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# *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.

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## Introduction

Worldwide, around 26% of the world land area is dominated by forage grass species for animal production systems[1]. Poaceae grasses (subfamily Pooidea), 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]. These endophytes are critical constitutents 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 alkaloid, 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[8]. 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[9]. 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[10,11]. 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 orchrogaster*) 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[7,41]. 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 Argentine stem weevil (*Listronotus bonariensis*) | Pasture mealybug (*Balanococcus poae*) | African black beetle (*Heteronychus arator*) | Root aphid (*Aploneura lentisci*) | Porina (*Wiseana* spp.) | Grass grub (*Costelytra zealandica*) | Black field cricket (*Teleogryllus commodus*) | Animal health disorders |
|---|---|---|---|---|---|---|---|---|---|
| Annual economic impact in a specific industry[20] | | Up to $200M dairy; $235M sheep & beef | Unknown | Up to $223M dairy; $19M sheep & beef | Unknown | Up to $84M dairy; $88M sheep & beef | $275M–$706M dairy; $75M–$205M sheep & beef | Unknown | |
| Diploid perennial ryegrass (*E. festucae* var. *lolii*) | | | | | | | | | |
| AR1 | Peramine | ++++[21] | ++++[22] | +[23] | –[2][24] | –[25] | –[26] | not tested | none[10] |
| AR37 | Epoxy-janthitrems | ++++[1][27] | ++++[22] | +++[28] | ++++[24] | +++[25] | +[26] | not tested | occasionally[29,30] |
| NEA2 | Peramine, ergovaline, lolitrem B | +++[26] | (++++)[26] | +++[26] | ++[24] | not tested | –[26] | not tested | none[26] |
| NEA4 | Peramine, ergovaline | +++[26] | (++++)[26] | +++[26] | ++[26] | not tested | not tested | not tested | none[26] |
| Edge | Peramine, ergovaline | (++++)* | (++++)* | (+++)* | (+++)* | (–)* | not tested | not tested | none* |
| Avanex® | Peramine, ergovaline, lolitrem B | # | # | # | # | # | # | # | # |
| Diploid perennial ryegrass (*E. siegelii*) | | | | | | | | | |
| Happe | Lolines | (+++)* | (++++)* | (+++)* | (++++)* | (++++)* | not tested | not tested | not tested |
| Tetraploid perennial ryegrass (*E. festucae* var. *lolii*) | | | | | | | | | |
| AR1 | Peramine | (+++)[26] | (++++)[26] | +[26] | –[2][26] | –[26] | – | not tested | none |
| AR37 | Epoxy-janthitrems | (+++)[1][26] | (++++)[26] | +++[26] | ++++[26] | (+++)[26] | + | not tested | occasionally[29,30] |
| Italian and hybrid ryegrass (*E. festucae* var. *lolii*) | | | | | | | | | |
| AR1 | Peramine | ++[26] | (++++)[26] | +[26] | –[26] | not tested | – | not tested | none |
| NEA | Peramine, ergovaline, lolitrem B | Not tested | (++++)[26] | +++[26] | not tested | not tested | – | not tested | none |
| AR37 | Epoxy-janthitrems | +++[1][26] | (++++)[26] | +++[26] | not tested | not tested | – | not tested | occasionally[29,30] |
| Festulolium (*E. uncinata*) | | | | | | | | | |
| U2 | Lolines | ++++[31] | (++++)[32] | ++++[3][26] | ++++[26] | (++)[26] | +++[33] | +++[26] | none |
| Meadow fescue (*E. uncinata*)[4] | | | | | | | | | |
| Tall fescue (*E. coenophiala*) | | | | | | | | | |
| MaxP/MaxQ | Peramine, lolines | (++++)[34] | (++++)[32] | ++++[26] | (++++)[26] | (++T)[35] | +++R[35] | ++++[36] | none[36] |
| Protek | Lolines | (++++)* | (++++)* | (++++)* | (++++)* | (++++)* | (++++)* | (++++)* | none* |

– 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. Damage might 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.
[1] AR37 only deters the more damaging ASW larvae not adult.
[2] AR1 plants are more harmed than plants without endophyte.
[3] Active against Black beetle adult and larvae.
[4] A new meadow fescue cultivar infected with *E. 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[37−39]
* 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[40].

