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

Dariusz P. Malinowski
David P. Belesky

Follow this and additional works at: https://researchrepository.wvu.edu/faculty_publications
Epichloë (formerly Neotyphodium) fungal endophytes increase adaptation of cool-season perennial grasses to environmental stresses

Dariusz Piotr Malinowski1*, David Paul Belesky2
1 Texas A&M AgriLife Research P.O. Box 1658 11708 Highway 70 South Vernon, TX 76384-1658, USA
2 Division of Plant and Soil Sciences, West Virginia University, 1082 Agricultural Sciences Building, P.O. Box 6108, 101 Research Way, Morgantown, WV 26506-6108, USA

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, epichloë 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 epichloë 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 epichloë 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 *Neothyphodium 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 endophytes 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. & Schardl [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 vasconstrictive 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-acetylloline, N-formylloline) 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].

Pyrrolizidine 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 lolitem 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 (Hetegonychus 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 antitherbivore 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 antitherbivory 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 Philogophora 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 form 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 NH₄⁺ 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 H₂O₂ 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 epichloë 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 epichloë 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 epichloë endophyte transmission between grass host generations [213]. Alkaloids produced by the epichloë 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
avoids a mechanism that 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 those 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 Max Q 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 epichloë endophytes with those of native epichloë 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 epichloë 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 epichloë 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. Epichloë 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 epichloë 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.

Acknowledgments

Scientific article No. 3356 of the West Virginia Agricultural and Forestry Experiment Station, Morgantown.
References

1. Downie JA, Brewin NJ. Plant–microorganism symbiosis. In: Russo VEA, Cove DJ, Edgar LG, Jaenisch R, Salamini F, editors. Development. Genetics, epigenetics and environmental regulation. Berlin: Springer; 1999. p. 211–230. https://doi.org/10.1007/978-3-642-59828-9_14

2. Harley JL, Smith SE. Mycorrhizal symbiosis. London: Academic Press; 1983.

3. Wurzburger N, Miniat CF. Drought enhances symbiotic dinitrogen fixation and competitive ability of a temperate forest tree. Oecologia. 2014;174:1117–1126. https://doi.org/10.1007/s00442-013-2851-0

4. Moora M, Zobel M. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia. 1996;108:79–84. https://doi.org/10.1007/BF00333217

5. Leuchtmann A, Bacon CW, Schardl CL, White JF Jr, Tadych M. Nomenclatural realignment of Neotyphodium species with genus Epichloë. Mycologia. 2014;106:202–215. https://doi.org/10.3852/106.2.202

6. Morgan-Jones G, Gams W. Notes on Hyphomycetes: XLI. An endophyte of Festuca arundinacea and the anamorph of Epichloë typhina, new taxa in one of two new sections of Acremonium. Mycotaxon. 1982;15:311–318.

7. Latch GCM, Christensen MJ. Ryegrass endophyte, incidence and control. New Zealand Journal of Agricultural Research. 1982;25:443–448. https://doi.org/10.1080/00288233.1982.10417910

8. Gams W, Petrini O, Schmidt D. Acremonium uncinatum, a new endophyte in Festuca pratensis. Mycotaxon. 1990;37:67–71.

9. Young CA, Hume DE, McCulley RL. Fungal endophytes of tall fescue and perennial ryegrass: pasture friend or foe? J Anim Sci. 2013;91:2379–2394. https://doi.org/10.2527/jas2012-5951

10. Moon CD, Craven KD, Leuchtmann A, Clement SL, Schardl CL. Prevalence of interspecific hybrids amongst asexual fungal endophytes of grasses. Mol Ecol. 2004;13:1455–1467. https://doi.org/10.1111/j.1365-294X.2004.02138.x

11. Selosse, MA, Schardl, CL. Fungal endophytes of grasses: hybrids rescued by vertical transmission? An evolutionary perspective. New Phytol. 2007;173:452–458. https://doi.org/10.1111/j.1469-8137.2007.01978.x

12. Tsai HF, Liu JS, Staben C, Christensen MJ, Latch GC, Siegel MR, et al. Evolutionary diversification of fungal endophytes of tall fescue grass by hybridization with Epichloë species. Proc Natl Acad Sci USA. 1994;91:2542–2546. https://doi.org/10.1073/pnas.91.7.2542

13. Norton MR, Malinowski DP, Volaire F. Plant drought survival under climate change and strategies to improve perennial grasses. A review. Agron Sustain Dev. 2016;36:29. https://doi.org/10.1007/s11359-016-0362-1

14. Christensen MJ, Leuchtmann A, Rowan DD, Tapper BA. Taxonomy of Acremonium endophytes of tall fescue (Festuca arundinacea), meadow fescue (F. pratensis), and perennial ryegrass (Lolium perenne). Mycol Res. 1993;97:1083–1092. https://doi.org/10.1016/S0953-7562(93)80509-1

15. Takach JE, Mittal S, Swoboda GA, Bright SK, Trammell MA, Hopkins AA, et al. Genotypic and chemotypic diversity of Neotyphodium endophytes in tall fescue from Greece. Appl Environ Microbiol. 2012;78:5501–5510. https://doi.org/10.1128/AEM.01084-12

16. Moon CD, Tapper BA, Scott B. Identification of Epichloë endophytes in planta by a microsatellite-based PCR fingerprinting assay with automated analysis. Appl Environ Microbiol. 1999;65:1268–1279.

17. Saikkonen K, Young CA, Helander M, Schardl CL. Endophytic Epichloë species and their grass hosts: from evolution to applications. Plant Mol Biol. 2016;6:665–675. https://doi.org/10.1007/s11103-015-0399-6

18. Saikkonen K, Ahlholm J, Helander M, Lehtimäki S, Niemeläinen O. Endophytic fungi in wild and cultivated grasses in Finland. Ecography. 2000;23:360–366. https://doi.org/10.1046/j.1600-0587.2000.tb00292.x

19. Song H, Nan Z. Origin, divergence, and phylogeny of asexual Epichloë endophyte in Elymus species from Western China. PLoS One. 2015;10:e0127096. https://doi.org/10.1371/journal.pone.0127096
20. Bastías DA, Martínez-Ghersa MA, Newman JA, Card SD, Mace WJ, Gundel PE. The plant hormone salicylic acid interacts with the mechanism of anti-herbivory conferred by fungal endophytes in grasses. Plant Cell Environ. 2018;41:395–405. https://doi.org/10.1111/pce.13102

21. Hamilton CE, Gundel PE, Helander M, Saikkonen K. Endophytic mediation of reactive oxygen species and antioxidant activity in plants: a review. Fungal Divers. 2012;54:1–10. https://doi.org/10.1007/s13225-012-0158-9

22. Saikkonen K, Gundel PE, Helander M. Chemical ecology mediated by fungal endophytes in grasses. J Chem Ecol. 2013;39:962–968. https://doi.org/10.1007/s10886-013-0310-3

23. Malinowski DP, Belesky DP. Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance. Crop Sci. 2000;40:923–940. https://doi.org/10.2135/cropsci2000.404923x

24. Malinowski DP, Belesky DP. Ecological importance of Neotyphodium spp. grass endophytes in agroecosystems. Grassl Sci. 2006;52:1–14. https://doi.org/10.1111/j.1744-697X.2006.00041.x

25. Bacon CW, Hinton DM, Glenn AE. Endophytic niche and grass defense. In: White JF Jr, Torres MS, editors. Defensive mutualism in microbial symbiosis. Boca Raton, FL: CRC Press; 2009. p. 385–404. https://doi.org/10.1201/9781420069327.ch23

26. Huang WY, Cai YZ, Xing J, Corke H, Sun M. A Potential antioxidant resource: endophytic fungi from medicinal plants. Econ Bot. 2007;61:14–30. https://doi.org/10.1663/0013-0001(2007)61[14:APAREF]2.0.CO;2

27. White JF, Torres MS. Is plant endophyte-mediated defensive mutualism the result of oxidative stress protection? Physiol Plant. 2009;138:440–446. https://doi.org/10.1111/j.1399-3054.2009.01332.x

28. Qawasmeh A, Obied HK, Raman A, Wheatley W. Influence of fungal endophyte infection on phenolic content and antioxidant activity in grasses: Interaction between Lolium perenne and different strains of Neotyphodium lolii. Journal of Agriculture and Food Chemistry. 2012;60:3381–3388. https://doi.org/10.1021/jf204105k

29. Latch GCM, Christensen MJ, Samuels GJ. Five endophytes of Lolium and Festuca in New Zealand. Mycotaxon. 1984;20:535–550.

30. An ZQ, Siegel MR, Hollin W, Tsai HF, Schmidt D, Schardl CL. Relationships among non-Acremonium sp. fungal endophytes in five grass species. Appl Environ Microbiol. 1993;59:1540–1548.

31. Tadych M, White JF. Endophytic microbes. In: Schaechter M, editor. Eukaryotic microbes. San Diego, CA: Academic Press; 2012. p. 54–64.

