




Entry

Asexual *Epichloë* Fungi—Obligate Mutualists

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Definition: Asexual *Epichloë* are obligate fungal mutualists that form symbiosis with many temperate grass species, providing several advantages to the host. These advantages include protection against vertebrate and invertebrate herbivores (i.e., grazing livestock and invertebrate pests, respectively), improved resistance to phytopathogens, increased adaptation to drought stress, nutrient deficiency, and heavy metal-containing soils. Selected *Epichloë* strains are utilised in agriculture mainly for their pest resistance traits, which are moderated via the production of *Epichloë*-derived secondary metabolites. For pastoral agriculture, the use of these endophyte infected grasses requires the balancing of protection against insect pests with reduced impacts on animal health and welfare.

Keywords: alkaloids; animal toxicosis; biocontrol; endophyte; fescue; ryegrass



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1. History

Microbial endophytes, primarily comprising archaea, bacteria, fungi, or viruses, are associated with most plant species [1,2]. The term ‘endophyte’ was derived from the Greek words ‘endon’ (within) and ‘phyton’ (plant) [3], and initially included both pathogenic and beneficial microorganisms [4]. However, the term endophyte has now become synonymous with mutualism in reference to microbes that spend all or part of their life cycle within the plant host while causing no apparent disease symptoms [5,6], and provides a net benefit outcome to both itself and the host plant [7].

Asexual *Epichloë* endophytes (previously belonging to the taxonomic genus *Neotyphodium* [8]) were identified in the 1980/90s as the cause of two economically important diseases that affected livestock that grazed fescue in the USA and perennial ryegrass in New Zealand, namely fescue toxicosis [9] and ryegrass staggers [10], respectively (Figure 1). These obligate symbionts are mutualistic, relying on the host plant for their growth, survival, and transmission through hyphal colonisation of the host’s seed [11]. These endophytes exhibit a degree of host-specificity within the cool-season grasses of the Pooideae, whereby *Epichloë* species are naturally restricted to a host grass genus or closely related genera within a grass tribe [12–14]. Asexual *Epichloë* spend their entire life cycle within the plant host growing systemically within shoot tissues between plant cells [15–17] (Figure 2). However, their bioactivity towards certain pests in the rhizosphere [18] can be attributed to the mobility of fungal secondary metabolites in the roots, produced during the symbiosis, within the plant vascular system [15,16].

Epichloë-derived secondary metabolites protect the host plant from herbivores—both vertebrates and invertebrates. However, the effect on ruminants and several non-ruminants including horses, camels, white rhinoceros, and alpacas [19] can be detrimental and, when first discovered, removal of these endophytes from grasses was considered the best solution. However, in many temperate regions of the world, such as New Zealand, these *Epichloë* endophytes are essential for pasture persistence. Novel endophyte strains have now been identified and commercialised that provide the host grass with tolerance/resistance to

pests, diseases, and some abiotic stresses while reducing or eliminating the debilitating animal health and welfare issues [20]. These endophytes can be transferred between plants through artificial infection [21].

