Epichloë – a lifeline for temperate grasses under combined drought and insect pressure

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Abstract
Fungal Epichloë endophytes form symbiotic associations with many temperate grasses, such as Lolium and Festuca, giving their host grasses an ecological advantage. The importance of specific Epichloë endophytes in providing varying levels of protection against invertebrate pests has been well documented. Similarly, but with fewer studies, the benefits of Epichloë to host grasses in drought events has been shown. Endophyte-infected grasses show an improved persistence against herbivore insect attack as well as resilience under drought. However, there are relatively few studies that investigate the interaction between drought and insect pressure, and yet it is these combined pressures that can prove detrimental for a ryegrass or fescue crop. This review examines the current state of knowledge on the effects of Epichloë on the interactions of insects and drought in temperate grasses.

Introduction
Worldwide, around 26% of the world land area is dominated by forage grass species for animal production systems[1]. Poaceae grasses (subfamily Pooideae), such as Lolium and Festuca, are often used in managed pasture systems throughout temperate zones[2,3]. Along with other cool-season grasses, they are capable of forming both sexual and asexual associations with fungal Epichloë endophytes that range from mutualistic to antagonistic. The mutalistic outcomes of the relationship for their Lolium and Festuca hosts are considered to be a major factor in the evolution of maternal transmission of the endophyte[4,6]. These endophytes are critical constituents of agricultural ecosystems and likely have an important role in regulating communities in natural grasslands although these have been less well studied. Living only in the above-ground tissues, endophyte infection in these temperate grasses can increase the plants’ ability to tolerate herbivory attack through the production of a large range of secondary metabolites such as alkaloids[5]. Four main classes of alkaloids are recognised as being produced by Epichloë endophytes; peramine, indole diterpenes, ergot alkaloids, and lolines[6]. All of these alkaloid classes are involved in invertebrate deterrence and/or toxicity[7], while ergot alkaloids as well as indole diterpenes can also impair grazing animal performance[5]. Removal of the fungal endophyte from the host grass to counter the toxic effect on grazing livestock is a logical approach. However, such endophyte-free plants were not viable in New Zealand and other countries that suffer from high invertebrate pest pressure[8]. The economic loss and reduced animal performance of livestock grazing pastures containing a toxic endophyte led to the identification of endophyte strains that retain insect-active alkaloids while minimising the production of the mammalian active toxins[5,10]. The anti-herbivory properties have been utilised and commercialised in agriculturally managed agroecosystems that use perennial ryegrass (Lolium perenne L.) and tall fescue (Festuca arundinacea Schreb.), two dominant plant species sown for ruminant livestock production[12–15] (Table 1 and Table 2). In addition to the invertebrates affected by endophyte, in the USA, mammalian-toxic E. coenophiala also affects grazing and reproduction of the prairie vole (Microtus ochrogaster) which in turn modifies community structure[16]. Fungal Epichloë endophytes have become a fundamental and essential management tool in integrated pest management in New Zealand, Australia, and the USA to maintain and/or increase pasture production and persistence[17–19].

Farmers are facing an increasingly complex operating environment through changes in climate as well as increased global demand for more sustainable farming systems. Resource limitations, such as drought, can significantly impact managed grassland productivity. Numerous studies have investigated if Epichloë endophyte infection improves the ability of the grass host to withstand abiotic stress factors and resource limitations such as drought[5,20]. Although there is evidence that E. coenophiala promotes drought tolerance in its tall fescue host, the information for this occurring in ryegrass is more equivocal. In addition, there is the likelihood of interactions occurring between invertebrates and abiotic stress which we do not yet fully understand. For example,
Table 1. Summary of *Epichloë* endophyte brands in ryegrass and fescue grasses available in New Zealand, Australia, and the USA: alkaloid profile, insect resistance properties, and livestock toxicity for each.

| Insect                              | Adult and larvae weevil (Listronotus bonariensis) | Pasture mealybug (Balanococcus poae) | African black beetle (Heteronychus arator) | Root aphid (Aploneura lenticis) | Porina (Wisana spp.) | Grass grub (Costelytra zealandica) | Black field cricket (Teleogryllus commodus) | Animal health disorders |
|-------------------------------------|--------------------------------------------------|--------------------------------------|---------------------------------------------|-------------------------------|----------------------|-----------------------------------|---------------------------------------------|-------------------------------|
|                                     | Up to $200M$ dairy; $235M$ sheep & beef           | Unknown                              | Up to $223M$ dairy; $19M$ sheep & beef       | Unknown                       | Up to $84M$ dairy; $88M$ sheep & beef | $275M$–$570M$ dairy; $75M$–$205M$ sheep & beef | Unknown                       |                               |
| Annual economic impact in a specific industry [26] | Up to $200M$ dairy; $235M$ sheep & beef           | Unknown                              | Up to $223M$ dairy; $19M$ sheep & beef       | Unknown                       | Up to $84M$ dairy; $88M$ sheep & beef | $275M$–$570M$ dairy; $75M$–$205M$ sheep & beef | Unknown                       |                               |
| Diploid perennial ryegrass (F. festucae var. lolii) | AR1 Peramine (+++) [21]  ++++ [22]  ++++ [23]  ++++ [24]  ++++ [25]  ++++ [26]  not tested  not tested  none [30]  | AR37 Epoxy-janthitrems (+++) [27]  ++++ [22]  ++++ [23]  ++++ [24]  ++++ [25]  ++++ [26]  not tested  not tested  occasionally [29,30]  | NE2 Peramine, ergovaline, lolitrem B  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  not tested  not tested  not tested  none [36]  | NE4 Peramine, ergovaline  (+++)  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  not tested  not tested  not tested  none  | Edge Peramine, ergovaline  (+++)  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  not tested  not tested  not tested  none  | Avanex® Peramine, ergovaline, lolitrem B (++)  (++)  (++)  (++)  (++)  (++)  (++)  (++)  None  | Happe Lolines  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  not tested  not tested  not tested  | Tetraploid perennial ryegrass (F. festucae var. lolli) |
| Italian and hybrid ryegrass (F. festucae var. lolli) | AR1 Peramine  (+++) [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  | AR37 Epoxy-janthitrems  (+++) [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  | NEA Peramine, ergovaline, lolitrem B  Not tested  Not tested  Not tested  Not tested  Not tested  Not tested  Not tested  Not tested  Occasionally [29,30]  | NE4 Peramine, ergovaline  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  None  | Edge Peramine, ergovaline  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  None  | Avanex® Peramine, ergovaline, lolitrem B (++)  (++)  (++)  (++)  (++)  (++)  (++)  (++)  None  | Happe Lolines  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  not tested  not tested  not tested  | Meadow fescue (F. uncinata) |
| Tall fescue (F. comophila) | MaxP/MaxQ Peramine, lolines  (+++) [24]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  | Protek Lolines  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  ++++ [26]  ++++ [26]  ++++ [26]  | U2 Lolines  (+++) [31]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  | MaxP/MaxQ Peramine, lolines  (+++) [24]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  | Protek Lolines  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  ++++ [26]  ++++ [26]  ++++ [26]  | U2 Lolines  (+++) [31]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  ++++ [32]  | MaxP/MaxQ Peramine, lolines  (+++) [24]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  ++++ [26]  | Protek Lolines  (+++)  (+++)  (+++)  (+++)  (+++)  (+++)  ++++ [26]  ++++ [26]  ++++ [26]  |

- No protection.
- Low level of control: Endophyte may provide a measurable effect, but is unlikely to give control in the field.
- Moderate level of control: Endophyte may provide some protection in the field, with a low to moderate reduction of pest population.
- Good level of control: Endophyte significantly reduces insect damage under low to moderate insect pressure. Disease may occur during high insect pressure.
- Very good control: Endophyte significantly reduces insect damage and pest population even under high pest pressure.