**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*) *E. festucae* var. *lolii* | Increased tiller number and shoot weight | 15% higher osmotic potential | [64] |
| | | Leaf water content not affected | [65] |
| | | 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 endophyte improved drought tolerance | Increased tiller number and yield | [69] |
| | 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 | [72] |
| | | No effect on stomatal conductance | [62,73,74] |
| | | No involvement to withstand or recover from drought | [75–78] |
| | Higher seedling survival when released from drought | No effect on reactive oxygen species | [79] |
| Tall fescue (*F. arundinacea*) *E. coenophiala* | Endophyte responses vary with genotype | Pseudostem, root and dead leaf yield increased with endophyte in some cases; no effect on non-structural carbohydrates | [80] |
| | | 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 plant survival under severe soil moisture deficit | 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 osmotic 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 enhances drought tolerance | [90,94] |
| | | Increased plant available water | [95] |
| | | Reduced reactive oxygen species | [96] |
| | Improved recovery after drought | Improved tiller and whole plant survival | [62,87,90,97–99] |
| | | Improved root growth | [100] |
| Meadow fescue (*F. pratensis*) *E. uncinatum* | Improved growth in drought | Reduced stomatal conductance | [101,102] |
| | | Increased water uptake capacity | [103] |
| | | Production of larger but fewer tillers | [104] |
| Strong creeping red fescue (*F. rubra* ssp. *rubra*) – turf type *E. festucae* | No improvement under drought | | [105] |
| **Native grasses** | | | |
| Drunken horse grass (*Achnatherum inebrians*) *E. gansuense* | Improved tolerance to drought and recovery from drought | Increased leaf proline, root/leaf growth, tiller number | [106] |

(to be continued)

**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 |
|---|---|---|---|
| | | Improved photosynthetic efficiency and nutrient absorption | [107] |
| | | Increased ergovaline and ergine alkaloid concentrations | [108] |
| | | Reduced disease incidence of *Blumeria graminis* | [109] |
| *Achnatherum sibiricum* *Epichloë* spp. | Endophyte benefit greatest when well-watered and fertilised | Higher root: shoot ratio and photosynthetic rate under drought and fertiliation | [110] |
| *Hordelymus europaeus* *E. hordelymi* | Improved recovery from drought | Increased tiller number and plant dry weight | [111] |
| Grove bluegrass (*Poa alsodes*) *Epichloë* spp. | Improved the negative effects of drought stress | Endophytic plants under drought had 24% more root biomass, 14% more shoot biomass; 29% more leaf senescence in non-endophytic plants | [112] |
| Arizona fescue (*Festuca arizonica)* *Epichloë* spp. | Endophyte infection beneficial in drought | Increased growth rates; low net photosynthesis and stomatal conductance | [113] |
| *Bromus auleticus* *E. pampeanum* and *E. tembladerae* | Improved survival in summer | Higher regrowth rate | [114] |
| *Roegneria kamoji* *E. sinica* | Improved seedling establishment in drought | Improved germination and seedling growth | [115] |
| *Elymus dahuricus* *Epichloë* spp. | Improved yield and tiller numbers under drought | Endophyte caused anti-oxidative enzyme activities and contents of proline and chlorophyll a + b increased under drought | [116] |
| | | Increased germination at moderate osmotic potentials | [117] |
| *Elymus virginicus* *E. elymi* | Improved drought tolerance, but also benefited well-watered plants | No effect on root: shoot ratio; improved tiller number | [118] |
| *Leymus chinensis* *E. bromicola* | Improved yield under drought | Increased photosynthetic rate | [119] |
| *Festuca sinensis* *Epichloë* spp. | Endophytes enhanced drought tolerance | Increased yield, root: shoot ratio | [120] |

moderate drought events can promote insect herbivory driven by elevated nutrient levels in plant tissues[42,43] and lowered plant defences[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[45]. Climate change has shifted the frequency of drought in some agricultural regions[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[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[51]. Perennial ryegrass, the mainstay of the New Zealand agricultural industry, fails to produce and thrive under a hot-dry climate[52], due at least in part to having a shallow root system[53] and therefore relying on constant water availability in the topsoil. Thus, drought in New Zealand reduces perennial ryegrass production, causing feed shortages for livestock requiring additional cost as alternative feed needs to be purchased[54,55]. Selecting for improved drought tolerance to maintain sustainable production is a priority plant breeding target[56]. Plants have evolved mechanisms to maintain function and/or survival under reduced soil moisture conditions[57], such as stomatal closure, reduction in leaf growth, as well as leaf abscission to reduce water loss via transpiration[58]. The plant accumulates solutes, such as carbohydrates, amino acids, sugars, and proline, to thereby draw water into the cells to re-establish turgor pressure. Even though this effect enables the plant to overcome short-term drought, it cannot be sustained for longer drought periods[59].

## *Epichloë* and drought

Endophyte-infected perennial ryegrass and tall fescue are considered to perform better in challenging environments than endophyte-free[60−62]. The presence of *Epichloë* can induce mechanisms of drought avoidance (morphological adaptions), 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[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)[61,63].