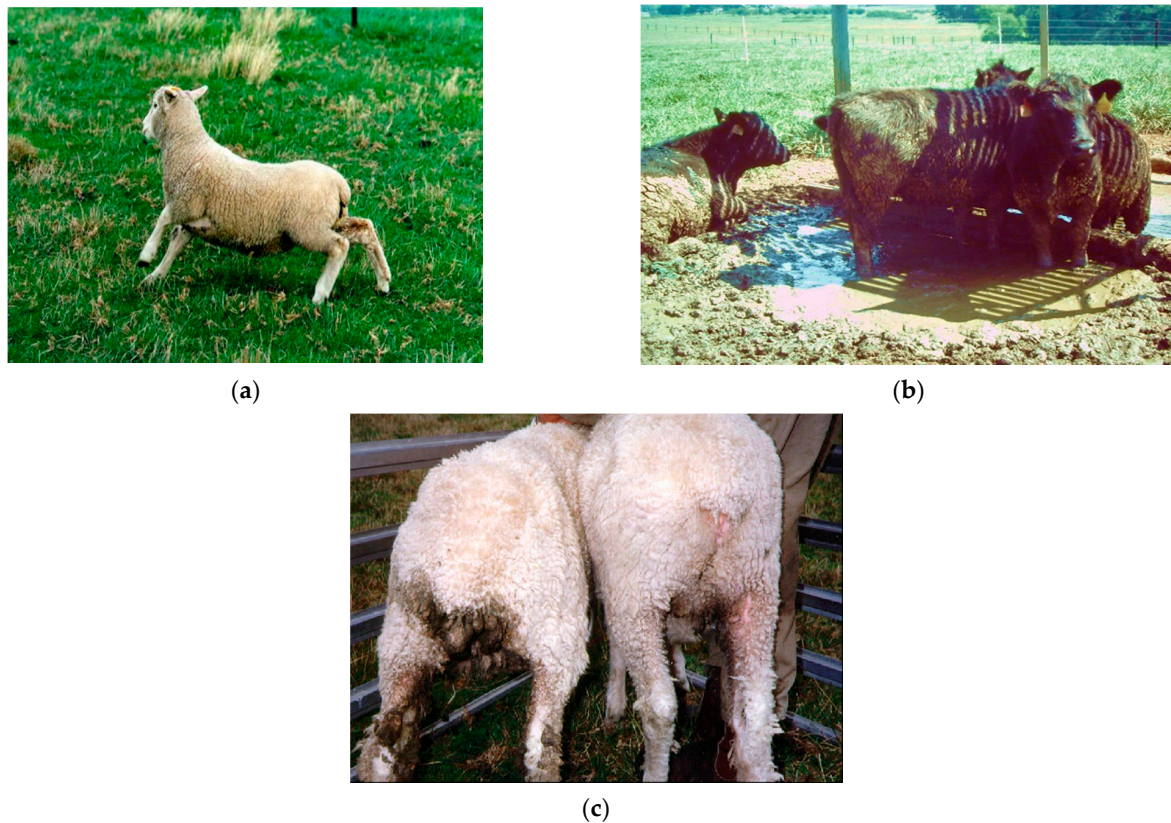


Figure 1. Animal ailments caused by some *Epichloë* secondary metabolites: (a) ryegrass staggers caused by lolitrem B, and (b) fescue toxicosis caused by ergovaline; (c) fecal soiling in the breech area ('dags') of sheep exacerbated, on left, by a combination of secondary metabolites. (Images (a,c) courtesy of L. Fletcher; image (b) courtesy of J. Bouton).

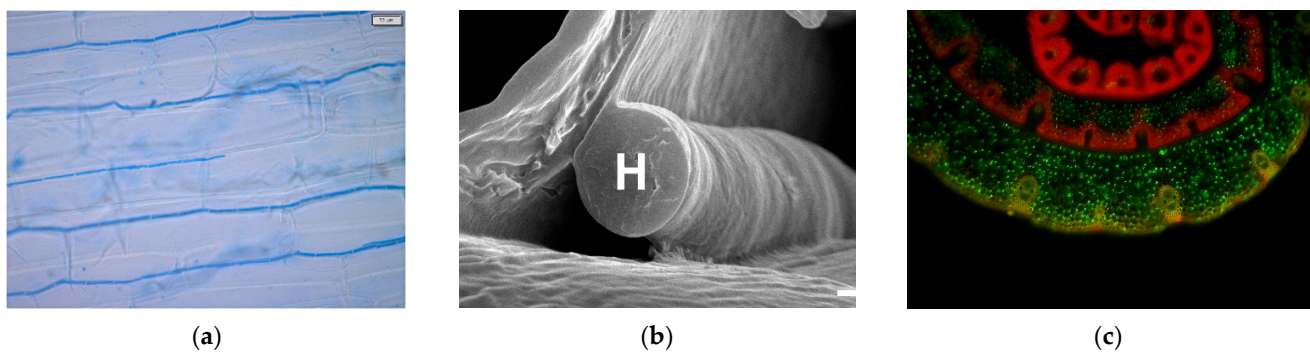


Figure 2. *Epichloë* hyphae, (a) stained with aniline blue (bar top right is 20 μ m) (image courtesy of W. Zhang), and (b) shown in a transmission electron micrograph growing between leaf cells with the hyphae labelled H (image courtesy of W. Zhang); and (c) a cross section of a grass tiller showing hyphae of a strain modified to express green fluorescent protein (image courtesy of M. Christensen).