* Provisional rating: Testing is ongoing, further data is required to support rating.
* AR1 plants are more harmed than plants without endophyte.
* A new meadow fescue cultivar infected with *F. uncinata* is now commercially available but has yet to be formally rated for its effects on insect pests. Previous work has shown that natural meadow fescue endophytes provide strong protection against a range of insect pests including black beetle, Argentine stem weevil and crickets.
* DLF Seeds & Science; ratings have not been approved by the New Zealand Plant Breeding & Research Association.
* T - Higher plant growth compared with endophyte-free control but no difference in larval weight.
* R - Reduced weight gain of grass grub larvae.
* Toxic endophyte used at airports and sports fields to reduce the number of birds on or near sports fields and airfields.

(1) Provisional rating: Testing is ongoing, further data is required to support rating.
(2) AR37 only deter the more damaging ASW larvae not adult.
(3) Active against Black beetle adult and larvae.
(4) A new meadow fescue cultivar infected with *F. uncinata* is now commercially available but has yet to be formally rated for its effects on insect pests. Previous work has shown that natural meadow fescue endophytes provide strong protection against a range of insect pests including black beetle, Argentine stem weevil and crickets.
(5) DLF Seeds & Science; ratings have not been approved by the New Zealand Plant Breeding & Research Association.
(6) T - Higher plant growth compared with endophyte-free control but no difference in larval weight.
(7) R - Reduced weight gain of grass grub larvae.
(8) Toxic endophyte used at airports and sports fields to reduce the number of birds on or near sports fields and airfields.

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Table 2. The impact of *Epichloë* endophyte on the drought tolerance of a range of cultivated and native temperate grasses.

| Species of grass and endophyte | Impact of endophyte | Physiological and/or structural changes to host plant and endophyte in response to drought | Reference |
|-------------------------------|---------------------|-----------------------------------------------------------------------------------------|-----------|
| **Cultivated grasses**        |                      |                                                                                         |           |
| Perennial ryegrass (L. perenne) | Increased tiller number and shoot weight | 15% higher osmotic potential, leaf water content not affected | [64]      |
| *E. festucae var. lolii*       |                      | Reduced leaf dehydration in moderately droughted plants                                 | [66]      |
|                               | Variable effect related to original habitat of collection | Increased root dry weight and root/shoot ratio                                           | [67]      |
|                               | Lower dry weight, but less wilting | Lower water use efficiency                                                              | [68]      |
| In 4 of 6 Mediterranean populations |                       | Increased tiller number and yield                                                       | [69]      |
| *E. festucae*                 | Beneficial for combined stresses of drought and *Bipolaris sorokiniana* | Increased growth, and photosynthetic parameter, but decreased proline content           | [70]      |
|                               | Provides physiological protection against drought | Drought increased ergovaline and lolitrem B levels but endophyte had no effect on proline levels improved water use efficiency, relative water content and osmotic potential | [71]      |
|                               | No effect            | No effect on osmotic potential, no effect on stomatal conductance, no involvement to withstand or recover from drought | [72, 62, 73, 74] |
| Higher seedling survival when released from drought | No effect on reactive oxygen species |                                                                                 | [79]      |
| **Tall fescue** (F. arundinacea) | Endophyte responses vary with genotype | Pseudostem, root and dead leaf yield increased with endophyte in some cases; no effect on non-structural carbohydrates | [80]      |
| *E. coenophiala*              | Improved plant survival under severe soil moisture deficit | No consistent endophyte effect on dry weight per tiller, stomatal conductance; endophyte reduced leaf rolling in drought, but increased water content and delayed desiccation | [81]      |
|                               |                      | No effect on leaf osmotic potential and minimal effect on plant water-soluble mineral and sugar concentrations | [82]      |
|                               | Improved recovery after drought | Leaf rolling under drought stress greater for endophytic plants; regrowth greater for endophytic plants when re-watered | [83]      |
|                               |                      | Increased alkaloid levels                                                               | [80, 84, 85] |
|                               |                      | Increased soluble carbohydrates in leaves                                                | [63, 86, 87] |
|                               |                      | Shedding of older leaves and rolling of younger leaves; low stomatal conductance; increased cellular turgor pressure | [63, 88] |
|                               |                      | No effect on leaf rolling                                                               | [89]      |
|                               |                      | Enhanced tiller density and plant survival                                             | [90]      |
|                               |                      | Maintained water use efficiency and photosynthetic rate better under drought            | [91]      |
|                               |                      | Enhanced stomatal adjustment in meristem; reduced stomatal conductance and transpiration | [92, 93] |
|                               |                      | Reduced stomatal conductance; maintained higher water content of tiller bases           | [93]      |
|                               |                      | Root nematode inhibition by endophyte                                                  | [90, 94] |
|                               |                      | Increased drought tolerance                                                             | [95]      |
|                               |                      | Improved plant available water                                                          | [96]      |
|                               |                      | Reduced reactive oxygen species                                                         |           |
|                               | Improved recovery after drought | Improved tiller and whole plant survival, improved root growth                          | [62, 87, 90, 97–99] |
| **Meadow fescue** (F. pratensis) | Improved growth in drought | Reduced stomatal conductance, increased water uptake capacity, production of larger but fewer tillers | [101, 102] |
| *E. uncinitum*                |                      |                                                                                         | [103]     |
| **Strong creeping red fescue** (F. rubra ssp. rubra) – turf type *E. festucae* | No improvement under drought |                                                                                         | [104]     |
| **Native grasses**            |                      |                                                                                         |           |
| Drunken horse grass (Achnatherum inebrians) | Improved tolerance to drought and recovery from drought | Increased leaf proline, root/leaf growth, tiller number                                  | [106]     |
| *E. gansuense*               |                      |                                                                                         |           |

*Interactions – drought, insects, and endophytes*

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moderate drought events can promote insect herbivory driven by elevated nutrient levels in plant tissues\cite{42,43} and lowered plant defences\cite{42,44}. There is, however, a major gap in our understanding of the role of *Epichloë* endophytes under combined effects of both drought and insect pressure.

The questions to be examined in this review are:

I. Many *Epichloë* endophyte strains improve plant persistence in the presence of some insect pests and when plants are drought-stressed, but is this a three-way interaction that needs to be better understood?

II. Can endophyte-infected plants survive a combination of insect pest pressure and drought stress or is their protection only effective when plants are challenged by one or other of these stresses? Are there likely to be differences depending on the *Epichloë* endophyte strains used? Is there a cost to the plant from hosting *Epichloë* endophytes when challenged by drought and other stress factors?

**Impact of drought**

Water is essential for herbaceous plants, giving the plant the ability to take up nutrients while maintaining turgor pressure. When water supply reduces or ceases for a period of time plants are subjected to unsuitable growing conditions resulting in a significant impact on plant production\cite{45}. Climate change has shifted the frequency of drought in some agricultural regions\cite{46,47}. While the predictions are highly variable between countries and regions, in temperate grass-producing regions of countries like New Zealand, Australia, and the USA, the overall trend is for increased likelihood of soil moisture depletion, increases in temperature, and more frequent extreme weather events\cite{48−50}. These changes are of particular significance to the agricultural sector. With such changes in temperature and precipitation, pastures are projected to have an earlier growth start in late winter while drying out more quickly in late spring\cite{51}. Perennial ryegrass, the mainstay of the New Zealand agricultural industry, fails to increase yield, root: shoot ratio; improved tiller number

| Table 2. (continued) |
|----------------------|
| **Species of grass and endophyte** | **Impact of endophyte** | **Physiological and/or structural changes to host plant and endophyte in response to drought** | **Reference** |
| *Achnatherum sibiricum* *Epichloë* spp. | Endophyte benefit greatest when well-watered and fertilised | Improved photosynthetic efficiency and nutrient absorption  | [107] |
| *Hordelymus europaeus* *E. hordelymi* | Improved recovery from drought | Increased ergovaline and ergine alkaloid concentrations | [108] |
| *Grove bluegrass* (*Poa alsodes*) *E. bromicola* sp. | Improved the negative effects of drought stress | Reduced disease incidence of *Blumeira graminis* | [109] |
| *Arizona fescue* (*Festuca arizonica*) *E. pampeanum* sp. | Endophyte infection beneficial in drought | Higher root: shoot ratio and photosynthetic rate under drought and fertilisation | [110] |
| *Bromus auleticus* *E. pampeanum* and *E. tembladerae* | Improved survival in summer | Increased tiller number and plant dry weight | [111] |
| *Roegneria kamooji* *E. sinica* | Improved seedling establishment in drought | Improved germination and seedling growth | [112] |
| *Elymus dahuicus* *E. bromicola* sp. | Improved yield and tiller numbers under drought | Endophyte caused anti-oxidative enzyme activities and contents of proline and chlorophyll | [113] |
| *Elymus virginitus* *E. elymi* | Improved drought tolerance, but also benefited well-watered plants | Increased germination at moderate osmotic potentials | [114] |
| *Leymus chinesis* *E. tembladerae* | Improved yield under drought | No effect on root: shoot ratio; improved tiller number | [115] |
| *Festuca sinensis* *E. pampeanum* | Endophytes enhanced drought tolerance | Increased photosynthetic rate | [116] |