32. Schmidt D. Effects of Acremonium uncinatum and a Phialophora-like endophyte on vigour, insect and disease resistance of meadow fescue. In: Hume DE, Latch GCM, Easton HS, editors. Proceedings of the 2nd International Symposium on Acremonium/Grass Interactions; 1993 Feb 4–6; Palmerston North, New Zealand. Palmerston North: AgResearch Grasslands Research Centre; 1993. p. 185–187.

33. Philipson MN. A symptomless endophyte of ryegrass (Lolium perenne) that spores on its host- a light microscope study. N Z J Bot. 1989;27:513–519. https://doi.org/10.1080/0028825X.1989.10414136

34. Naffaa W, Ravel C, Boyer N, Guillaumin JJ. Peroxidase activity of perennial ryegrass and tall fescue seedlings artificially infected with endophytes. Agronomy, EDP Sciences. 1999;19:611–619. https://doi.org/10.1051/agro:19990705

35. Philipson MN. Ultrastructure of the Gliocladium-like endophyte of perennial ryegrass (Lolium perenne L.). New Phytol. 1991;117:271–280. https://doi.org/10.1111/j.1469-8137.1991.tb04908.x

36. Siegel MR, Latch GCM. Expression of antifungal activity in agar culture by isolates of grass endophytes. Mycologia. 1991;83:525–537. https://doi.org/10.1080/00275514.1991.1020647

37. Malinowski D, Leuchtmann A, Schmidt D, Nösberger J. Growth and water status in meadow fescue is affected by Neotyphodium and Phialophora species endophytes. Agron J. 1997;89:673–678. https://doi.org/10.2134/agronj1997.00021962008900040021x

38. Tadych M, Ambrose KV, Bergen MS, Belanger FC, White JF. Taxonomic placement of Epichloë poae sp. nov. and horizontal dissemination to seedlings via conidia. Fungal Divers. 2012;54:117–131. https://doi.org/10.1007/s13225-012-0170-0

39. Clay K. Fungal endophytes of grasses – a defensive mutualism between plants and fungi.
40. Clay K. Defensive mutualism and grass endophytes: still valid after all these years? In: Torres M, White JF Jr, editors. Defensive mutualism in symbiotic association. Oxford: Taylor and Francis Publications; 2009. p. 9–20. https://doi.org/10.1201/9781420069327.ch2

41. Clay K, Holah J. Fungal endophyte symbiosis and plant diversity in successional fields. Science. 1999;285:1742–1744. https://doi.org/10.1126/science.285.5434.1742

42. Rudgers JA, Koslow JM, Clay K. Endophytic fungi alter relationships between diversity and ecosystem properties. Ecol Lett. 2004;7:42–51. https://doi.org/10.1046/j.1461-0248.2003.00543.x

43. Torres MS, White JF Jr. Grass endophyte-mediated plant stress tolerance: alkaloids and their functions. In: Seckbach J, Grube M, editors. Symbioses and stress. Dordrecht: Springer; 2010. p. 477–493. (Cellular Origin, Life in Extreme Habitats and Astrobiology; vol 17). https://doi.org/10.1007/978-90-481-9449-0_24

44. Schardl CL, Young CA, Faulkner JR, Florea S, Pan J. Chemotypic diversity of epichloae, fungal symbionts of grasses. Fungal Ecol. 2012;5:331–344. https://doi.org/10.1016/j.funeco.2011.04.005

45. Schardl CL, Florea S, Pan J, Nagabhyyru P, Bec S, Calie PJ. The epichloae: alkaloid diversity and roles in symbiosis with grasses. Curr Opin Plant Biol. 2013;16:480–488. https://doi.org/10.1016/j.pbi.2013.06.012

46. Schardl CL, Grossman RB, Nagabhyyru P, Faulkner JR, Mallik UP. Loline alkaloids: currencies of mutualism. Phytochemistry. 2007;68:980–996. https://doi.org/10.1016/j.phytochem.2007.01.010

47. Young CA, Scharld CL, Panaccione DG, Florea S, Takach JE, Charlton ND, et al. Genetics, genomics and evolution of ergot alkaloid diversity. Toxins. 2015;7:1273–1302. https://doi.org/10.3390/toxins7041273

48. Belesky DP, Stringer WC, Plattner RD. Influence of endophyte and water regime upon tall fescue accessions. II. Pyrrolizidine and ergopeptine alkaloids. Ann Bot. 1989;64:343–349. https://doi.org/10.1093/oxfordjournals.aob.a087850

49. Robbins JD, Wilkinson SR, Burdick D. Loline alkaloids of tall fescue seed and forage. In: Proceedings of the Fescue Toxicity Conference; 1973 May 31 – Jun 1; Lexington, KY, USA. Lexington, KY: University of Kentucky; 1993. p. 98–107

50. Ball OJ, Prestidge RA, Sprosen JM. Interrelationships between Acremonium lolii, peramine, and lolitrem B in perennial ryegrass. Appl Environ Microbiol. 1995;61:1527–1533.

51. Justus M, Witte L, Hartmann T. Levels and tissue distribution of loline alkaloids in endophyte-infected Festuca pratensis. Phytochemistry. 1997;44:51–57. https://doi.org/10.1016/S0031-9422(96)00535-3

52. Ryan GD, Rasmussen S, Xue H, Parsons AJ, Newman JA. Metabolite analysis of the effects of elevated CO2 and nitrogen fertilization on the association between tall fescue (Schedonorus arundinacea) and its fungal symbiont Neotyphodium coenophialum. Plant Cell Environ. 2014;37:204–212. https://doi.org/10.1111/pce.12146

53. Hennessy LM, Popay AJ, Finch SC, Clearwater MJ, Cave VM. Temperature and plant genotype alter alkaloid concentrations in ryegrass infected with an Epichloë endophyte and this affects an insect herbivore. Front Plant Sci. 2016;7:1097. https://doi.org/10.3389/fpls.2016.01097

54. Yoshihara T, Togiya S, Koshino H, Sakamura S, Shimanuki T, Sato T, et al. Three fungitoxic cyclopentanoidesquiterpenes from stromata of Epichloë typhina. Tetrahedron Lett. 1985;26:5551–5554. https://doi.org/10.1016/0040-4039(85)80885-6

55. Koshino, H, Terada S, Yoshihara T, Sakamura S, Shimanuki T, Sato T, et al. Three phenolic acid derivates from stromata of Epichloë typhina on Phleum pratense. Phytochemistry. 1988;27:1333–1338. https://doi.org/10.1016/0031-9422(88)80188-2

56. Koshino H, Yoshihara T, Sakamura S, Shimanuki T, Sato T, Tajimi A. A ring B aromatic sterol from stromata of Epichloë typhina. Phytochemistry. 1999;28:771–772. https://doi.org/10.1016/S0031-9422(89)80112-8

57. Ju Y, Sacalis JN, Still CC. Bioactive flavonoids from endophyte-infected bluegrass (Poa ampla). Journal of Agriculture and Food Chemistry. 1998;46:3785–3788. https://doi.org/10.1021/jf980189m

58. Bacon CW, Porter JK, Robbins JD, Luttrell ES. Epichloë typhina from toxic tall fescue
grasses. Appl Environ Microbiol. 1977;34:576–581.

59. Porter JK. Chemical constituents of grass endophytes. In: Bacon CW, White JF, Jr, editors. Biotechnology of endophytic fungi of grasses. Boca Raton, FL: CRC Press; 1994. p. 103–123.

60. Hoffmann A, Tscherner H. Isolierung von Lysergsaurealkaloiden aus der mexikanischen Zauberdroge “ololiuqui” [Rivea corymbosa (L.) Hall.]. Experientia. 1960;16:414. https://doi.org/10.1007/BF02178840

61. Crosignani PG. Current treatment issues in female hyperprolactinaemia. European Journal of Obstetrics, Gynecology and Reproductive Biology. 2006;125:152–164. https://doi.org/10.1016/j.ejogrb.2005.10.005

62. Eich E, Pertz H. Antimicrobial and antitumor effects of ergot alkaloids and their derivatives. In: Kren V, Cvak L, editors. Ergot: the genus Claviceps. Amsterdam: Harwood Academic Publishers; 1999. p. 441–449.

63. Raisbeck MF, Rottinghaus GE, Kendall JD. Effects of naturally occurring mycotoxins on ruminants. In: Smith JE, Henderson RS, editors. Mycotoxins and animal foods. Boca Raton, FL: CRC Press; 1991. p. 647–677.

64. Thompson FN, Stuedemann JA. Pathophysiology of fescue toxicosis. Agriculture, Ecosystems and Environment. 1993;44:263–281. https://doi.org/10.1016/0167-8809(93)90050-Y

65. Tor-Agbidye J, Blethe LL, Craig AM. Correlation of endophyte toxins (ergovaline and lolitrem B) with clinical disease: fescue foot and perennial ryegrass staggers. Vet Hum Toxicol. 2001;43:140–146.