2. *Epichloë* Endophytes—A Necessity for the Pastoral Industry?

2.1. Taxonomy and Distribution

Epichloë fungi are found in the Clavicipitaceae family [22]. As a result of taxonomists being required to have a single genus name for all stages of the development of a fungal species [23], the *Epichloë* genus contains both sexual (teleomorph) and asexual (anamorph)

forms. The latter had previously been classified as *Neotyphodium* [8]. More than 100 cool-temperate grass species host *Epichloë*, with the majority originating from Europe and Asia, and with many fewer from Australasia, sub-Saharan Africa, and South America (Table 1).

Asexual *Epichloë* strains are either hybrid as a result of a cross between two or more species, or are non-hybrid [14,24]. While all hybrid types are asexual, those classified as non-hybrid types are also incapable of sexual reproduction [25,26]. Compared with other fungal genera, *Epichloë* has the greatest number of interspecific hybrids [27].

Table 1. *Epichloë* species found in different grass genera across a range of territories.

Grass Genus (Common Names)	<i>Epichloë</i> Species	Region	Reference
<i>Achnatherum</i>	<i>E. gansuensis</i> , <i>E. sibirica</i> ; <i>E. chisosa</i> ; <i>E. inebrians</i> ; <i>E. funkii</i>	Asia	[8,24,28,29]
<i>Agropyron</i>	<i>E. bromicola</i>	Europe/North Africa	[30]
<i>Agrostis</i> (browntop)	<i>E. baconii</i> , <i>E. amarillans</i>	Europe/North Africa	[31]
<i>Ammophila</i>	<i>E. amarillans</i>	North America	[32]
<i>Anthoxanthum</i>	<i>E. typhina</i>	Europe/North Africa	[31]
<i>Brachyelytrum</i>	<i>E. brachyelytri</i>	Europe/North Africa; North America	[31,33]
<i>Brachypodium</i>	<i>E. sylvatica</i> ; <i>E. typhina</i> ; <i>E. bromicola</i>	Europe/North Africa; Asia	[29,31]
<i>Briza</i>	<i>E. tembladera</i>	South America	[34]
<i>Bromus</i>	<i>E. bromicola</i> ; <i>E. cabralii</i> ; <i>E. typhina</i> subsp. <i>poae</i> var. <i>aonikenkana</i> ; <i>E. typhina</i> ; <i>E. tembladera</i> ; <i>E. pampeana</i>	Europe/North Africa; Asia; North America; South America	[8,29,31,34–37]
<i>Calamagrostis</i>	<i>E. stromatolonga</i>	Asia	[29]
<i>Cinna</i>	<i>E. schardlii</i>	North America	[38]
<i>Dactylis</i> (cocksfoot)	<i>E. typhina</i>	Europe/North Africa	[31]
<i>Dichelachne</i>	<i>E. australiensis</i>	New Zealand	[39]
<i>Echinopogon</i>	<i>E. australiensis</i> ; <i>E. aotearoae</i>	Australia; New Zealand	[40,41]
<i>Elymus</i>	<i>E. elymi</i> ; <i>E. bromicola</i> ; <i>E. canadensis</i>	Europe/North Africa; Asia; North America	[8,24,29,31,33,42]
<i>Elytrigia</i>	<i>E. spp.</i>	Asia	[29]
<i>Festuca</i> (fescue)	<i>E. coenophiala</i> ; <i>E. festucae</i> ; <i>E. uncinata</i> ; <i>E. siegelii</i> ; <i>E. sinofestucae</i> ; <i>E. typhinum</i> var. <i>huerfana</i> , <i>E. tembladera</i>	Europe/North Africa; Asia; North America; South America	[29,31,43–45]
<i>Glyceria</i>	<i>E. glyceriae</i>	Europe/North Africa; North America	[31,33]
<i>Holcus</i>	<i>E. typhina</i> subsp. <i>clarkii</i> ; <i>E. mollis</i>	Europe/North Africa	[8,31,46]
<i>Hordelymus</i>	<i>E. disjuncta</i> , <i>E. danica</i> , <i>E. hordelymi</i> , <i>E. sylvatica</i> subsp. <i>pollinensis</i> ,	Europe/North Africa	[8,26]
<i>Hordeum</i>	<i>E. tembladera</i> , <i>E. amarillans</i> , <i>E. typhina</i> hybrids	South America	[47]
<i>Lolium</i> (ryegrass)	<i>E. occultans</i> ; <i>E. typhina</i> var. <i>canariensis</i> ; <i>E. hybrida</i> ; <i>E. festucae</i> var. <i>lolii</i> , <i>E. typhina</i> ,	Europe/North Africa	[8,27,31,48]
<i>Leymus</i>	<i>E. bromicola</i>	Europe/North Africa; Asia	[29,31]
<i>Melica</i>	<i>E. melicicola</i> ; <i>E. guerinii</i> ; <i>E. tembladera</i>	South America; Sub-Saharan Africa; South America	[8,24,34,41]
<i>Phleum</i> (timothy)	<i>E. typhina</i> ; <i>E. cabralii</i> ; <i>E. tembladera</i>	Europe/North Africa; South America	[8,31,34,37]
<i>Poa</i>	<i>E. typhina</i> ; <i>E. liyangensis</i> ; <i>E. alsodes</i> ; <i>E. typhina</i> subsp. <i>poae</i> ; <i>E. tembladera</i> ; <i>E. novae-zelandiae</i>	Europe/North Africa; Asia; North America; South America; New Zealand	[31,34,39,43,49]
<i>Roegneria</i>	<i>E. sinica</i> ; <i>E. bromicola</i>	Asia	[29,50]
<i>Sphenopholis</i>	<i>E. amarillans</i>	Europe/North Africa	[31]
<i>Stipa</i>	<i>E. spp.</i>	Asia	[29]