**Table 2.** (continued)

**Species of grass and endophyte** | **Impact of endophyte** | **Physiological and/or structural changes to host plant and endophyte in response to drought** | **Reference** |
| *Bromus auleticus* *E. pampeanum* and *E. tembladerae* | Improved survival in summer | Higher regrowth rate | [117] |
| *Roegneria kamooji* *E. sinica* | Improved seedling establishment in drought | Improved germination and seedling growth | [118] |
| *Elymus dahuicus* *E. bromicola* sp. | Improved yield and tiller numbers under drought | Endophyte caused anti-oxidative enzyme activities and contents of proline and chlorophyll | [119] |
| *Elymus virginitus* *E. elymi* | Improved drought tolerance, but also benefited well-watered plants | Increased germination at moderate osmotic potentials | [120] |
| *Leymus chinesis* *E. tembladerae* | Improved yield under drought | No effect on root: shoot ratio; improved tiller number | [121] |
| *Festuca sinensis* *E. pampeanum* | Endophytes enhanced drought tolerance | Increased photosynthetic rate | [122] |
Epiclóë and drought

Endophyte-infected perennial ryegrass and tall fescue are considered to perform better in challenging environments than endophyte-free\(^\text{[60−62]}\). The presence of Epiclóë can induce mechanisms of drought avoidance (morphological adaptations), drought tolerance (biochemical and physiological adaptations) as well as drought recovery for both domesticated and wild cool-temperate grasses (Table 3). However, the wide natural genetic variability of tall fescue and perennial ryegrass at the population level and its interaction with the endophyte strains has provided some inconsistent results on the effect of the endophyte on forage production under variable soil water availability\(^\text{[63]}\), which has also been complicated by whether trials are undertaken using pots in glasshouses/growth rooms, small plots under cutting, or large paddocks under grazing. Despite this, there is general acceptance that in the field, endophyte infection improves plant persistence and fitness in at least the most responsive combinations under severe water deficit (Fig. 1)\(^\text{[61,63]}\).

### Table 3. Impact of Epiclóë on the interaction between drought and insect herbivory

| Endophyte type and trial protocol | Known alkaloid expression | Insect pest | Drought effect | Reference |
|----------------------------------|--------------------------|------------|----------------|-----------|
| **Ryegrass**                     |                          |            |                |           |
| Italian ryegrass (L. multiflorum) | Lolines and peramine     | Grass aphid (Sipha maydis) | Endophyte reduced aphid numbers but only on drought stressed plants. Aphid herbivory detrimental to endophyte infected well-watered plants. Interactions between drought and aphids affected reproductive tillering in endophyte-free plants only. | [138] |
| L. occultans (presumably) Pot trial in a glasshouse | | Cherry-oat aphid (Rhopalosiphum padi) | | |
| **Perennial ryegrass** (L. perenne) E. festucae var. lolii Field trial; visual assessment of larval damage scored | Dependent on endophyte strain: ergovaline, peramine, lolitrem B | Black beetle (Heteronychus arator) | Summer/early autumn drought plus differences in black beetle root damage decreased plant survival and growth of susceptible plant-endophyte combinations compared with a resistant one. | [139] |
| **Fescue**                       |                          |            |                |           |
| Tall fescue (F. arundinacea) E. coenophiala Pot trial in a glasshouse | N-acetyl and N-formyl lolines | Number of cherry-oat aphids (Rhopalosiphum padi) | Aphid density reduced by endophyte, and by drought stress in endophyte-free plants only. Growth and development reduced by endophyte-infected drought stressed herbage compared with well-watered. No effect on larvae fed Nil herbage. | [140] |
| **Tall fescue** (F. arundinacea) E. coenophiala AR84 Excised roots from treated plants feed to 3\(^{rd}\) instar grass grub | Lolines | Grass grub (Costelytra given) 3\(^{rd}\) instar larvae | Root consumption of endophyte-free plants higher if plants droughted compared with well-watered endophyte-free; larval weight change reduced by endophyte fed droughted plant roots. Loline concentration in roots higher in droughted than in well-watered plants. Endophyte reduced root consumption, frass output, and larval weight change; effects greatest for well-watered plants; Loline concentration higher in roots of well-watered plants than droughted plants. | [142] |
| Meadow fescue (F. pratensis) E. uncinata Excised roots fed to 3\(^{rd}\) instar grass grub | | | | |
| Red fescue (F. rubra) E. festucae Field survey and common garden experiment | Ergovaline | Locusts (Locusta migratoria) | Endophyte significantly reduced weight and survival of locusts | [143], [144] |

Insect responses to drought

Reduced soil moisture influences herbivorous invertebrates as well as plants. Drought can, directly and indirectly, affect insects. A direct influence is seen when insects are exposed to an environmental change. For example, reduced soil moisture content changes the physical properties of soils, influencing the behaviour of soil-dwelling insects\(^\text{[121]}\). In comparison, an indirect influence of drought affects the insect’s host and in due course the insect itself. Drought-stressed plants experience chemical changes in which the water content reduces, subsequently leading to lower turgor pressure, a more viscous phloem sap\(^\text{[122]}\), and a higher nitrogen content in the plant tissue\(^\text{[123−125]}\), which is generally a limiting factor for herbivorous insects\(^\text{[126,127]}\). Such physiological changes in the plant can impact the suitability as a food source for insect pests. An increase in the presence of insects has been linked with drought-stressed plants\(^\text{[128–130]}\). However, this may be moderated by the insect species and the feeding guilds involved\(^\text{[123]}\). For example, phloem feeders...
(e.g. aphids, planthoppers) and cambium feeders (e.g. bark beetles) were predicted to positively respond to drought-stressed plants, in contrast to free-living chewing insects (e.g. caterpillars) and gall formers (e.g. gall wasps)[131]. However, such effects are dependent on water deficit intensity and duration. In dry soil moisture conditions, populations of the lucerne weevil (Sitona discoideus), a major pest of this plant, increased significantly resulting in even higher yield loss[132]. Foliage feeding Spodoptera litura increased significantly in drought-stressed Piper betel and Ricinus communis, which is believed to be linked with an increase in flavonoid and amino acid content[133]. Phloem-feeding below ground aphid species have been found to reproduce rapidly in dry soil conditions[134−136], likely utilising the drought-induced weakening of the plant in which nitrogen content is increased.

Despite higher nitrogen content in the plant sap during times of drought, phytophagous herbivores that feed on the sap can be negatively affected by continued drought. This is caused by reduced turgor pressure which interferes with the insect’s ability to utilise available nitrogen[123].

**Interaction between drought, insect herbivory and *Epichloë* endophyte**

Despite the importance of insect-plant-endophyte interactions, little research has focused on the interaction between drought, endophytes, and insect herbivory. Plant defence theory predicts that plants under moisture deficit should increase their resource allocation toward the production of plant-derived secondary metabolites that deter herbivores[137]. This theory is also seen in endophyte-infected plants, which increase their alkaloid concentration under drought stress[118]. It is however unclear to what extent the plant can mediate drought tolerance and herbivore pressure simultaneously. Insects can be affected in different ways by the endophyte, and this can be further influenced by the additional resource limitation of the host (Table 3). However, this demonstrates that there are a limited number of studies to definitively conclude that it is often the combination of both insect herbivory pressure and drought, rather than each individually that finally impacts ryegrass persistence.