66. Spiers DE, Zhang Q, Eichen PA, Rottinghaus GE, Garner GB, Ellersieck MR. Temperature-dependent responses of rats to ergovaline derived from endophyte-infected tall fescue. J Anim Sci. 1995;73:1954–1961. https://doi.org/10.2527/1995.7371954x

67. Bush LP, Wilkinson HH, Schardl CL. Bioprotective alkaloids of grass–fungal endophyte symbioses. Plant Physiol. 1997;114:1–7. https://doi.org/10.1104/pp.114.1.1

68. Wilkinson HH, Siegel MR, Blankenship JD, Mallory AC, Bush LP, Schardl CL. Contribution of fungal loline alkaloids to protection from aphids in a grass–endophyte mutualism. Mol Plant Microbe Interact. 2000;13:1027–1033. https://doi.org/10.1094/MPMI.2000.13.10.1027

69. Spiering MJ, Moon CD, Wilkinson HH, Schardl CL. Gene clusters for insecticidal loline alkaloids in the grass–endophytic fungus Neotyphodium uncinatum. Genetics. 2005;169:1403–1414. https://doi.org/10.1534/genetics.104.035972

70. Huizing HJ, van der Molen W, Kloock W, Den Nijs APM. Detection of loline alkaloids in endophyte-containing meadow fescue in the Netherlands and the effect of elevated temperature on induction of loline alkaloids in endophyte-infected perennial ryegrass. Grass Forage Sci. 1999;46:441–445. https://doi.org/10.1111/j.1365-2494.1999.tb02405.x

71. Strickland JR, Bailey EM, Abney LK, Oliver JW. Assessment of the mitogenic potential of the alkaloids produced by endophyte (Acrogenium coenophialum)-infected tall fescue (Festuca arundinacea) on bovine vascular smooth muscle in vitro. J Anim Sci. 1996;74:1664–1671. https://doi.org/10.2527/1996.7471664x

72. Clay K, Schardl C. Evolutionary origins and ecological consequences of endophyte symbiosis with grasses. Am Nat. 2002;160(4 suppl):S99–S127. https://doi.org/10.1086/342161

73. Dahlman DL, Siegel MR, Bush LP. Insecticidal activity of N-formyloline. In: Proceedings of the XVIII International Grassland Congress; 1997 Jun 8–19; Winnipeg, Manitoba, Saskatchewan, Saskatchewan, Canada. Calgary: International Grassland Congress; 1997. p. 13.5–13.6.

74. Riedell WE, Kieckhefer RE, Petroski RJ, Powell RG. Naturally occurring and synthetic loline alkaloid derivatives: insect feeding behavior modification and toxicity. J Entomol Sci. 1991;26:122–129. https://doi.org/10.18474/0749-8004-26.1.122

75. Johnson MC, Dahlman DL, Siegel MR, Bush LP, Latch GCM, Potter DA, et al. Insect feeding deterrents in endophyte-infected tall fescue. Applied Environmental Microbiology. 1985;49:568–571.

76. Poole DP, Littler RA, Smith BL, McLeay LM. Effects and mechanisms of action of the ergopeptides ergotamine and ergovaline and the effects of peramine on reticulum motility of sheep. Am J Vet Res. 2009;70:270–276. https://doi.org/10.2460/ajvr.70.2.270

77. Siegel, MR, Bush, LP. Defensive chemicals in grass–fungal endophyte associations.
78. Schardl CL, Leuchtmann A, Spiering MJ. Symbioses of grasses with seedborne fungal endophytes. Annu Rev Plant Biol. 2004;55:315–340. https://doi.org/10.1146/annurev.arplant.55.031903.141735

79. Philippe G. Lolitrems B and indole diterpene alkaloids produced by endophytic fungi of the genus *Epichloë* and their toxic effects in livestock. Toxins. 2016;8:47. https://doi.org/10.3390/toxins8020047

80. Rowan DD. Lolitrems, peramine and pxalline: mycotoxins of the ryegrass/endophyte interaction. Agriculture, Ecosystems and Environment. 1993;44:103–122. https://doi.org/10.1016/0167-8809(93)90041-M

81. Di Menna ME, Finch SC, Popay AJ, Smith BL. A review of the *Neotyphodium lolii* / *Lolium perenne* symbiosis and its associated effects on animal and plant health, with particular emphasis on ryegrass staggers. N Z Vet J. 2012;60:315–328. https://doi.org/10.1080/00480169.2012.697429

82. Tapper BA, Lane GA. *Janthitrems* found in a *Neotyphodium* endophyte of perennial ryegrass. In: Kallenbach R, Rosenkrans CJ, Lock TR, editors. Proceedings of the 5th International Symposium on *Neotyphodium* / Grass Interactions; 2004 May 23–26; Fayetteville, AR, USA. Fayetteville, AR: University of Arkansas Press; 2004. p. 301.

83. Thom ER, Waugh CD, Minnee EMK, Waghorn GC. A new generation ryegrass endophyte – the first results from dairy cows fed AR37. In: Popay AJ, Thom ER, editors. Proceedings of the 6th International Symposium on Fungal Endophytes of Grasses; 2007 Mar 25–28; Christchurch, New Zealand. Dunedin: New Zealand Grassland Association; 2007. p. 293–296.

84. Ball OJP, Christensen MJ, Prestidge RA. Effect of selected isolates of *Acremonium* endophytes on adult black beetle (*Heteronychus arator*) feeding. N Z Plant Prot. 1994;47:227–231.

85. Popay AJ, Wyatt RT. Resistance to argentine stem weevil in perennial ryegrass infected with endophytes producing different alkaloids. N Z Plant Prot. 1995;48:229–236.

86. Popay A, Silvester WB, Gerard PJ. New endophyte isolate suppresses root aphid, *Aploneura lentisci*, in perennial ryegrass. In: Kallenbach R, Rosenkrans CJ, Lock TR, editors. Proceedings of the 5th International Symposium on *Neotyphodium* / Grass Interactions; 2004 May 23–26; Fayetteville, AR, USA. Fayetteville, AR: University of Arkansas Press; 2004. p. 317

87. Jensen JG, Popay AJ. Perennial ryegrass infected with AR37 endophyte reduces survival of porina larvae. N Z Plant Prot. 2004;57:323–328.

88. Hiroiuki K, Satoshi T, Shun-ichi T, Yoshihara T, Sakamura S, Shimanuki T, et al. New fungitoxic sesquiterpenoids, chokoils A–G, from stromata of *Epichloe typhina* and the absolute configuration of chokol E. Agric Biol Chem. 1989;53:789–796. https://doi.org/10.1080/00021369.1989.10869341

89. Qawasmeh A, Raman A, Wheatley W, Nicol H. Antioxidative capacity of phenolic compounds extracted from *Lolium perenne* and *Lolium arundinaceum* infected with *Neotyphodium* (Hypocreales: Clavicipitaceae). Acta Physiol Plant. 2012;34:827–833. https://doi.org/10.1007/s11738-011-0878-6

90. Simmonds MSJ. Flavonoid–insect interactions: recent advances in our knowledge. Phytochemistry. 2003;64:21–30. https://doi.org/10.1016/S0031-9422(03)00293-0

91. Leuchtmann A. Systematics, distribution, and host specificity of grass endophytes. Nat Toxins. 1992;1:150–162. https://doi.org/10.1002/nt.2620001030

92. Belesky DP, Malinowski DP. Morphological plasticity and chemical adaptations of *Neotyphodium*-infected tall fescue. In: White, JF Jr, Bacon CW, editors. Microbial endophytes. New York, NY: Marcel Dekker; 2000. p. 455–484.

93. Popay AJ, Bonos SA. Biotic responses in endophytic grasses. In: Roberts CA, West CP, Spiers DE, editors. *Neotyphodium* in cool-season grasses. Ames, IA: Blackwell Publishing; 2005. p. 163–185. https://doi.org/10.1002/9780470384916.ch7

94. Rudgers JA, Mattingly WB, Koslow JM. Mutualistic fungus promotes plant invasion into diverse communities. Oecologia. 2005;144:463–471. https://doi.org/10.1007/s00442-005-0039-y

95. Schardl CL, Phillips TD. Protective grass endophytes: where are they from and where are they going? Plant Dis. 1997;81:430–437. https://doi.org/10.1094/PDIS.1997.81.5.430

96. Latch GCM. Physiological interactions of endophytic fungi and their hosts: biotic stress
97. Miles CO, Lane GA, di Menna ME, Garthwaite I, Piper EL, Ball OJP, et al. High levels of ergonovine and isysergic acid amide in toxic *Achnatherum inebrians* accompany infection by an *Acremonium*-like endophytic fungus. J Agric Food Chem. 1996;44:1285–1290. https://doi.org/10.1021/jf950410k

98. Miles CO, Menna ME, Jacobs SWL, Garthwaite I, Lane GA, Prestidge RA, et al. Endophytic fungi in indigenous Australasian grasses associated with toxicity to livestock. Appl Environ Microbiol. 1998;64:601–606.

99. Cabral D, Cafaro MJ, Saidman B, Lugo M, Reddy PV, White JF Jr. Evidence supporting the occurrence of a new species of endophyte in some South American grasses. Mycologia. 1999;91:315–325. https://doi.org/10.2307/3761376

100. Giuliano WM, Elliott CL, Sole JD. Significance of tall fescue in the diet of the eastern cottontail. Prairie Naturalist. 1994;26:53–60.