2.2. Life Cycle

In planta, asexual *Epichloë* spp. complete their entire life cycle within the host plant's tissues (Figure 3). Dissemination of *Epichloë* to the next plant generation occurs through vertical transmission of fungal hyphae via the seed of the host plant [51] and is mod-

erated by the compatibility of the endophyte strain with the host's genetics. Asexual *Epichloë* generally do not produce spores except when grown axenically within a laboratory environment [52].

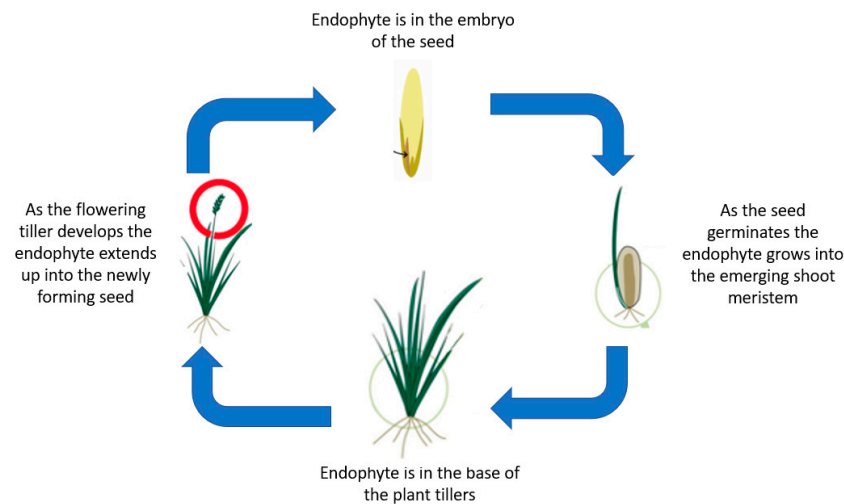


Figure 3. Schematic diagram of the asexual *Epichloë* endophytic life cycle in cool-season grasses of the Pooideae.

When used in managed pastoral ecosystems, viability of the endophyte in seed can be threatened if the seed is stored at ambient temperatures and humidity [53]. However, storage of seed with a moisture level below 8% at temperatures below 5 °C and relative humidity of less than 30% will ensure long term endophyte viability [54].