Harbouring a systemic endophyte may represent a net cost to the plant in the absence of other stress factors[145]. However, observations of field-grown plants have prompted the opinion that it is when pressure on plants from both insects and drought is greatest, that endophytes provide the greatest advantage[139]. The benefits of endophyte-grass symbioses may enhance the plants’ ability to tolerate interactions between biotic and abiotic stressors[143,145]. In New Zealand, this effect occurs most often during late summer and autumn[21,146,147], the time of the year when alkaloid concentration is generally at its highest[148,149]. *Epichloë* strain effects can also be important at times when both insect and drought stress are threatening grass survival. A comparison of strains AR37, standard endophyte and AR1 showed that during hot dry summers the overriding impact of pasture pests, predominantly African black beetle (Heteronychus arator), was greater on AR1 than AR37 and standard endophyte[150]. The use of irrigation has been shown to slow the loss of endophyte-free plants even though insect pressures can still be present[151].

It has been hypothesised that key environmental factors can affect the presence and frequency of *Epichloë* endophytes in natural populations[152]. Importantly, they concluded for biotic factors endophyte infection frequency in a population is negatively associated with a degree of insect damage. In New Zealand, it is recognised that without the appropriate endophyte strains in perennial ryegrass, the persistence of perennial ryegrass in many regions of the country would be poor[153], as demonstrated in Fig. 2.

In trials undertaken in Germany where endophyte-free and infected plants were transplanted into two environments the effect of endophyte on aphid presence was dependent on the region in which the trial was run and therefore the environment[154]. The site with the lowest rainfall over the 3 months of the trial (281 mm compared with 327 mm) had the highest bird-cherry oat aphid levels and was the only region where endophyte presence had a significant effect in reducing aphid numbers.

The compatibility of an endophyte strain with the host plant is an important consideration for improving host plant fitness against both biotic and abiotic stresses[152]. The more compatible a strain is with a host plant the greater the likelihood of enhanced vegetative biomass, tiller number, and

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**Fig. 1** A proposed schematic diagram of endophyte-infected and endophyte-free plant responses to increasing soil water deficit. Figure adapted from Assuero et al.[63].

**Table 3**

| Condition          | Endophyte-infected plants | Endophyte-free plants |
|--------------------|---------------------------|-----------------------|
|                    | increase growth and senescence while accumulating osmoprotectant in tiller base | may show delayed or/and less intense physiological responses |
|                    | higher survival rate and faster drought recovery due to lower exposed leaf areas and higher osmoprotectant concentration in meristems | die because of low dehydration tolerance |

None | Moderate | Severe

Water deficit continuum
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Conflict of interest

J.R.C. is employed by Grasslanz Technology Limited, a company that is a part-owner of the intellectual property associated with Epichloë strains marketed under the brands AR1™, AR3™, Endo9™, MaxQ®, MaxQII™, MaxP®, MaxR™, Avanex®, Happe™ and Protek™.

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REFERENCES

1. Food and Agriculture Organization of the United Nations. 2021. Grasslands, Rangelands and Forage Crops. http://www.fao.org/agriculture/crops/thematic-sitemap/theme/spi/grasslands-rangelands-and-forage-crops/en/
2. Turner LR, Donaghy DJ, Lane PA, Rawnsley RP. 2006. Effect of defoliation management, based on leaf stage, on perennial ryegrass (Lolium perenne L.), prairie grass (Bromus wildenowii Kunth.) and cocksfoot (Dactylis glomerata L.) under dryland conditions. 1. Regrowth, tillering and water-soluble carbohydrate concentration. Grass and Forage Science 61:164–74
3. Hartley W. 1973. Studies on the origin, evolution, and distribution of the Gramineae. V. The subfamily Festucoideae. Australian Journal of Botany 21:201–34
4. Clay K, Schardl C. 2002. Evolutionary origins and ecological consequences of endophyte symbiosis with grasses. The American Naturalist 160:599–5127
5. Caradus JR, Johnson LJ. 2020. Epichloë fungal endophytes – From a biological curiosity in wild grasses to an essential component of resilient high performing ryegrass and fescue pastures. Journal of Fungi 6:322
6. Panaccione DG, Beaulieu WT, Cook D. 2014. Bioactive alkaloids in vertically transmitted fungal endophytes. Functional Ecology 28:299–314
7. Johnson LJ, de Bonth ACM, Briggs LR, Caradus JR, Finch SC, et al. 2013. The exploitation of epichloë endophytes for agricultural benefit. Fungal Diversity 60:171–88
8. Hume DE, Ryan GD, Gibert A, Helderan M, Mirlohi A, et al. 2016. Epichloë fungal endophytes for grassland ecosystems. In Sustainable Agriculture Reviews, ed. Lichtfouse E, 19:vi, 399. Switzerland: Springer International Publishing. pp 233–305. https://doi.org/10.1007/978-3-319-26777-7_6
9. Easton HS. 2007. Grasses and Neotyphodium endophytes: co-adaptation and adaptive breeding. Euphytica 154:295–306
10. Fletcher LR. 1999. “Non-toxic” endophytes in ryegrass and their effect on livestock health and production. In Proc. Ryegrass Endophyte - An Essential New Zealand Symbiosis, eds. Woodfield DR, Matthew C, Napier, New Zealand: New Zealand Grassland Association. pp133–39.https://doi.org/10.33584/rps.7.1999.3393
11. Finch SC, Prinsep MR, Popay AJ, Wilkins AL, Webb NG, et al. 2020. Identification and structure elucidation of epoxyjanthitremes from Lolium perenne infected with the endophytic fungus Epichloë festucae var. lolii and determination of the tremorgenic and anti-insect activity of epoxyjanthitrem I. Toxins (Basel) 12:526
12. Nixon CG. 2016. How Valuable is that Plant Species?: Application of a Method for Enumerating the Contribution of Selected Plant Species to New Zealand’s GDP. Wellington: Ministry for Primary Industries https://www.mpi.govt.nz/dmsdocument/14527 diret
13. Hendriks SJ, Donaghy DJ, Matthew C, Bretherton MR, Sneddon NW, et al. 2016. Dry matter yield, nutritive value and tiller density of tall fescue and perennial ryegrass swards under grazing. *Journal of New Zealand Grasslands* 78:149–56

14. Caradus JR, Johnson LJ. 2019. Improved adaptation of temperate grasses through mutualism with fungal endophytes. In *Endophyte biotechnology: potential for agriculture and pharmacology*, ed. Schouten A, Wallingford, UK: CAB. pp 85–108. https://doi.org/10.1079/9781786399427.0085

15. Caradus J, Chapman D, Cookson T, Cotching B, Deighton M, et al. 2021. *Epichloë* endophytes – new perspectives on a key ingredient for resilient perennial grass pastures. In *Proceeding Resilient Pastures Symposium*, Napier, New Zealand: New Zealand Grasslands Association. pp. 57–70. https://doi.org/10.33584/17.2021.3435

16. Clay K. 2001. Symbiosis and the regulation of communities. *American Zoologist* 41:810–24

17. Johnson LJ, Voisey C, Faville M, Moon CD, Simpson WR, et al. 2019. Advances and perspectives in breeding for improved grass-endophyte associations. Improving sown grasslands through breeding and management, Joint Symposium EFG/Eucarpia, Zurich, Switzerland. 2019. Grassland Science in Europe 24:351–63

18. Woodfield DR, Judson HJ. 2019. Balancing pasture productivity with environmental and animal health requirements. In *Improving grassland and pasture management in temperate agriculture*, UK: Burleigh Dodds Science Publishing, pp 237–52. https://doi.org/10.19130/as.2017.002408

19. Hume DE, Stewart AV, Simpson WR, Johnson RD. 2020. *Epichloë* fungal endophytes play a fundamental role in New Zealand grasslands. *Journal of the Royal Society of New Zealand* 50:279–98

20. Ferguson CM, Barratt BIP, Bell N, Goldson SL, Hardwick S, et al. 2019. Quantifying the economic cost of invertebrate pests to New Zealand’s pastoral industry. *New Zealand Journal of Agricultural Research* 62:255–315