101. Lopez JE, Faeth SH, Miller M. Effect of endophytic fungi on herbivory by redlegged grasshoppers (Orthoptera: Acrididae) on Arizona fescue. Environ Entomol. 1995;24:1576–1580. https://doi.org/10.1093/ee/24.6.1576

102. Fortier GM, Bard N, Jansen M, Clay K. Effects of tall fescue endophyte infection and population density on growth and reproduction in prairie voles. J Wildl Manage. 2000;64:122–128. https://doi.org/10.2307/3802981

103. Conover MR, Messmer TA. Feeding preferences and changes in mass of Canada geese grazing endophyte-infected tall fescue. Condor. 1996;98:859–862. https://doi.org/10.2307/1369872

104. Madej CW, Clay K. Avian seed preference and weight loss experiments: the effect of fungal endophyte-infected tall fescue seeds. Oecologia. 1991;88:296–302. https://doi.org/10.1007/BF00320825

105. Knoch TR, Faeth SH, Arnott DL. Endophytic fungi alter foraging and dispersal by desert seed-harvesting ants. Oecologia. 1993;95:470–475. https://doi.org/10.1007/BF00317429

106. Elmi AA, West CP, Robbins RT, Kirkpatrick TL. Endophyte effects on reproduction of a root-knot nematode (*Meloidogyne marylandi*) and osmotic adjustment in tall fescue. Grass Forage Science. 2000;55:166–172. https://doi.org/10.1007/j.1365-2494.2000.00210.x

107. West CP, Izekor E, Oosterhuis DM, Robbins RT. The effect of *Acremonium coenophialum* on the growth and nematode infestation of tall fescue. Plant Soil. 1998;112:3–6. https://doi.org/10.1007/BF02181745

108. Kimmons CA, Gwinn KD, Bernard EC. Nematode reproduction on endophyte-infected and endophyte-free tall fescue. Plant Dis. 1990;74:757–761. https://doi.org/10.1094/CPDIS-74-0757

109. Panaccione DG, Kotcon JB, Schardl CL, Johnson RD, Morton JB. Ergot alkaloids are not essential for endophytic fungus-associated population suppression of the lesion nematode, *Pratylenchus scribneri*, on perennial ryegrass. Nematology. 2006;8:583–590. https://doi.org/10.1163/156854106778614074

110. Rogers JK, Walker NR, Young CA. The effect of endophytic fungi on nematode populations in summer-dormant and summer-active tall fescue. J Nematol. 2016;48:88–94. https://doi.org/10.21307/jofnem-2017-013

111. Rowan DD, Hunt MB, Gaynor DL. Peramine, a novel insect feeding deterrent from ryegrass infected with the endophyte *Acremonium lolaeae*. J Chem Soc Chem Commun. 1986;142:935–936. https://doi.org/10.1039/c39860000935

112. Craven KD, Blankenship JD, Leuchtmann A, Hignight K, Schardl CL. Hybrid fungal endophytes symbiotic with the grass *Lolium pratense*. Sydowia. 2001;53:44–73.

113. Siegel M, Latch G, Bush L, Fannin F, Rowan D, Tapper B, et al. Fungal endophyte-infected grasses: alkaloid accumulation and aphid response. J Chem Ecol. 1990;16:3301–3315. https://doi.org/10.1007/BF00982100

114. Hartley SE, Gange AC. Impacts of plant symbiotic fungi on insect herbivores: mutualism in a multitrophic context. Annual Reviews in Entomology. 2009;54:323–342. https://doi.org/10.1146/annurev.ento.54.110807.090614

115. Lehtonen P, Helander M, Saikkonen K. Are endophyte-mediated effects on herbivores conditional on soil nutrients? Oecologia. 2005;142:38–45. https://doi.org/10.1007/s00442-004-1701-5

116. Finkes LK, Cady AB, Mulroy JC, Clay K, Rudgers JA. Plant–fungus mutualism...
affects spider composition in successional fields. Ecol Lett. 2006;9:347–356. https://doi.org/10.1111/j.1461-0248.2005.00882.x

117. Zabalgogeazcoa I. Review. Fungal endophytes and their interaction with plant pathogens. Spanish Journal of Agricultural Research. 2008;6:138–146. https://doi.org/10.5424/sjar/200806S1-382

118. Stovall ME, Clay K. Fungitoxic effects of Balansia cyperi (Clavicipitaceae). Mycologia. 1991;83:288–295. https://doi.org/10.1080/00275514.1991.12026012

119. Panka D, West CP, Guerber CA, Richardson MD. Susceptibility of tall fescue to Rhizoctonia zeae infection as affected by endophyte symbiosis. Ann Appl Biol. 2013;163:257–268. https://doi.org/10.1111/aab.12051

120. Ford VL, Kirkpatrick TL. Effects of Acremonium coenophialum in tall fescue on host disease and insect resistance and allelopathy to Pinus taeda seedlings. In: West CP, editor. Proceedings of the Arkansas fescue toxicosis conference. Fayetteville, AR: Arkansas Agricultural Experiment Station; 1989. p. 29–34. (Arkansas Agricultural Experiment Station Special Report; vol 140).

121. Tian P, Nan ZB, Li CJ. Effect of the endophyte Neotyphodium lolii on susceptibility and host physiological response of perennial ryegrass to fungal pathogens. Eur J Plant Pathol. 2008;122:593–602. https://doi.org/10.1007/s10658-008-9329-7

122. Clay K, Cheplick GP, Marks SM. Impact of the fungus Balansia henningsiana on the grass Panicum agrostoides: frequency of infection, plant growth and reproduction, and resistance to pests. Oecologia. 1989;80:374–380. https://doi.org/10.1007/BF00379039

123. Shimamuni T. Studies on the mechanisms of the infection of timothy with purple spot disease caused by Cladosporium phlei (Gregory) de Vries. Research Bulletin of Hokkaido National Agricultural Experiment Station. 1987;148:1–56.

124. Wang X, Qin J, Chen W, Zhou Y, Ren A, Gao Y. Pathogen resistant advantage of endophyte-infected over endophyte-free Leymus chinensis is strengthened by pre-drought treatment. Eur J Plant Pathol. 2016;144:477–486. https://doi.org/10.1007/s10658-015-0788-3

125. Welty RE, Barker RE, Azevedo MD. Reaction of tall fescue infected and noninfected by Acremonium coenophialum to Puccinia graminis subsp. graminicola. Plant Dis. 1991;75:883–886. https://doi.org/10.1094/PD-75-0883

126. Rochow WF, Duffus JE. Luteoviruses and yellows diseases. In: Kurstak E, editor. Handbook of plant virus infections and comparative diagnosis. Amsterdam: Elsevier; 1981. p. 147–170.

127. Mahmood T, Gergerich RC, Milus EA, West CP, D’Arcy CJ. Barley yellow dwarf viruses in wheat, endophyte-infected and endophyte-free tall fescue, and other hosts in Arkansas. Plant Dis. 1993;77:225–228. https://doi.org/10.1094/PD-77-0225

128. Lehtonen PT, Helander M, Siddiqui SA, Lehto K, Saikkonen K. Endophytic fungus decreases plant virus infections in meadow ryegrass (Lolium pratense). Biol Lett. 2006;2:620–623. https://doi.org/10.1098/rsbl.2006.0499

129. Romo M, Leuchtmann A, García B, Zabalgogeazcoa I. A totivirus infecting the mutualistic fungal endophyte Epichloë festucae. Virus Res. 2007;124:38–43. https://doi.org/10.1016/j.virusres.2006.09.008

130. Herrero N, Sánchez S, Zabalgogeazcoa I. Mycoviruses are common among different species of fungal endophytes of grasses. Arch Virol. 2009;154:327–330. https://doi.org/10.1007/s00705-008-0293-5

131. Smith SE, Gianinazzi-Pearson V. Physiological interactions between symbionts in vesicular-arbuscular mycorrhizal plants. Annual Reviews of Plant Physiology and Plant Molecular Biology. 1988;39:221–244. https://doi.org/10.1146/annurev.pp.39.060188.001253

132. Vignale MV, Iannone LJ, Scervino JM, Novas MV. Epichloë exudates promote in vitro and in vivo arbuscular mycorrhizal fungi development and plant growth. Plant Soil. 2018;422:267–281. https://doi.org/10.1007/s11104-017-3173-5

133. Chu-Chou M, Guo B, An ZQ, Hendrix JW, Ferris RS, Siegel MR, et al. Suppression of mycorrhizal fungi in fescue by the Acremonium coenophialum endophyte. Soil Biology and Biochemistry. 1992;24:633–637. https://doi.org/10.1016/0038-0717(92)90041-U

134. Müller J. Artificial infection by endophytes affect growth and mycorrhizal colonisation of Lolium perenne. Funct Plant Biol. 2003;30:419–424. https://doi.org/10.1071/FP02189

135. Omacini M, Eggers T, Bonkowski M, Gange AC, Jones TH. Leaf endophytes affect
mycorrhizal status of co-infected and neighbouring plant. Funct Ecol. 2006;20:226–232. https://doi.org/10.1111/j.1365-2435.2006.01099.x

136. Mack KML, Rudgers JA. Balancing multiple mutualists: asymmetric interactions among plants, arbuscular mycorrhizal fungi, and fungal endophytes. Oikos. 2008;117:310–320. https://doi.org/10.1111/j.2007.0030-1299.15973.x

137. Novas MV, Cabral D, Godeas AM. Interaction between grass endophytes and mycorrhizas in Bromus setifolius from Patagonia, Argentina. Symbiosis. 2005;40:23–30.