2.3. Secondary Metabolite Bioactivity and Its Consequences

The impact of *Epichloë* in natural and agricultural ecosystems is largely driven by chemistry. The genome of the endophyte strain determines the types (quality) of secondary metabolites expressed, but the host plant genome largely regulates the amount (quantity) [55,56]. Considerable information is known about four types of these secondary metabolite compounds (Figure 4) [55–57]:

1. Ergot alkaloids—can be divided into four groups based on their chemical structure: clavines (e.g., chanoclavine, agroclavine), lysergic acid, lysergic acid amides (e.g., ergonovine, ergine), and ergopeptines (e.g., ergovaline, ergotamine, ergocornine, ergocristine, ergosine, ergocryptine).
2. Indole diterpenoids—lolitrems, epoxyjanthitrems, terpendoles, paxilline.
3. Lolines—N-formyl loline (NFL), N-acetyl loline (NAL), N-acetylnorloline (NANL).
4. Pyrrolopyrazine—peramine.

Seasonal climatic effects can also have an overriding effect on the concentrations of secondary metabolites expressed [58–60]. These tend to be higher in the warmer drier periods of summer and autumn and lower through the cooler winter period (Figure 5).

Secondary metabolite distribution within the plant can vary with compounds and among host species. In ryegrass, ergovaline is concentrated in the stem and basal leaf sheath of intermediate aged tillers, lolitrem B accumulates in older tissues, and peramine is distributed evenly across all leaf tissues [63]. In meadow fescue, lolines are found in both shoot and root tissues [64].

The bioactive impacts of *Epichloë* strains can vary depending on the quality and quantity of secondary metabolites expressed. Secondary metabolites causing most of the negative effects on mammals have been elucidated, but research continues to understand the role of beneficial secondary metabolites that provide advantages to host plant persistence (Table 2).

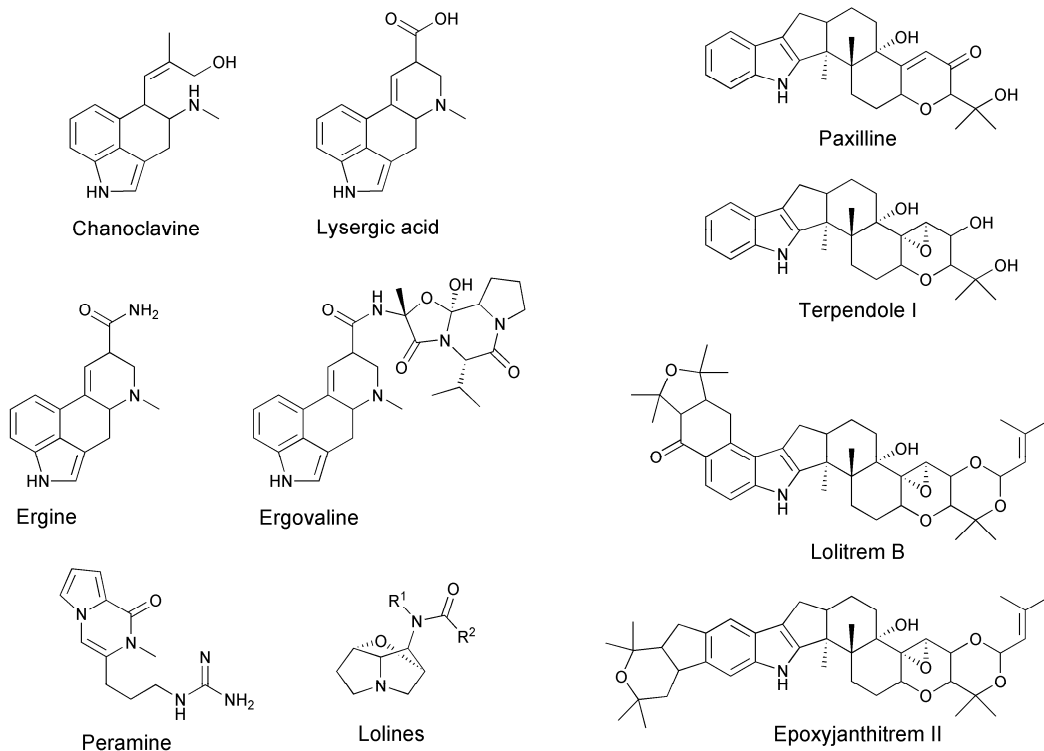


Figure 4. Molecular structures of the known secondary metabolites produced by *Epichloë*, *in planta*. Ergot alkaloids include chanoclavine, lysergic acid, ergine, and ergovaline; indole diterpenes include paxilline, terpendole I, lolitrem B, and epoxyjanthitrem II; peramine; and the lolines. (Figure provided courtesy of W. Mace).