21. Popay AJ, Hume DE, Baltus JG, Latch GCM, Tapper BA, et al. 1999. Field performance of perennial ryegrass (*Lolium perenne*) infected with toxin-free fungal endophytes (*Neotyphodium* spp.). *Proc. Ryegrass Endophyte: An Essential New Zealand Symbiosis*, Napier, New Zealand: Palmerston North, New Zealand: New Zealand Grassland Association. pp. 113–22. https://doi.org/10.33584/rps.7.1999.3388

22. Pennell CGL, Popay AJ, Ball OJP, Hume DE, Baird DB. 2005. Occurrence and impact of pasture mealybug (*Balanococcus paeoni*) and root aphid (*Aploneura lenticis*) on ryegrass (*Lolium spp.*) with and without infection by *Neotyphodium* fungal endophytes. *New Zealand Journal of Agricultural Research* 48:329–37

23. Popay AJ, Baltus JG. 2001. Black beetle damage to perennial ryegrass infected with AR1 endophyte. *Proc. New Zealand Grassland Association, Hamilton, New Zealand*, 2001, 63: 267–71. New Zealand Grassland Association. https://doi.org/10.33584/jnzz.2001.63.2415

24. Popay AJ, Cox NR. 2016. *Aploneura lenticis* (Homoptera: Aphididae) and its interactions with fungal endophytes in perennial ryegrass (*Lolium perenne*). *Frontiers in Plant Science* 7:1395

25. Jensen JS, Popay AJ. 2004. Perennial ryegrass infected with AR37 endophyte reduces survival of porina larvae. *Proc. New Zealand Plant Protection, Rotorua, New Zealand*, 2004, 57: 323–28. New Zealand Plant Protection Society https://doi.org/10.30843/nzpzp.2004.57.6930

26. New Zealand Plant Breeding & Research Association. 2020. Fact sheet - Endophyte Insect Control. https://beeflambnz.com/knowledge-hub/PDF/endophyte-update.pdf

27. Popay AJ, Wyatt RT. 1995. Resistance to Argentine stem weevil in perennial ryegrass infected with endophytes producing different alkaloids. *Proc. New Zealand Plant Protection, Hastings, New Zealand*, 1995, 48: 229–36. New Zealand Plant Protection Society. https://doi.org/10.33584/nzpzp.2004.57.6930

28. Ball OJP, Christensen MJ, Prestidge RA. 1994. Effect of selected isolates of *Acremonium* endophytes on adult black beetle (*Heteronychus arator*) feeding. *Proc. New Zealand Plant Protection, Rotorua, New Zealand*, 1994, 47: 227–31: New Zealand Plant Protection Society. https://doi.org/10.30843/nzpzp.1994.47.11101

29. Fletcher LR, Sutherland BL. 2009. Sheep responses to grazing ryegrass with AR37. *Proc. New Zealand Grassland Association*, 2009, 71: 127–32: New Zealand Grassland Association. https://doi.org/10.33584/nzap.1999.52.11582

30. Thom ER, Waugh CD, Minnkk EMK, Waghorn GC. 2007. A new generation ryegrass endophyte - the first results from dairy cows fed AR37. *Proc. Proceedings of the 6th International Symposium on Fungal Endophytes of Grasses.*, Christchurch, New Zealand, 13: 293–96. New Zealand Grassland Association. https://doi.org/10.33584.rps.13.2006.3146

31. Patchett BJ, Chapman RB, Fletcher LR, Gooneratne SR. 2008. Endophyte-infected Festuca pratensis containing loline alkaloids deters feeding by Lixostrobus bonariensis. *New Zealand Plant Protection* 61:205–9

32. Pennell C, Ball OJP. 1999. The effects of *Neotyphodium* endophytes in tall fescue on pasture mealy bug (*Balancoecoccus paeoni*). *Proc. New Zealand Plant Protection, Auckland, New Zealand*, 1999, 52: 259–63. New Zealand Plant Protection Society. https://doi.org/10.30843/nzpzp.1999.52.11582

33. Patchett BJ, Gooneratne RB, Chapman B, Fletcher LR. 2011. Effects of loline-producing endophyte-infected meadow fescue ecotypes on New Zealand grass grub (*Costelytra zealandica*). *New Zealand Journal of Agricultural Research* 54:303–13

34. Jensen JG, Popay AJ, Tapper BA. 2009. Argentine stem weevil adults are affected by meadow fescue endophyte and its loline alkaloids. *Proc. New Zealand Plant Protection, 2009, 62: 12–8*. New Zealand Plant Protection Society. https://doi.org/10.30843/nzpzp.2009.62.4800

35. Popay AJ, Lane GA. 2000. The effect of crude extracts containing loline alkaloids on two New Zealand insect pests. *Proceedings of the 4th International Neotyphodium/Grass Interactions Symposium, Soest, Germany*, 2000: 471–75

36. Stewart A, Kerr GA, Lissaman W, Rowarth JS. 2014. Chapter 8 – Endophyte in ryegrass and fescue. In *Pasture and forage plants for New Zealand. Grassland Research and Practice Series*, 8 ed. Stewart A, Kerr G, Lissaman W, Rowarth J. New Zealand Grassland Association. pp 66–77. https://www.nzgajournal.org.nz/index.php/rps/issue/view/112

37. Barker GM, Patchett BJ, Cameron NE. 2015. *Epichloë uncinata* infection and loline content afford Festulolium grasses protection from black beetle (*Heteronychus arator*). *New Zealand Journal of Agricultural Research* 58:35–56

38. Barker GM, Patchett BJ, Cameron NE. 2015. *Epichloë uncinata* infection and loline content protect Festulolium grasses from crickets (Orthoptera: Gryllidae). *Journal of Economic Entomology* 108:789–97

39. Barker GM, Patchett BJ, Gillanders TJ, Brown GS, Montel S, et al. 2015. Feeding and oviposition by Argentine stem weevil on Festulolium grasses. *Proceedings of the 6th International Neotyphodium/Grass Interactions Symposium, Soest, Germany*. 2000: 471–75

40. Pennell CG, Rolston MP. 2019. *Avanex*™ Unique endophyte technology-bird deterrent endophytic grass for amenity turf and airports. *Proceeding 22nd International Grasslands Congress, Sydney, Australia*, 2019: 405–8 https://www.grassland.org.nz/publications/nzgrassland_publication_2590.pdf
41. Malinowski DP, Belesky DP. 2000. Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance. *Crop Science* 40:923–40

42. Rhoades DF. 1983. Herbivore population dynamics and plant chemistry. In *Variable Plants and Herbivores in Natural and Managed Systems*, eds. Denno RF, McClure MS, 6:717. Orlando, FL: Academic Press NY. pp 155–220. https://doi.org/10.1016/b978-0-12-209160-5.50012-x

43. White TCR. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90–105

44. Rhoades DF. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *The American Naturalist* 125:205–38

45. Lambers H, Chapin III FS, Pons TL. 2008. *Plant physiological ecology*. Springer Science & Business Media

46. Mullan B, Porteous A, Wratt D, Hollis M. 2005. Changes in drought risk with climate change. Wellington, New Zealand https://docs.niwa.co.nz/library/public/WLG2005-23execsum.pdf

47. Strzepek K, Yohe G, Neumann J, Boehlert B. 2010. Characterizing changes in drought risk for the United States from climate change. *Environmental Research Letters* 5:044012

48. Reisinger A, Mullan A, Manning M, Wratt D, Nottage R. 2010. Global and local climate change scenarios to support adaptation in New Zealand. In *Climate change adaptation in New Zealand: Future scenarios and some sectoral perspectives*, eds. Nottage RAC, Wratt DS, Borman LF, Jones K. Wellington, New Zealand: New Zealand Climate Change Centre, Victoria University of Wellington, pp 26–43

49. Trenberth KE, Dai A, van der Schrier G, Jones PD, Barichivich J, et al. 2014. Global warming and changes in drought. *Nature Climate Change* 4:17–22