138. Novas MV, Iannone LJ, Godeas A, Cabral D. Positive association between mycorrhiza and foliar endophytes in Poa bonariensis, a native grass. Mycol Prog. 2009;8:75–81. https://doi.org/10.1007/s11557-008-0579-8

139. Cheplick GP, Faeth SH. Ecology and evolution of the grass–endophyte symbiosis. New York, NY: Oxford University Press, Inc.; 2009. https://doi.org/10.1093/acprof:oso/9780195308082.001.0001

140. Barker GM. Mycorrhizal infection influences Acremonium-induced resistance to argentine stem weevil in ryegrass. In: Popay AJ, editor. Proceedings of the 40th N. Z. Weed and Pest Control Conference; 1987 Aug 11–13; Nelson, New Zealand. Nelson: The New Zealand Weed and Pest Control Society Inc.; 1987. p. 199–203.

141. Vicari M, Hatcher PE, Ayres PG. Combined effect of foliar and mycorrhizal endophytes on an insect herbivore. Ecology. 2002;83:2452–2464. https://doi.org/10.1890/0012-9658(2002)083[2452:CEOFAM]2.0.CO;2

142. Asao T, Hasegawa K, Sueda Y, Tomita K, Taniguchi K, Hosoki T, et al. Autotoxicity of root exudates from taro. Scienta Horticulturae. 2003;97:389–396. https://doi.org/10.1016/S0304-4238(02)00197-8

143. Kalinova J, Vrchotova N, Triska J. Exudation of allelopathic substances in buckwheat (Fagopyrum esculentum Moench). Journal of Agriculture and Food Chemistry. 2007;55:6453–6459. https://doi.org/10.1021/jf070795u

144. Guo J, McCulley RL, McNear DH Jr. Tall fescue cultivar and fungal endophyte combinations influence plant growth and root exudate composition. Front Plant Sci. 2015;6:183. https://doi.org/10.3389/fpls.2015.00183

145. Yu JQ, Matsu Y. Phytotoxic substances in root exudates of cucumber (Cucumis sativus L.). J Chem Ecol. 1994;20:21–31. https://doi.org/10.1007/BF02065988

146. Al-Sherif E, Hegazy AK, Gomaa NH, Hassan MO. Allelopathic effect of black mustard tissues and root exudates on some crops and weeds. Planta Daninha. 2013;31:11–19. https://doi.org/10.1590/0100-83582013000100002

147. Renne IJ, Rios BG, Fehmi JS, Tracy BF. Low allelopathic potential of an invasive forage grass on native grassland plants: a cause for encouragement? Basic Appl Ecol. 2004;5:261–269. https://doi.org/10.1016/j.baae.2003.11.001

148. van Hecke MM, Treonis AM, Kaufman JR. How does the fungal endophyte Neotyphodium coenophialum affect tall fescue (Festuca arundinacea) rhizodeposition and soil microorganisms? Plan Soil. 2005;275:101–109. https://doi.org/10.1007/s11104-005-0380-2

149. Arraudeau MA. Breeding strategies for drought resistance. In: Baker FWC, editor. Drought resistance in cereals. Wallingford: CAB International; 1989. p. 107–116.

150. Latch GCM, Hunt WF, Musgrave DR. Endophytic fungi affect growth of perennial ryegrass. New Zealand Journal of Agricultural Research. 1985;28:165–168. https://doi.org/10.1080/00288233.1985.10427011

151. de Battista JP, Bouton JH, Bacon CW, Siegel MR. Rhizome and herbage production of endophyte removed tall fescue clones and populations. Agron J. 1990;82:651–654.

152. Marks S, Clay K, Cheplick GP. Effects of fungal endophytes on interspecific and intraspecific competition in the grasses Festuca arundinacea and Lolium perenne. J Appl Ecol. 1991;28:194–204. https://doi.org/10.2307/2404125

153. Malinowski D, Leuchtmann A, Schmidt D, Nösberger J. Symbiosis with Neotyphodium uncinatum endophyte may increase the competitive ability of meadow fescue. Agron J. 1997;89:833–839. https://doi.org/10.2134/agronj1997.00021962008900050019x

154. Elmi AA, West CP. Endophyte infection effects on stomatal conductance, osmotic adjustment and drought recovery of tall fescue. New Phytol. 1995;131:61–67. https://doi.org/10.1111/j.1469-8137.1995.tb03055.x

155. Buck GW, West CP, Elbersen HW. Endophyte effect on drought tolerance in diverse Festuca species. In: Bacon CW, Hill NS, editors. Neotyphodium/
156. Elbersen HW, West CP. Growth and water relations of field-grown tall fescue as influenced by drought and endophyte. Grass Forage Sci. 1996;51:333–342. https://doi.org/10.1111/j.1365-2494.1996.tb02068.x

157. Richardson MD, Chapman GW Jr, Hovelands CS, Bacon CW. Sugar alcohols in endophyte-infected tall fescue. Crop Sci. 1992;32:1060–1061. https://doi.org/10.2135/cropsci1992.0011183X003200040045x

158. Bayat F, Mirlohi A, Khodambashi M. Effects of endophytic fungi on some drought tolerance mechanisms of tall fescue in a hydroponics culture. Russ J Plant Physiol. 2009;56:510–516. https://doi.org/10.1134/S1021443709040104

159. Nagabhryu P, Dinkins RD, Wood CL, Bacon CW, Schardl CL. Tall fescue endophyte effects on tolerance to water-deficit stress. BMC Plant Biol. 2013;13:127. https://doi.org/10.1471-2229/13/127

160. Barker DJ, Sullivan CY, Moser LE. Water deficit effects on osmotic potential, cell wall elasticity and proline in five forage grasses. Agron J. 1993;85:270–275. https://doi.org/10.2134/agronj1993.00021962008500020020x

161. Abernethy GA, McManus MT. Biochemical responses to an imposed water deficit in mature leaf tissue of Festuca arundinacea. Environmental Experimental Botany. 1998;40:17–28. https://doi.org/10.1016/S0098-8472(98)00017-3

162. West CP, Carson RD, Guerber CA, de los Reyes B. Endophyte effects on antioxidants and membrane leakage in tall fescue during drought. In: Proceedings of the 4th International Symposium on the Molecular Breeding of Forage and Turf, a satellite workshop of the XXth International Grassland Congress; 2005 Jul; Aberystwyth, Wales; Wageningen: Wageningen Academic Publishers; 2005. p. 217–218.

163. Malinowski D. Rhizomatous ecotypes and symbiosis with endophytes as new possibilities of improvement in competitive ability of meadow fescue (Festuca pratensis Huds.) [PhD thesis]. Zurich: Swiss Federal Institute of Technology; 1995. https://doi.org/10.3929/ethz-a-001575829

164. Johnson RC, Tieszen LL. Carbon isotope discrimination, water relations, and gas exchange in temperate grass species and accessions. In: Ehleringer JR, Hall AE, Farquhar GD, editors. Stable isotopes and plant carbon–water relations. San Diego, CA: Academic Press, Inc; 1993. p. 281–296. https://doi.org/10.1016/B978-0-08-091801-3.50027-1

165. Eerens JPJ, Lucas RJ, Easton HS, White JGH. Influence of the endophyte (Neotyphodium lolii) on morphology, physiology, and alkaloid synthesis of perennial ryegrass during high temperature and water stress. New Zealand Journal of Agricultural Research. 1998;41:219–226. https://doi.org/10.1080/00288233.1998.9513305

166. West CP, Carson RD, Guerber CA, de los Reyes B. Endophyte effects on antioxidants and membrane leakage in tall fescue during drought. In: Proceedings of the 4th International Symposium on the Molecular Breeding of Forage and Turf, a satellite workshop of the XXth International Grassland Congress; 2005 Jul; Aberystwyth, Wales; Wageningen: Wageningen Academic Publishers; 2005. p. 217–218.

167. Zhang YP, Nan ZB. Growth and anti-oxidative systems changes in Elymus dahuricus is affected by Neotyphodium endophyte under contrasting water availability. J Agron Crop Sci. 2007;193:377–386. https://doi.org/10.1111/j.1439-037X.2007.00279.x

168. Torres MS, White JC Jr, Zhang X, Hinton DM, Bacon CW. Endophyte-mediated adjustments in host morphology and physiology and effects on host fitness traits in grasses. Fungal Ecol. 2012;5:322–330. https://doi.org/10.1016/j.funeco.2011.05.006

169. West CP, Elbersen HW, Elmi AA, Buck GW. Acremonium effects on tall fescue growth: parasite or stimulant? In: Brink GE, editor. Proceedings of the 50th Southern Pasture Forage Crop Improvement Conference; 1994 May 23–25; Knoxville, TN, USA. Knoxville, TN: [publisher unknown]; 1994. p. 102–111.