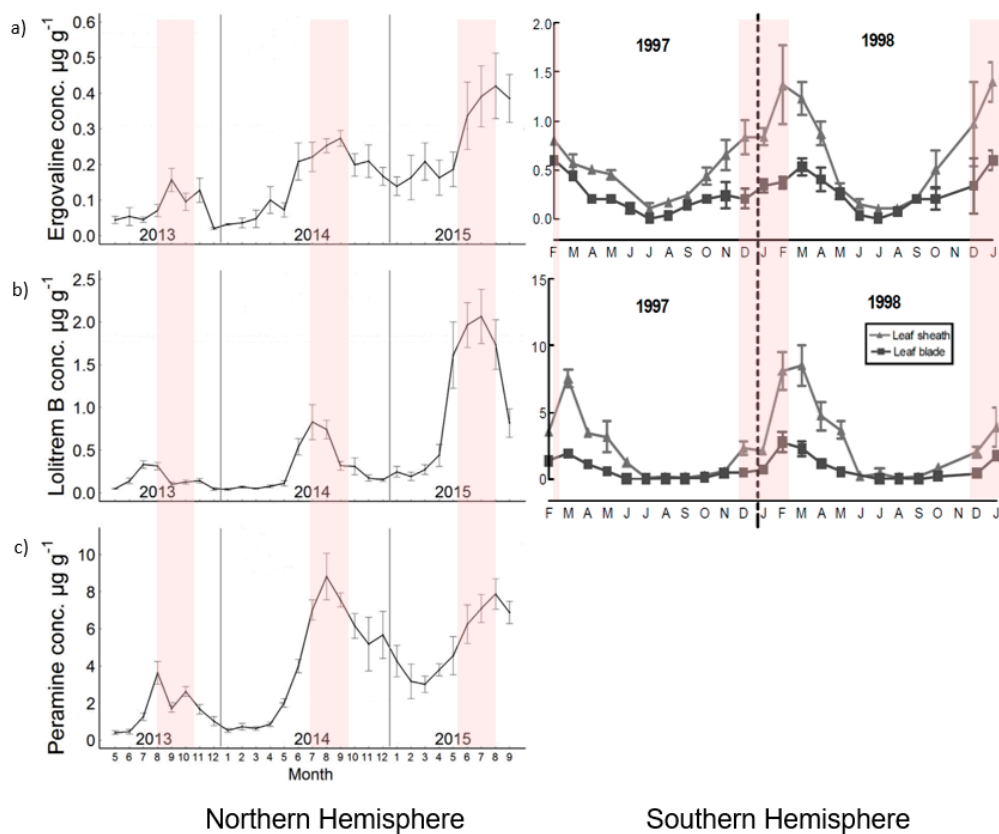


Figure 5. Seasonal trends in expression of ergovaline (a), lolitrem B (b), and peramine (c). Red shaded area represents summer months for the Northern and Southern Hemisphere. Figures modified from Fuchs et al [61] and Watson et al [62].

Table 2. Bioactivity of asexual *Epichloë* endophyte in grasses.