50. King AD, Pitman AJ, Henley BJ, Ukkola AM, Brown JR. 2020. The role of climate variability in Australian drought. *Nature Climate Change* 10:177–9

51. Palmer JA. 2009. The future of pastoral farming in a changing climate. *Proc. New Zealand Grassland Association, Waitangi*, New Zealand, 2009, 71:69–72. New Zealand Grasslands Association. https://doi.org/10.33584/jnzg.2009.71.2773

52. Hunt WF, Easton HS. 1989. Fifty years of ryegrass research in New Zealand. *Proc. New Zealand Grassland Association, Wanganui*, New Zealand, 1989, 50: 11–23. New Zealand Grassland Association. https://doi.org/10.33584/jnzg.1989.50.1876

53. Matthew C, van der Linden A, Hussain S, Easton HS, Hatier JHB, et al. 2012. Which way forward in the quest for drought tolerance in perennial ryegrass? *Proc. New Zealand Grassland Association, Gore*, New Zealand, 2012, 74: 195–200: New Zealand Grassland Association https://doi.org/10.33584/jnzg.2012.74.2854

54. Macdonald KA, Matthew C, Glassey CB, McLean N. 2011. Dairy farm systems to aid persistence. *Proc. Pasture Persistence Symposium Hamilton*, New Zealand, 2011, 15: 199–209. New Zealand’s Grasslands Association https://doi.org/10.33584/rrps.15.2011.3199

55. Korte CJ, Chu ACP. 1983. Some effects of drought on perennial ryegrass swards. *Proc. New Zealand Grassland Association, Blenheim, New Zealand*, 1983, 44: 211–16. New Zealand’s Grasslands Association. https://doi.org/10.33584/jnzg.1983.44.1625

56. Cui Y, Wang J, Wang X, Jiang Y. 2015. Phenotypic and genotypic diversity for drought tolerance among and within perennial ryegrass accessions. *HortScience* 50:1148–54

57. Fang Y, Xiong L. 2015. General mechanisms of drought response and their application in drought resistance improvement in plants. *Cellular and Molecular Life Sciences* 72:673–89

58. Munné-Bosch S, Alegre L. 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology* 31:203–16

59. Reid JB, Crush JR. 2013. Root turnover in pasture species: perennial ryegrass (Lolium perenne L.). *Crop and Pasture Science* 64:165–77

60. Thom ER, Popay AJ, Waugh CD, Minnée ÉMK. 2014. Impact of novel endophytes in perennial ryegrass on herbage production and insect pests from pastures under dairy cow grazing in northern New Zealand. *Grass and Forage Science* 69:191–204

61. Decunqua FA, Pérez LI, Malinowski DP, Molina-Montenegro MA, Gundel PE. 2021. A systematic review on the effects of *Epichloë* fungal endophytes on drought tolerance in cool-season grasses. *Frontiers in Plant Science* 12:380

62. West CP. 1994. Physiology and drought tolerance of endophyte-infected grasses. In *Biotechnology of Endophytic Fungi of Grasses*, eds. Bacon CW, White JF, 87. Boca Raton, FL: CRC Press. pp 87–99. https://doi.org/10.1201/9781351070324-7

63. Assuero SG, Tognetti JA, Colabelli MR, Agnusdei MG, Petroni EC, et al. 2006. Endophyte infection accelerates morphophysiological responses to water deficit in tall fescue. *New Zealand Journal of Agricultural Research* 49:359–70

64. Ravel C, Courty C, Coudret A, Charmet G. 1997. Beneficial effects of *Neotyphodium lolii* on the growth and the water status in perennial ryegrass cultivated under nitrogen deficiency or drought stress. *Agronomie* 17:173–81

65. Vahid J, Bihantma MR, Islam M, Farrokh D. 2015. The effect of endophytic fungi in drought resistance of *Lolium Perenne* in Iran (Isfahan) condition. *Advanced Studies in Biology* 7:245–57

66. He L, Hatier J, Card S, Matthew C. 2013. Endophyte-infection reduces leaf dehydration of ryegrass and tall fescue plants under moderate water deficit. *Proceedings of the New Zealand Grasslands Association, Tauranga, New Zealand, 2013*: 5–7. New Zealand Grasslands Association https://doi.org/10.33584/jnzg.2013.75.2936

67. Hesse U, Schöberlein W, Wittenmayer L, Förster K, Warnstorf K, et al. 2003. Effects of *Neotyphodium* endophytes on growth, reproduction and drought-stress tolerance of three *Lolium perenne* genotypes. *Grass and Forage Science* 58:407–15

68. Eerens JPJ, Lucas RJ, Easton S, White JGH. 1998. 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* 41:219–26

69. Kane KH. 2011. Effects of endophyte infection on drought stress tolerance of *Lolium perenne* accessions from the Mediterranean region. *Environmental and Experimental Botany* 71:337–44

70. Li F, Duan T, Li Y. 2020. Effects of the fungal endophyte *Epichloë festucae var. lolii* on growth and physiological responses of perennial ryegrass *cv. fairway* to combined drought and pathogen stresses. *Microorganisms* 8:1917

71. Hahn H, McManus MT, Warnstorf K, Monahan BJ, Young CA, et al. 2008. *Neotyphodium* fungal endophytes confer physiological protection to perennial ryegrass (*Lolium perenne* L.) subjected to a water deficit. *Environmental and Experimental Botany* 63:183–99

72. Hume DE, Popay AJ, Barker DJ. 1993. Effect of *Acremonium* endophyte on growth of ryegrass and tall fescue under varying levels of soil moisture and Argentine stem weevil attack. *Proc. 2nd International Symposium on Acremonium/Grass Interactions, Palmerston North, New Zealand, 1993*: 161–4.
73. Barker DJ, Hume DE, Quigley PE. 1997. Negligible physiological responses to water deficit in endophyte-infected and uninfected perennial ryegrass. *Neotyphodium/Grass Interactions*, eds. CW Bacon, NS Hill. New York: Plenum Press. pp 137–39. https://doi.org/10.1007/978-1-4899-0271-9_20

74. Malinowski DP, Belesky DP, Lewis GC. 2005. Abiotic Stresses in Endophytic Grasses. *Neotyphodium in Cool-Season Grasses*, eds. Roberts CA, West CP, Spiers DE. Ames, IA: Blackwell Publishing. pp 187–99 https://doi.org/10.1002/9780470384916.ch8

75. MacLean B, Matthew C, Latch GCM, Barker DJ. 1993. The effect of endophyte on drought resistance in tall fescue. *Proc. 2nd International Symposium on Acremonium/Grass Interactions*, Palmerston North New Zealand, 1993: 165–69

76. Cheplick GP, Perera A, Koulouri K. 2000. Effect of drought on the growth of *Lolium perenne* genotypes with and without fungal endophytes. *Functional Ecology* 14:657–67

77. Marks S, Clay K. 2007. Low resource availability differentially affects the growth of host grasses infected by fungal endophytes. *International Journal of Plant Sciences* 168:1269–77

78. He L, Hatier JHB, Matthew C. 2017. Drought tolerance of two perennial ryegrass cultivars with and without AR37 endophyte. *New Zealand Journal of Agricultural Research* 60:173–88

79. Briggs L, Crush J, Ouyang L, Sprosen J. 2013. *Neotyphodium* endophyte strain and superoxide dismutase activity in perennial ryegrass plants under water deficit. *Acta Physiologiae Plantarum* 35:1513–20

80. Belesky DP, Stringer WC, Hill NS. 1989. Influence of endophyte and water regime upon tall fescue accesses. I. Growth characteristics. *Annals of Botany* 63:495–503

81. Elbersen HW, West CP. 1996. Growth and water relations of field-grown tall fescue as influenced by drought and endophyte. *Grass and Forage Science* 51:333–42

82. Hill NS, Pachon JG, Bacon CW. 1996. *Acremonium coenophialum*-mediated short- and long-term drought acclimation in tall fescue. *Crop Science* 36:665–72

83. Archevaleta M, Bacon CW, Hoveland CS, Radcliffe DE. 1989. Effect of the tall fescue endophyte on plant response to environmental stress. *Agronomy Journal* 81:83–90