170. Volaire F. Drought survival, summer dormancy and dehydrin accumulation in contrasting cultivars of Dactylis glomerata. Physiol Plant. 2002;116:42–51. https://doi.org/10.1034/j.1399-3054.2002.1160106.x

171. Allagulova CR, Gimalov FR, Shakirova FM, Vakhitov VA. The plant dehydrins: structure and putative functions. Biochemistry (Moscow). 2003;68:945–951. https://doi.org/10.1023/A:1026077825584

172. Koag MC, Fenton RD, Winklen S, Close TJ. The binding of maize DHN1 to lipid vesicles. Gain of structure and lipid specificity. Plant Physiol. 2003;131:309–316. https://doi.org/10.1104/pp.011171
173. Carson RD. Biochemical responses of tall fescue to endophyte infection during water deficit [Master thesis]. Fayetteville: University of Arkansas Library; 2004.

174. Guerber CA, West CP, Carson RD, Havel AM. Dehydrin expression in drought-stressed tall fescue. In: Popay AJ, Thom ER, editors. Proceedings of the 6th International Symposium on Endophyte–Grass Interactions; 2006 Mar 26–28; Christchurch, New Zealand. Christchurch: New Zealand Grassland Association; 2007. p. 225–227. (Grassland Research and Practice Series; vol 13).

175. Jiang Y, Huang B. Protein alterations in tall fescue in response to drought stress and abscisic acid. Crop Sci. 2002;42:202–207. https://doi.org/10.2135/cropsci2002.2020

176. Carrow RN. Drought avoidance characteristics of diverse tall fescue cultivars. Crop Sci. 1996;36:371–377. https://doi.org/10.2135/cropsci1996.0011183X0036000020026x

177. Crush JR, Popay AJ, Waller J. Effect of different Neotyphodium endophytes on root distribution of a perennial ryegrass (Lolium perenne L.) cultivar. New Zealand Journal of Agricultural Research. 2004;47:345–349. https://doi.org/10.1080/00288233.2004.9513603

178. Ding N, Kupper JV, McNear DH Jr. Phosphate source interacts with endophyte strain to influence biomass and root system architecture in tall fescue. Agron J. 2015;107:662–670. https://doi.org/10.2134/agronj2014.0135

179. Malinowski DP, Belesky DP. Neotyphodium coenophialum endophyte infection affects the ability of tall fescue to use sparingly available phosphorus. J Plant Nutr. 1999;22:835–853. https://doi.org/10.1080/01904169909365675

180. Malinowski DP, Zuo H, Belesky DP, Alloush GA. Evidence for copper binding by extracellular root exudates of tall fescue but not perennial ryegrass infected with Neotyphodium spp. endophytes. Plant Soil. 2004;267:1–12. https://doi.org/10.1007/s11104-005-2575-y

181. Belesky DP, Stuedemann JA, Plattner RD, Wilkinson SR. Ergopeptide alkaloids in grazed tall fescue. Agron J. 1988;80:209–212. https://doi.org/10.2134/agronj1988.00021962008000020014x

182. Lyons PC, Evans JJ, Bacon CW. Effects of the fungal endophyte Acremonium coenophialum on nitrogen accumulation and metabolism in tall fescue. Plant Physiol. 1990;92:726–732. https://doi.org/10.1104/pp.92.3.726

183. Belesky DP, Wilkinson SR, Pallas JE Jr. Response of four tall fescue cultivars grown at two nitrogen levels to low soil water availability. Crop Sci. 1982;22:93–97. https://doi.org/10.2135/cropsci1982.0011183X002200010021x

184. Belesky DP, Wilkinson SR, Evans JJ. Amino acid composition of fractions of ‘Kentucky-31’ tall fescue as affected by N fertilization and mild water stress. Plant Soil. 1984;81:257–267. https://doi.org/10.1007/BF02197159

185. Malinowski DP, Alloush GA, Belesky DP. Evidence for chemical changes on the root surface of tall fescue in response to infection with the fungal endophyte Neotyphodium coenophialum. Plant Soil. 1998;205:1–12. https://doi.org/10.1023/A:1004331932018

186. Malinowski DP, Belesky DP. Tall fescue aluminum tolerance is affected by Neotyphodium coenophialum endophyte. J Plant Nutr. 1999;22:1335–1349. https://doi.org/10.1080/01904169909365716

187. Malinowski DP, Alloush GA, Belesky DP. Leaf endophyte Neotyphodium coenophialum modifies mineral uptake in tall fescue. Plant Soil. 2000;227:115–126. https://doi.org/10.1023/A:1026518828237

188. Ren AZ, Gao YB, Zhou F. Response of Neotyphodium lolii-infected perennial ryegrass to phosphorus deficiency. Plant Soil Environ. 2007;53:113–119. https://doi.org/10.17221/2225-PSE

189. Appel HM. Phenolics in ecological interactions: the importance of oxidation. J Chem Ecol. 1993;19:1521–1552. https://doi.org/10.1007/BF00984985

190. Kalkafi U, Bar-Yosef B, Rosenberg R, Sposito G. Phosphorus adsorption by kaolinite and montmorillonite: II. Organic anion competition. Soil Sci Soc Am J. 1988;52:1585–1589. https://doi.org/10.2136/sssaj1988.0361599500520000060012x

191. Rahman MH, Saiga S. Endophyte effects on nutrient acquisition in tall fescue grown in andisols. J Plant Nutr. 2007;30:2141–2158. https://doi.org/10.1080/01904160701700632

192. Dennis SB, Allen VG, Saker KE, Fontenot JP, Ayad JY, Brown CP. Influence of Neotyphodium coenophialum on copper concentration in tall fescue. J Anim Sci. 1998;76:2687–2693. https://doi.org/10.2527/1998.76102687x

193. Marschner, H. Mineral nutrition in higher plants. 2nd ed. Orlando, FL: Academic Press;
199. van Hecke MM, Treonis AM, Kaufman JR. How does the fungal endophyte *Neotyphodium coenophialum* affect tall fescue (*Festuca arundinacea*) rhizodeposition and soil microorganisms? Plant Soil. 2005;275:101–109. https://doi.org/10.1007/s11104-005-0380-2

195. Fabien M, Nathalle V, Adnan H, Alain C, Huguette S. Endophytic *Neotyphodium lolii* induced tolerance to Zn stress in *Lolium perenne*. Plant Physiol. 2001;113:557–563. https://doi.org/10.1093/jxbot/113.3.557

196. Zamani N, Sabzalian MR, Khoshgoftarmanesh A, Afyuni M. *Neotyphodium* endophyte changes phytoextraction of zinc in *Festuca arundinacea* and *Lolium perenne*. Int J Phytoremediation. 2014;17:456–463. https://doi.org/10.1080/15226514.2014.922919

198. Mirzahosseini Z, Shabani L, Sabzalian MR, Sharifi Tehrani M. Effect of *Neotyphodium* endophyte symbiosis on growth, nickel uptake and photosynthetic pigments in two genotypes of tall fescue. Journal of Plant Processes and Function. 2014;2:25–37.

201. Bonnet M, Camares O, Veisseire P. Effects of zinc and influence of *Acremonium lolii* on growth parameters, chlorophyll a fluorescence and antioxidant enzyme activities of ryegrass (*Lolium perenne* L. cv Apollo). J Exp Bot. 2000;51:945–953. https://doi.org/10.1093/jexbot/51.346.945

202. Yin L, Ren A, Wei M, Wu L, Zhou Y, Li X, Gao Y. *Neotyphodium coenophialum*-infected tall fescue and its potential application in the phytoremediation of saline soils. Int J Phytoremediation. 2014;16:235–246. https://doi.org/10.1080/15226514.2013.773275

203. Belesky DP, Devine OJ, Pallas JE, Stringer WC. Photosynthetic activity of tall fescue as influenced by a fungal endophyte. Photosynthetica. 1987;21:82–87.

207. McLeod AR, Rey A, Newsham KK, Lewis GC, Wolferstan P. Effects of elevated ultraviolet radiation and endophytic fungi on plant growth and insect feeding in *Lolium perenne*, *Festuca rubra*, *F. arundinacea* and *F. pratensis*. Journal of Photochemistry and Photobiology. 2001;B62:97–107. https://doi.org/10.1016/S1011-1344(01)00151-8

208. Zhou F, Gao Y, Ma W. Effects of phosphorus deficiency on growth of perennial ryegrass–fungal endophyte symbiont and phenolic content in root. Plant Physiology Communications. 2003;39:321–324.