## 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[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[122], and a higher nitrogen content in the plant tissue[43,123−125], which is generally a limiting factor for herbivorous insects[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[128−130]. However, this may be moderated by the insect species and the feeding guilds involved[123]. For example, phloem feeders

**Table 3.** Impact of *Epichloë* 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*) *E. occultans* (presumably) Pot trial in a glasshouse | Lolines and peramine | Grass aphid (*Sipha maydis*) Cherry-oat aphid (*Rhopalosiphum padi*) | 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] |
| 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] |
| Perennial ryegrass (*L. perenne*) *E. festucae var. lolii* Field trial | Dependent on endophyte strain: ergovaline, peramine, lolitrem B, epoxy-janthitrems | Root aphid (*Aploneura lentisci*) Field measurements of population densities and ryegrass growth | Drought may have increased aphid populations and likely exacerbated their effect on plant growth. Two endophytes strongly reduced populations. Aphid populations correlated with plant growth. | [140] |
| **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. | [141] |
| | | Development time of fall armyworm (*Spodoptera frugiperda*) Growth of fall armyworm (*Spodoptera frugiperda*) | Growth and development reduced by endophyte-infected drought stressed herbage compared with well-watered. No effect on larvae fed Nil herbage. | [141] |
| Tall fescue (*F. arundinacea*) *E. coenophiala* AR584 Excised roots from treated plants feed to 3rd instar grass grub | Lolines | Grass grub (*Costelytra given*) 3rd 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. | [142] |
| Meadow fescue (*F. pratensis*) *E. uncinata* Excised roots fed to 3rd instar grass grub | | | 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] |
| 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] |

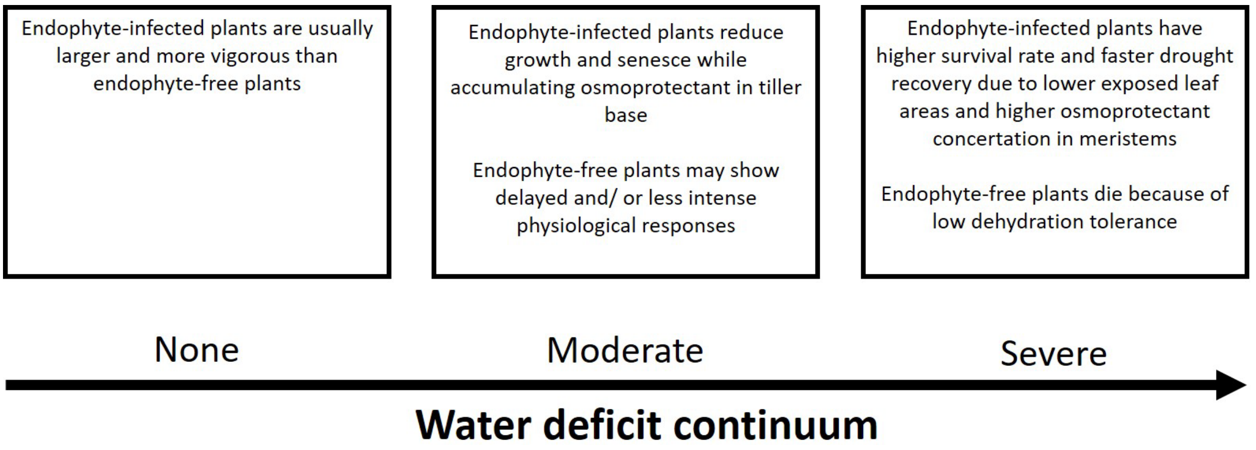


**Fig. 1** A proposed schematic diagram of endophyte-infected and endophyte-free plant responses to increasing soil water deficit. Figure adapted from Assuero et al.[63].

(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[71,83]. 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

**Fig. 2** Three-year-old perennial ryegrass trial in the Waikato, New Zealand. Plants in plots that have not survived were either endophyte-free or infected with an endophyte strain that did not protect the host plant against Argentine stem weevil or African black beetle during dry summers.

root mass which in turn will aid tolerance of drought[116] and insect pest pressures[139]. Host plant genotype also has a major effect on the outcomes of the symbiosis relating to drought stress[76].

## Concluding comment

Fungal *Epichloë* endophytes often increase host plant tolerance to water deficit as well as increase the ability to withstand herbivorous insect attack thereby making endophytes a critical component of temperate grasses in many intensively-managed pastoral systems. The majority of studies on endophyte-grass symbiosis focus on insect responses to endophyte presence or drought as a sole environmental stress factor. Less attention has been given to the combined impact of herbivore and environmental limitations, such as drought, on pasture production and resilience, even though in natural settings these biotic and abiotic stressors often occur concurrently. The positive effects of such endophytes on plant production, host fitness and resilience will become increasingly important with the projected increased frequency of drought combined with insect pressure due to climate change.

While in some temperate environments *Epichloë* symbionts are well established as an integrated pest management tool, their full potential for host plant adaption under multiple biotic or abiotic stress factors remains poorly described and understood. Yet it is these combined pressures that can prove terminal for temperate grasses. Understanding these interactions between resource limitation and herbivorous pressure on the host plant is required to better manage current *Epichloë* commercialised strains and to develop new agriculturally useful *Epichloë* – grass associations.

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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™, AR37®, Endo5™, MaxQ®, MaxQII™, MaxP®, MaxR™, Avanex®, Happe™ and Protek™.

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