84. Archevaleta M, Bacon CW, Plattner RD, Hoveland CS, Radcliffe DE. 1992. Accumulation of ergopeptide alkaloids in symbiotic tall fescue grown under deficits of soil water and nitrogen fertilizer. *Applied and Environmental Microbiology* 58:857–61

85. Kennedy CW, Bush LP. 1983. Effect of environmental and management factors on the accumulation of N-acetyl and N-formyl loline alkaloids in tall fescue. *Crop Science* 23:547–52

86. Richardson MD, Chapman GW Jr, Hoveland CS, Bacon CW. 1996. Sugar alcohols in endophyte-infected tall fescue under drought. *Crop Science* 32:1060–1

87. Nagabhyru P, Dinksin RD, Wood CL, Bacon CW, Schardl CL. 2013. Tall fescue endophyte effects on tolerance to water-deficit stress. *BMC Plant Biology* 13:127

88. Bacon CW. 1993. Abiotic stress tolerances (moisture, nutrients) and photosynthesis in endophyte-infected tall fescue. *Agriculture, Ecosystems and Environment* 44:123–41

89. White RH, Engelke MC, Morton SJ, Johnson-Calease JM, Rueemelé BA. 1992. *Acremonium* endophyte effects on tall fescue drought tolerance. *Crop Science* 32:1392–6

90. West CP, Gwinn KD. 1993. Role of *Acremonium* in drought, pest, and disease tolerances of grasses. *Proc. 2nd International Symposium on Acremonium/Grass Interactions*, Palmerston North, New Zealand, 1993: 131–40

91. Swarthout D, Harper E, Judd S, Gonthier D, Shyne R, et al. 2009. Measures of leaf-level water-use efficiency in drought stressed endophyte infected and non-infected tall fescue grasses. *Environmental and Experimental Botany* 66:88–93

92. Elmi A, West C. 1995. Endophyte infection effects on stomatal conductance, osmotic adjustment and drought recovery of tall fescue. *New Phytologist* 131:61–7

93. Buck GW, West CP, Elbersen HW. 1997. Endophyte effect on drought tolerance in diverse *Festuca* species. *Neotyphodium/Grass Interactions*, eds. Bacon CW, Hill NS. Boston, MA: Springer. pp 141–43.

94. Elmi A, West C, Robbins R, Kirkpatrick T. 2000. Endophyte effects on reproduction of a root-knot nematode (*Meloidogyne marylandii*) and osmotic adjustment in tall fescue. *Grass and Forage Science* 55:166–72

95. Hosseini F, Mosaddeghi M, Hajabassi MA, Sabzalian M. 2016. Role of fungal endophyte of tall fescue (*Epichloë coenophiala*) on water availability, wilting point and integral energy in texturally-different soils. *Agricultural Water Management* 163:197–211

96. Xu L, Li X, Han L, Li D, Song G. 2017. *Epichloë* endophyte infection improved drought and heat tolerance of tall fescue through altered antioxidant enzyme activity. *European Journal of Horticultural Science* 82:90–97

97. Read JC, Camp BJ. 1986. The effect of the fungal endophyte *Acremonium coenophialum* in tall fescue on animal performance, toxicity, and stand maintenance. *Agronomy Journal* 78:848–50

98. Read JC. 1990. The effect of the fungal endophyte *Acremonium coenophialum* on dry matter production and summer survival of tall fescue. *Proc. Proceedings of the international symposium on Acremonium/grass interactions, Baton Rou*, United States of America, 1990: 181–4

99. West CP, Izekor E, Oosterhuis DM, Robbins RT. 1988. The effect of *Acremonium coenophialum* on the growth and nematode infestation of tall fescue. *Plant and Soil* 1123–6

100. Knox J, Karnok K. 1992. Root and shoot growth of endophyte infected and endophyte free tall fescue under water stress and non-stress conditions. *Proc. Agronomy Abstracts. Madison, WI: American Society of Agronomy*, 1992, 171

101. Malinowski D, Leuchtman A, Schmidt D, Nössberger J. 1997. Growth and water status in meadow fescue is affected by *Neotyphodium* and *Philaophora* species endophytes. *Agronomy Journal* 89:673–8

102. Malinowski D, Leuchtman A, Schmidt D, Nössberger J. 1997. Symbiosis with *Neotyphodium uncinatum* endophyte may increase the competitive ability of meadow fescue. *Agronomy Journal* 89:833–9

103. Malinowski D. 1995. *Rhizomatosus ectotypes and symbiosis with endophytes as new possibilities of improvement in competitive ability of meadow fescue* (*Festuca pratensis* Huds.). Ph.D. ETH Zurich

104. Ahholm JU, Huelander M, Lehtimäki S, Wåli P, Salkkonen K. 2002. Vertically transmitted fungal endophytes: different responses of host-parasite systems to environmental conditions. *Oikos* 99:173–83

105. Tian Z, Huang B, Belanger FC. 2015. Effects of *Epichloë festucae* fungal endophyte infection on drought and heat stress responses of strong creeping red fescue. *Journal of the American Society for Horticultural Science* 140:257–64

106. Li C, Li F, Gou X, Nan Z. 2008. Effects of abiotic stresses on *Achnatherum inebrians* by symbiotic endophyte of *Neotyphodium gansuense*. *Proc. XXI International Grassland Congress/ VII International Rangeland Congress, Hohot, China*, 2008: 819. Guangdong People’s Publishing House

107. Xia C, Li N, Zhang Y, Li C, Zhang X, et al. 2018. Role of *Epichloë* endophytes in defense responses of cool-season grasses to pathogens: a review. *Plant Disease* 102:2061–73
108. Zhang X, Li C, Nan Z. 2011. Effects of salt and drought stress on alkaloid production in endophyte-infected drunken horse grass (Achnatherum inebrians). *Biochemical Systematics and Ecology* 39:471–6

109. Xia C, Zhang X, Christensen MJ, Nan Z, Li C. 2015. *Epichloë* endophyte affects the ability of powdery mildew (Blumeria graminis) to colonise drunken horse grass (Achnatherum inebrians). *Fungal Ecology* 16:26–33

110. Ren A, Li X, Han R, Yin L, Wei M, et al. 2011. Benefits of a symbiotic association with endophytic fungi are subject to water and nutrient availability in *Achnatherum sibiricum*. *Plant and Soil* 346:363–73

111. Oberhofer M, Güsewell S, Leuchtmann A. 2014. Effects of natural hybrid and non-hybrid *Epichloë* endophytes on the response of *Hordelymus europaeus* to drought stress. *New Phytologist* 201:242–53

112. Kannadan S, Rudgers JA. 2008. Endophyte symbiosis benefits a rare grass under low water availability. *Functional Ecology* 22:706–13

113. Morse LJ, Day TA, Faeth SH. 2002. Effect of Neotyphodium endophyte infection on growth and leaf gas exchange of *Arizona* rescue under contrasting water availability regimes. *Environmental and Experimental Botany* 48:257–68

114. Iannone LJ, Pinget AD, Nagabhyru P, Schardl CL, De Battista JP. 2012. Beneficial effects of *Neotyphodium* tembladerae and *Neotyphodium pampeanum* on a wild forage grass. *Grass and Forage Science* 67:382–90

115. Bu Y, Guo P, Ji Y, Zhang S, Yu H, et al. 2019. Effects of *Epichloë sinica* on *Roegneria kamoji* seedling physiology under PEG-6000 simulated drought stress. *Symbiosis* 77:123–32

116. Zhang YP, Nan ZB. 2007. Growth and anti-oxidative systems changes in *Elymus dahuricus* is affected by *Neotyphodium* endophyte under contrasting water availability. *Journal of Agronomy and Crop Science* 193:377–86

117. Zhang YP, Nan ZB. 2010. Germination and seedling anti-oxidative enzymes of endophyte-infected populations of *Elymus dahuricus* under osmotic stress. *Seed Science and Technology* 38:522–7