209. Blokhina O, Virolainen E, Fagerstedt KV. Antioxidants, oxidative damage and oxygen deprivation stress: a review. Ann Bot. 2003;91:179–194. https://doi.org/10.1093/aob/mcf118

210. Malinowski DP, Belesky DP, Lewis GC. Abiotic stresses in endophytic grasses. In: Roberts CA. West CP, Spiers DE, editors. *Neotyphodium* in cool season grasses. Ames, IA: Blackwell Publishing Professional; 2005. p. 187–199. https://doi.org/10.1002/9780470384916.ch18

211. Belesky DP, Bacon CW. Tall fescue and associated mutualistic toxic fungal endophytes in agroecosystems. Toxins Rev. 2009;28:102–117.
212. Spyreas G, Gibson DJ, Middleton BA. Effects of endophyte infection in tall fescue (Festuca arundinacea: Poaceae) on community diversity. Int J Plant Sci. 2001;162:1237–1245. https://doi.org/10.1086/323274

213. Gundel PE, Garibaldi LA, Martínez-Ghersa MA, Ghersa CM. Neotyphodium endophyte transmission to Lolium multiflorum seeds depends on the host plant fitness. Environ Exp Bot. 2011;71:359–366. https://doi.org/10.1016/j.envexpbot.2011.02.002

214. Iqbal J, Nelson JA, McCulley RL. Fungal endophyte presence and genotype affect plant diversity and soil-to-atmosphere trace gas fluxes. Plant Soil. 2013;364:15–27. https://doi.org/10.1007/s11104-012-1326-0

215. Franzluebbers AJ, Nazih N, Stuedemann JA, Fuhrmann JJ, Schomberg HH, Hartel PG. Soil carbon and nitrogen pools under low- and high-endophyte-infected tall fescue. Soil Sci Soc Am J. 1999;63:1687–1694. https://doi.org/10.2136/sssaj1999.6361687x

216. Omacini M, Chaneton EJ, Ghersa CM, Otero P. Do foliar endophytes affect grass litter decomposition? A microcosm approach using Lolium multiflorum. Oikos. 2004;104:581–590. https://doi.org/10.1111/j.0030-1299.2004.12915.x

217. Lemons A, Clay K, Rudgers JA. Connecting plant–microbial interactions above and belowground: a fungal endophyte affects decomposition. Oecologia. 2005;145:595–604. https://doi.org/10.1007/s00442-005-0163-8

218. Petroski RJ, Dornbos DL Jr, Powell RG. Germination and growth inhibition of annual ryegrass (Lolium multiflorum L.) and alfalfa (Medicago sativa L.) by loline alkaloids and synthetic N-acylloline derivatives. Journal of Agriculture and Food Chemistry. 1990;38:1716–1718. https://doi.org/10.1021/jf00098a019

219. Malinowski DP, Belesky DP, Fedders JM. Endophyte infection may affect the competitive ability of tall fescue grown with red clover. J Agron Crop Sci. 1999;183:91–101. https://doi.org/10.1046/j.1439-037x.1999.00322.x

220. Sutherland BL, Hume DE, Tapper BA. Allelopathic effects of endophyte-infected perennial ryegrass extracts on white clover seedlings. New Zealand Journal of Agricultural Research. 1999;42:19–26. https://doi.org/10.1080/00288233.1999.9531349

221. Matthews JW, Clay K. Influence of fungal endophyte infection on plant–soil feedback and community interactions. Ecology. 2001;82:500–509. https://doi.org/10.1890/0012-9658(2001)082[0500:IOFEIO]2.0.CO;2

222. Buyer JS, Zuberer DA, Nichols KA, Franzluebbers AJ. Soil microbial community function, structure, and glomalin in response to tall fescue endophyte infection. Plant Soil. 2011;339:401–412. https://doi.org/10.1007/s11104-010-0592-y

223. Casas C, Omacini M, Susana Montecchia M, Susana Correa O. Soil microbial community responses to the fungal endophyte Neotyphodium in Italian ryegrass. Plant Soil. 2011;340:347–355. https://doi.org/10.1007/s11104-010-0607-8

224. Hoveland CS, Bouton JH, Durham RG. Fungal endophyte effects on production of legumes in association with tall fescue. Agron J. 1999;91:897–902. https://doi.org/10.2134/agronj1999.916987x

225. Takai T, Sanada Y, Yamada T. Influence of the fungal endophyte Neotyphodium uncinatum on the persistency and competitive ability of meadow fescue (Festuca pratensis Huds.). Japanese Society of Grassland Science. 2010;56:59–64. https://doi.org/10.1111/j.1744-697X.2010.00175.x

226. Rudgers JA, Fischer, S, Clay K. Managing plant symbiosis: fungal endophyte genotype alters plant community composition. J Appl Ecol. 2010;47:468–477. https://doi.org/10.1111/j.1365-2664.2010.01788.x

227. Yurkonis KA, Shukla K, Holdenried J, Hager HA, Bolton KA, Klironomos JN, et al. Endophytes inconsistently affect plant communities across Schedonorus arundinaceus hosts. Plant Ecol. 2014;215:389–398. https://doi.org/10.1007/s11258-014-0309-z

228. Marks S, Clay K. Effects of CO2 enrichment, nutrient addition, and fungal endophyte infection on the growth of two grasses. Oecologia. 1990;84:207–214. https://doi.org/10.1007/BF00318273

229. Briggs L, Crush J, Ouyang L, Sprosen J. Neotyphodium endophyte strain and superoxide dismutase activity in perennial ryegrass plants under water deficit. Acta Physiol Plant. 2013;35:1513–1520. https://doi.org/10.1007/s11738-012-1192-7

230. Ambrose KV, Tian Z, Wang Y, Smith J, Zylstra G, Huang B, et al. Functional characterization of salicylate hydroxylase from the fungal endophyte Epichloë festucae.
231. Bastias DA, Alejandra Martínez-Ghersa M, Newman JA, Card SD, Mace WJ, Gundel PE. The plant hormone salicylic acid interacts with the mechanism of anti-herbivory conferred by fungal endophytes in grasses. Plant Cell Environ. 2018;41:395–405. https://doi.org/10.1111/pce.13102

232. Clay K. Effects of fungal endophytes on the seed and seedling biology of Lolium perenne and Festuca arundinacea. Oecologia. 1987;73:358–362. https://doi.org/10.1007/BF00385251

233. Pinkerton BW, Rice JS, Undersander DJ. Germination in Festuca arundinacea as affected by the fungal endophyte, Acremonium coenophialum. In: Quinsenberry SS, Joost RE, editors. Proceedings of the International Symposium on Acremonium/Grass Interactions; 1990 Nov 3; Baton Rouge, LA, USA. Baton Rouge, LA: Louisiana Agricultural Experiment Station; 1990. p. 176–180.

234. Novas MV, Gentile A, Cabral D. Comparative study of growth parameters on diaspores and seedlings between populations of Bromus setifolius from Patagonia, differing in Neotyphodium endophyte infection. Flora. 2003;198:421–426. https://doi.org/10.1078/0367-2530-00115

235. Li CJ, Nan ZB, Li F. Biological and physiological characteristics of Neotyphodium gansuense symbiotic with Achnatherum inebrians. Microbiol Res. 2008;163:431–440. https://doi.org/10.1016/j.micres.2006.07.007

236. Wang J, Zhou Y, Lin W, Li M, Wang M, Wang Z, et al. Effect of an Epichloë endophyte on adaptability to water stress in Festuca sinensis. Fungal Ecol. 2017;30:39–47. https://doi.org/10.1016/j.funeco.2017.08.005

237. Faeth SH, Helander ML, Saikkonen KT. Asexual Neotyphodium endophytes in a native grass reduce competitive abilities. Ecol Lett. 2004;7:304–313. https://doi.org/10.1111/j.1461-0248.2004.00578.x

238. Owens HT, Finneseth CH, Tillery TM, Phillips TD. Germination rate and seedling vigour of tall fescue as affected by endophyte status and seed density. In: Popay AJ, Thom ER, editors. Proceedings of the 6th International Symposium on Fungal Endophytes of Grasses; 2007 Mar 25–28; Christchurch, New Zealand. Dunedin: New Zealand Grassland Association; 2007. p. 271–274.

239. Wäli PR, Helander M, Saloniemi I, Ahlholm J, Saikkonen K. Variable effects of endophytic fungus on seedling establishment of fine fescues. Oecologia. 2009;159:49–57. https://doi.org/10.1007/s00442-008-1202-z

240. Hill NS, Stringer WC, Rottinghaus GE, Belesky DP, Parrot WA, Pope DD. Growth, morphological and chemical component responses of tall fescue to Acremonium coenophialum. Crop Sci. 1990;30:156–161. https://doi.org/10.2135/cropsci1990.0011183X003000010034x

241. Eerens JPJ, White JGH, Lucas RJ. The influence of Acremonium endophyte on the leaf extension rate of moisture stressed ryegrass plants. In: Hume DE et al., editors. Proceedings of the 2nd International Symposium on Acremonium/Grass Interactions; 1993 Feb 4–6; Palmerston North, New Zealand. Palmerston North: AgResearch, Grassland Research Centre; 1993. p. 200–204.