Bioactivity Trait	Consequence	Causation	References
Disadvantageous bioactivity			
Fescue toxicosis	Fescue foot, high core body temperature, increased respiration, low heart rate, altered fat metabolism, low serum prolactin, failure or reduced milk production produce milk, suppression of the immune system, reduced forage intake, low rate of weight gain, and reproductive problems.	Ergot alkaloids	[65–67]
Ryegrass staggers	Neurotoxic disease with symptoms ranging from slight muscular tremors through to staggering, and collapse. Can be associated with animal deaths.	Lolitrein B, other indole diterpenoids; sub-chronic threshold of 1.55 ppm for cattle and 2 to 2.5 ppm for sheep	[68–70]
Heat stress	Animals that are exposed to high concentrations of ergot alkaloids lose their ability to dissipate heat through restricted blood flow.	Ergovaline and other ergot alkaloids	[67,71,72]
Fecal soiling of the breech (dags)	Leads to higher incidence of myiasis (flystrike).	Ergovaline and lolitrein B	[73]
Reduced animal performance	Reduced liveweight gains and milk yields.	Ergovaline and lolitrein B	[73,74]
Ryegrass toxicosis	Can result in death through misadventure.	Documented only in Australia and likely to be a combination of ergot alkaloids and lolitrein B	[75–77]
Equine fescue oedema	Inappetence, depression, and subcutaneous oedema of the head, neck, chest, and abdomen in horses.	Only noted with endophytes in Mediterranean-type tall fescues	[78,79]
Reduced herbivore feeding	Deterrence to feeding.	Ergovaline and other ergot alkaloids	[80–82]
Livestock toxicosis (Australia, New Zealand)	Rare toxicosis in grazing livestock after <i>Poa matthewsii</i> and <i>Echinopogon</i> consumption.	Possible paxilline	[41,83]
Huecu toxicosis (Argentina)	Intoxication in grazing animals after <i>Poa</i> and <i>Festuca</i> grazing infected with <i>E. tembladerae</i> .	Indole-diterpenoid and ergot alkaloids	[84,85]
Sleepy grass toxicosis (USA)	Intoxication and narcosis in grazing livestock after <i>Stipa robusta</i> consumption.	Lysergic acid amide	[86,87]
Drunken horse grass toxicosis (Mongolia, China)	Intoxication and narcosis in horses, donkeys, sheep, goats, and cattle after <i>Achnatherum inebrians</i> consumption.	Ergot, ergonovine, lysergic acid, stipatoxin	[88]
Dronkgras toxicosis (South Africa)	Drunk-like behaviour of cattle, horses, donkeys consuming <i>Melica decumbens</i> .	Indole-diterpenoids	[89,90]
Advantageous bioactivity			
Insect pest resistance	Improved plant persistence and yield in presence of some insect pests.	Various alkaloids depending on insect species (Table 3)	[72,91,92]
Plant pathogen resistances	Reduced incidence to some fungal diseases.	Many known, but possible effects of peroxidase activity, phenolic compounds and antifungal proteins	[72,93–95]
Drought (low water supply) tolerance	Improved tolerance of drought through moderation of stomatal conductance, enhanced osmoregulation.	Largely unknown, but compounds implicated include polyols; increased levels of sugars and proline	[96–103]

Table 2. Cont.

Bioactivity Trait	Consequence	Causation	References
Allelopathy	Endophytic fescue plants reduce radicle elongation and growth of competing seedling species; but can detrimental on companion <i>Trifolium</i> species.	Total phenolic compound concentration was greater in endophytic than non-endophytic plants	[104]
Heavy metal tolerance	Improved growth in presence of cadmium, nickel.	Unknown; in case of cadmium improved translocation to shoot, but for nickel reduced translocation to shoot	[105,106]
Aluminium tolerance	Aluminium sequestration was greater on root surfaces and in root tissues of endophytic plants.	Increased exudation of phenolic-like compounds from roots of endophytic plants	[107]
Salinity tolerance	Improved leaf survival; changes of anatomical structures reducing water loss; and allowing water, nutrients, photosynthates translocation.	Unknown, but decreased sodium potassium and chlorine uptake	[108,109]
Nutrient uptake	Increased uptake of N and P from low levels of supply.	Unknown	[96,98,110,111]

Table 3. Mode of action of *Epichloë* secondary metabolites against invertebrates.

Secondary Metabolite	Mode of Action	Invertebrates Affected	Reference
Ergot alkaloids			
Ergovaline	Deterrent; anti-feeding; toxic	Argentine stem weevil (<i>Listronotus bonariensis</i>) adults; African black beetle (<i>Heteronychus arator</i>) adults; root aphid (<i>Aploneura lentisci</i>); Japanese beetle (<i>Popillia japonica</i>) larvae; black cutworm (<i>Agrostis ipsilon</i>); nematode (<i>Pratylenchus scribneri</i>)	[112–116]
Ergocryptine	Deterrent; anti-feeding; toxic	Argentine stem weevil adults and larvae; fall armyworm (<i>Spodoptera frugiperda</i>) larvae; nematode (<i>Pratylenchus scribneri</i>)	[117,118]
Indole diterpenoids			
Lolitre B	Deterrent; anti-feeding	Argentine stem weevil larvae; circumstantial effect on <i>Paratylenchus</i> nematode	[119]
Paxilline	Deterrent; anti-feeding	Argentine stem weevil larvae	[120]
Epoxyjanthitrens	Deterrent and toxic	Porina	[121]
Lolines			
N-formyl loline, N-acetyl loline, N-acetylnorloline	Deterrent; anti-feeding	Grass grub (<i>Costelytra giveni</i>); horn flies (<i>Haematobia irritans</i>); African black beetle; field cricket (<i>Gryllidae</i> spp.); Japanese beetle (<i>Popillia japonica</i>) larvae	[122–125]
	Deterrent and toxic	Argentine stem weevil larvae and adults; milkweed bug (<i>Oncopeltus fasciatus</i>); corn borer (<i>Ostrinia nubilalis</i>) larvae; aphid (<i>Rhopalosiphum padi</i> and <i>Schizaphis graminum</i>); fall armyworm (<i>Spodoptera frugiperda</i>) larvae; porina larvae (<i>Wiseana</i> spp.); nematode (<i>Pratylenchus scribneri</i>)	[126–130]
Pyrralopyrazine			
Peramine	Deterrent; anti-feeding	Argentine stem weevil adults and larvae	[120,131]
	Not a deterrent, but disrupted development	Cutworm (<i>Graphania mutans</i>)	[118]