118. Rudgers JA, Swafford AL. 2009. Benefits of a fungal endophyte in *Elymus virginicus* decline under drought stress. *Basic and Applied Ecology* 10:43–51

119. Ren A, Wei M, Yin L, Wu L, Zhou Y, et al. 2014. Benefits of a fungal endophyte in *Leymus chinensis* depend more on water than on nutrient availability. *Environmental and Experimental Botany* 108:71–8

120. Wang J, Zhou Y, Lin W, Li M, Wang M, et al. 2017. Effect of an *Epichloë* endophyte on adaptability to water stress in *Festuca sinensis*. *Fungal Ecology* 30:39–47

121. Sjursen H, Bayley M, Holmstrup M. 2001. Enhanced drought tolerance of a soil-dwelling springtail by pre-acclimation to a mild drought stress. *Journal of Insect Physiology* 47:1021–7

122. Premachandra GS, Hahn DT, Rhodes D, Joly RJ. 1995. Leaf water relations and solute accumulation in two grain sorghum lines exhibiting contrasting drought tolerance. *Journal of Experimental Botany* 46:1833–41

123. Huberty AF, Denno RF. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85:1383–98

124. Isaacs R, Byrne DN, Hendrix DL. 1998. Feeding rates and carbohydrate metabolism by *Bemisia tabaci* (Homoptera: Aleyrodidae) on different quality philom sap. *Physiological Entomology* 23:241–8

125. Mattson WJ, Haack RA. 1987. The role of drought in outbreaks of plant-eating insects. *Biological Journal of the Linnean Society* 37:110–8

126. Mattson WJ Jr. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–61

127. White JF Jr, Crawford H, Torres MS, Mattera R, Iizary I, et al. 2012. A proposed mechanism for nitrogen acquisition by grass seedlings through oxidation of symbiotic bacteria. *Symbiosis* 57:161–71

128. Brodebeck B, Strong D. 1987. Amino acid nutrition of herbi- vorous insects and stress to host plants. In *Insect Outbreaks: ecological and evolutionary perspectives*, eds. Barbosa P, Schultz JC. New York, USA: Academic Press. pp 547–64 https://doi.org/10.1016/B978-0-12-078148-5.50018-X

129. Mattson WJ, Haack RA. 1987. The role of drought stress in provoking outbreaks of phytophagous insects. In *Insect Outbreaks*, eds. Barbosa P, Schultz JC. New York, USA: Academic Press. pp 365–407 https://doi.org/10.1016/B978-0-12-078148-5.50019-1

130. White TCR. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50:905–9

131. Larsson S. 1989. Stressful times for the plant stress: insect performance hypothesis. *Oikos* 56:277–83

132. Goldson SL, Frampton ER, Jamieson PD. 1986. Relationship of *Sitona discoides* (Coleoptera: Curculionidae) larval density to *Sepranet*-induced potential soil moisture deficits. *New Zealand Journal of Agricultural Research* 29:275–9

133. Rani PU, Kanuparthi P. 2014. Water stress induced physiological and biochemical changes in *Piper betle* L. and *Ricinus communis* L. plants and their effects on *Spodoptera litura*. *Allelopathy Journal* 33:25–41

134. Kindler D, Hesler L, Elliott N, Royer T, Giles K. 2004. Seasonal abundance of rice root aphid in wheat and its effect on forage and grain yields. *Southwestern Entomologist* 29:245–52

135. Al-Antary TM, Akkawi M. 1987. The occurrence, economic importance and control of wheat root aphid (*Alpuneura lentisci* Passerini), Homoptera, *Aphididae*) on wheat in Jordan. *Diasetas* 2:83–8

136. Pretorius RJ, Heen GL, Bradshaw JD. 2016. Ecology and management of *Pemphigus betae* (Hemiptera: *Aphididae*) in sugar beet. *Journal of Integrated Pest Management* 7:10

137. Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67:283–335

138. Miranda MJ, Omacini M, Chaneton EJ. 2011. Environmental context of endophyte symbioses: Interacting effects of water stress and insect herbivory. *International Journal of Plant Sciences* 172:499–508

139. Popay AJ, Hume DE. 2011. Endophytes improve ryegrass persistence by controlling insects. *Proc. Pasture Persistence Symposium, Dunedin, New Zealand, 2011*, 15: 149–56. New Zealand Grassland Association https://doi.org/10.33584/rps.15.2011.3196

140. Popay AJ, Hume DE, Mace WJ, Faville MJ, Finch SC, et al. 2021. A root aphid, *Aploneura lentisci* is affected by *Epichloë* endophyte strain and impacts perennial ryegrass growth in the field. *Crop and Pasture Science* 72:155–64

141. Bultman TL, Bell GD. 2003. Interaction between fungal endophytes and environmental stressors influences plant resistance to insects. *Oikos* 103:182–90

142. Popay AJ, Jensen EJ, Mace WJ. 2020. Root herbivory: grass species, *Epichloë* endophytes and moisture status make a difference. *Microorganisms* 8:997

143. Saona NM, Albrechtson BR, Ericson L, Bazely DR. 2010. Environmental stresses mediate endophyte-grass interactions in a boreal arthropod. *Journal of Ecology* 98:470–9

144. Bazely DR, Vicari M, Emmerich S, Filpi L, Lin D, et al. 1997. Interactions between herbivores and endophyte-infected Festuca rubra from the Scottish islands of St. Kilda, Benbecula and Rum. *The Journal of Applied Ecology* 34:847–60
145. Rodríguez RJ, White JF Jr, Arnold AE, Redman RS. 2009. Fungal endophytes: Diversity and functional roles: Tansley review. New Phytologist 182:314–30
146. Hume DE, Popay AJ, Cooper BM, Eerens JPJ, Lyons TB, et al. 2004. Effect of a novel endophyte on the productivity of perennial ryegrass (Lolium perenne) in New Zealand. Proceeding 5th International Symposium on Neotyphodium/ Grass Interactions, Fayetteville, Arkansas, United States of America, 2004: Poster 313
147. Hume DE, Ryan DL, Cooper BM, Popay AJ. 2007. Agronomic performance of AR37-infected ryegrass in northern New Zealand. Proceeding New Zealand Grassland Association, Wairakei, New Zealand, 2007, 69: 201–5. Wairakei: New Zealand Grassland Association https://doi.org/10.33584/jnzg.2007.69.2673
148. Fletcher L, Lane G, Baird D, Davies E. 2001. Seasonal variations of alkaloid concentrations in two perennial ryegrass-endophyte associations. Proc. 4th International Neotyphodium/ Grass Interactions Symposium, Universität-Gesamthochschule Paderborn, Soest, Germany, 2001: S35–41
149. Fuchs B, Krischke M, Mueller MJ, Krauss J. 2017. Plant age and seasonal timing determine endophyte growth and alkaloid biosynthesis. Fungal Ecology 29:52–8
150. Popay AJ, Thom ER. 2009. Endophyte effects on major insect pests in Waikato dairy pasture. Proceeding Pasture Persistence Symposium, Hamilton, New Zealand, 2009, 71: 121–6. Dunedin, New Zealand: New Zealand Grassland Association. https://doi.org/10.33584/jnzg.2009.71.2758
151. Francis SM, Baird DB. 1989. Increase in the proportion of endophyte-infected perennial ryegrass plants in overdrilled pastures. New Zealand Journal of Agricultural Research 32:437–40
152. Shymonovich T, Faeth SH. 2019. Environmental factors affect the distribution of two Epichloë fungal endophyte species inhabiting a common host grove bluegrass (Poa alsodes). Ecol. Evol. 9:6624–42
153. Caradus J, Chapman D, Cookson T, Cotching B, Deighton M, et al. 2021. Epichloë endophytes–new perspectives on a key ingredient for resilient perennial grass pastures. Proc. Pasture Resilience Symposium, Hamilton, New Zealand, 2021, 17: 57–70. New Zealand Grasslands Association. https://doi.org/10.33584/rps.17.2021.3435
154. Börschig C, Klein AM, Krauss J. 2014. Effects of grassland management, endophytic fungi and predators on aphid abundance in two distinct regions. Journal of Plant Ecology 7:490–8.

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