242. Malinowski DP, Brauer DK, Belesky DP. The endophyte Neotyphodium coenophialum affects root morphology of tall fescue grown under phosphorus deficiency. J Agron Crop Sci. 1999;183:53–60. https://doi.org/10.1046/j.1439-037x.1999.00321.x

243. Vázquez-de-Aldana BR, Zabalgogeazcoa I, García-Ciudad A, García-Criado B. An Epichloë endophyte affects the competitive ability of Festuca rubra against other grassland species. Plant Soil. 2013;362:201–213. https://doi.org/10.1007/s11104-012-1283-7

244. Chen W, Liu H, Wurihan, Gao Y, Card SD, Ren A. The advantages of endophyte-infected over uninfected tall fescue in the growth and pathogen resistance are counteracted by elevated CO2. Sci Rep. 2017;7:6952. https://doi.org/10.1038/s41598-017-07183-y

245. Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, et al, editors. Climate Change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press; 2013.

246. Hunt MG, Rasmussen SPCD, Parsons AJ, Newman JA. Near-term impacts of elevated CO2, nitrogen and fungal endophyte-infection on Lolium perenne L. growth, chemical composition and alkaloid production. Plant Cell Environ. 2005;28:1345–1354. https://doi.org/10.1111/j.1365-3040.2005.01367.x
247. Newman JA, Abner ML, Dado RG, Gibson DJ, Brookings A, Parson AJ. Effects of elevated CO₂, nitrogen and fungal endophyte-infection on tall fescue growth, photosynthesis, chemical composition and digestibility. Glob Chang Biol. 2003;9:425–437. https://doi.org/10.1046/j.1365-2486.2003.00601.x

248. Volaire F, Norton M. Summer dormancy in perennial temperate grasses. Ann Bot. 2006;98:927–933. https://doi.org/10.1093/aob/mcl195

249. Clement SL, Elberson LR, Youssef NN, Davitt CM, Doss RP. Incidence and diversity of Neotyphodium fungal endophytes in tall fescue from Morocco, Tunisia, and Sardinia. Crop Sci. 2001;41:570–576. https://doi.org/10.2135/cropsci2001.412570x

250. Piano E, Bertoli FB, Romani M. Specificity of host-endophyte association in tall fescue populations from Sardinia, Italy. Crop Sci. 2005;45:1456–1463. https://doi.org/10.2135/cropsci2004.0287

251. Pecetti L, Romani M, Carroni AM, Annicchiarico P, Piano E. The effect of endophyte infection on persistence of tall fescue (Festuca arundinacea Schreb.) populations in two climatically contrasting Italian locations. Aust J Agric Res. 2007;58:893–899. https://doi.org/10.1071/AR06423

252. Pecetti L, Annicchiarico P, Porqueddu C, Khedim A, Abdelguerfi A. Fitting germplasm types of tall fescue and orchardgrass to different cropping environments of the Mediterranean region. Crop Sci. 2009;49:2393–2399. https://doi.org/10.2135/cropsci2009.06.0333

253. Malinowski DP, Butler TJ, Belesky DP. Competitive ability of tall fescue against alfalfa as a function of summer dormancy, endophyte infection, and soil moisture availability. Crop Sci. 2011;51:1282–1290. https://doi.org/10.2135/cropsci2010.08.0456

254. Brem D, Leuchtmann A. Intraspecific competition of endophyte infected vs uninfected plants of two woodland grass species. Oikos. 2002;96:281–290. https://doi.org/10.1034/j.1600-0706.2002.960210.x

255. Saikkonen K, Lehtonen P, Helander M, Koricheva J, Faeth SH. Model systems in ecology: dissecting the endophyte-grass literature. Trends Plant Sci. 2006;11:428–433. https://doi.org/10.1016/j.tplants.2006.07.001

256. Tapper BA, Latch GCM. Selection against toxin production in endophyte-infected perennial ryegrass. In: Woodfield DR, Matthew C, editors. Ryegrass endophyte: an essential New Zealand symbiosis. Palmerston North: New Zealand Grassland Association; 1999. p. 107–111. (Grassland Research and Practice Series; vol 7).

257. Bouton JH, Latch GCM, Hill NS, Hoveland CS, McCann MA, Watson RH, et al. Reinfection of tall fescue cultivars with non-ergot alkaloid-producing endophytes. Agron J. 2002;94:567–574. https://doi.org/10.2134/agronj2002.5670

258. Parish JA, McCann MA, Watson RH, Hoveland CS, Hawkins LL, Hill NS, et al. Use of nonergot alkaloid-producing endophytes for alleviating tall fescue toxicosis in sheep. J Anim Sci. 2003;81:1316–1322. https://doi.org/10.2527/2003.811316x

259. Parish JA, McCann MA, Watson RH, Paiva NN, Hoveland CS, Parks AH, et al. Use of nonergot alkaloid-producing endophytes for alleviating tall fescue toxicosis in stocker cattle. J Anim Sci. 2003;81:2856–2868. https://doi.org/10.2527/2003.81112856x

260. Nihsen ME, Piper EL, West CP, Crawford RJ Jr, Denard TM, Johnson ZB, et al. Growth rate and physiology of steers grazing tall fescue inoculated with novel endophytes. J Anim Sci. 2004;82:878–883. https://doi.org/10.1093/ansci/82.3.878

261. Gunter SA, Beck PA. Novel endophyte-infected tall fescue for growing beef cattle. J Anim Sci. 2004;82:E75–E82.

262. Hopkins AA, Young CA, Panaccione DG, Simpson WR, Mittal S, Bouton JH. Agronomic performance and lamb health among several tall fescue novel endophyte combinations in the South-Central USA. Crop Sci. 2009;50:1552–1561. https://doi.org/10.2135/cropsci2009.08.0473

263. Gundel PE, Pérez LI, Helander M, Saikkonen K. Symbiotically modified organisms: nontoxic fungal endophytes in grasses. Trends Plant Sci. 2013;18:420–427. https://doi.org/10.1016/j.tplants.2013.03.003

264. Macoon B, Vann RC, Perkins JD III, Withers FT Jr. Steer performance and forage production on novel-endophyte fescue compared to ryegrass pastures. In: Kallenbach R, Rosenkrans C Jr, Lock TR, editors. Proceedings of the 5th International Symposium on Neotyphodium/Grass Interactions; 2004 May 23–26; Fayetteville, AR, USA. Fayetteville, AR: University of Arkansas; 2004. Poster No. 504.
265. Hopkins AA, Young CA, Butler TJ, Bouton JH. Registration of ‘Texoma’ MaxQ II tall fescue. J Plant Regist. 2011;5:14–18. https://doi.org/10.3198/jpr2010.02.0082cr

266. New Zealand Agriseeds. Endophyte options [Internet]. 2018 [cited 2018 Sep 27]. Available from: https://www.agriseeds.co.nz/ryegrassendophyte/endophyte-options.htm

267. Heritage Seeds. Seed guide [Internet]. 2018 [cited 2018 Sep 27]. Available from: https://www.heritageseeds.com.au/brochures-publications

268. Popay AJ, Hume DE, Baltus JG, Latch GCM, Tapper BA, Lyons TB, et al. Field performance of perennial ryegrass (Lolium perenne) infected with toxin-free fungal endophytes (Neotyphodium spp.). Grassland Research and Practice Series. 1999;7:113–122.

269. Popay AJ, Baltus JG. Black beetle damage to perennial ryegrass infected with AR 1 endophyte. Proceedings of the New Zealand Grassland Association. 2001;63:267–271.

270. Hunt MG, Newman JA. Reduced herbivore resistance from a novel grass–endophyte association. J Appl Ecol. 2005;42:762–769. https://doi.org/10.1111/j.1365-2664.2005.01061.x

271. Timper P, Bouton JH. Effect of endophyte status and tall fescue cultivar on reproduction of lesion and stubby-root nematodes. In: Kallenbach R, Rosenkranz C Jr, Lock TR, editors. Proceedings of the 5th International Symposium on Neotyphodium/Grass Interactions, 2004 May 23–26; Fayetteville, AR, USA. Fayetteville, AR: University of Arkansas; 2004. Poster No. 406.

272. Malinowski DP, Kigel J, Pinchak WE. Water deficit, heat tolerance, and persistence of summer-dormant grasses in the U.S. Southern Plains. Crop Sci. 2009;49:2363–2370. https://doi.org/10.2135/cropsci2009.06.0316

273. Ju HJ, Hill NS, Abbot T, Ingram KT. Temperature influences on endophyte growth in tall fescue. Crop Sci. 2006;46:404–412. https://doi.org/10.2135/cropsci2005.06.0328

Epichloë (dawniej Neotyphodium) grzybowe endofyty 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 kręgowe i bezkręgowe, pasożytnicze nicienie, patogeny i konkurencję z innymi roślinami). Niektóre szczepy endofytów wytwarzają szereg alkaloидów i innych wtórnych związków chemicznych, które mogą mieć szkodliwy wpływ na zwierzęta wypasane na symbiotycznych trawach. W ciągu ostatnich dwóchdekad 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 konkurowania symbiotycznych odmian traw z chwastami. W niniejszej pracy omawiamy mechanizmy odpowiedzialne za większą zdolność konkurencyjną symbiotycznych traw oraz konsekwencje tej symbiozy dla ekosystemów roślinnych.