The mode of action of secondary metabolites against insect pests continues to be understood as new endophyte strains are discovered and improved control of insect pests is achieved (Table 3).

However, there are also many unidentified secondary metabolites that are known to exist through bioactivity against invertebrates that cannot be attributed to known chemistry. In addition, *Epichloë* endophytes boost the jasmonic acid pathway, which in turn, enhances the host plant's immunity to chewing insects [132]. Grass emitted volatile organic compounds triggered by an aphid infestation can also be enhanced through *Epichloë* endophyte infection [133]. These volatiles have been shown to attract syrphid flies, which are natural enemies of aphids [134].

2.4. Application and Value to the Pastoral Industry

In a pastoral agriculture context, *Epichloë* endophytes are essential for temperate grass persistence in New Zealand, Australia, the USA, South America, and, to a lesser extent, Europe [135]. The absence of an *Epichloë* endophyte or use of an inappropriate strain can result in complete pasture loss, as shown in a comparative trial in the Waikato region of New Zealand (Figure 6). However, to ensure the disadvantageous impacts of *Epichloë* on animal health and welfare are minimised, strains of endophyte that do not express those secondary metabolites at levels causing these issues have been identified, isolated, and then re-inoculated into high yielding plant germplasm [72,136]. This has resulted in several novel *Epichloë* strain-host associations being commercialised [137–142]. Table 4 summarises the performance of these commercialised strains and their known chemistry.

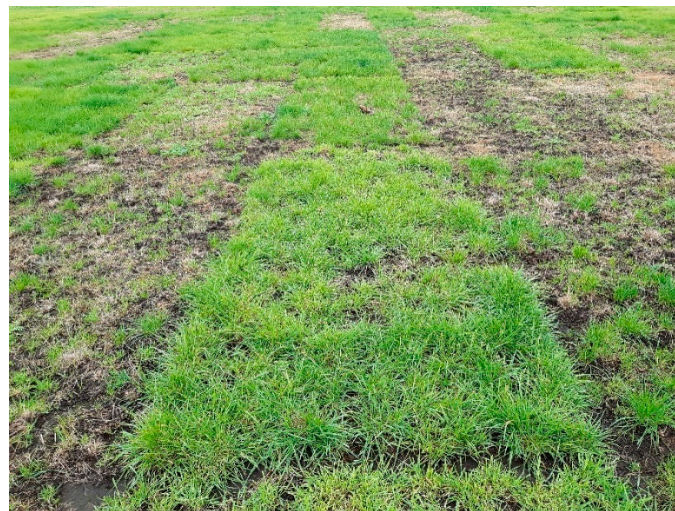


Figure 6. The loss of persistence due to insect pests and drought on ryegrass with either no *Epichloë* endophyte or an ineffective strain on ryegrass persistence in the Waikato region of New Zealand.

Table 4. Summary of known chemistry, impacted insect pests, and animal performance of commercialised *Epichloë* endophyte strains (reviewed in Caradus et al [142]).

<i>Epichloë</i> Brand (or Strain)	Known Chemistry	Insect Pest Affects Significantly Reduced	Animal Performance	References
Ryegrass; endophytes are <i>E. festucae</i> var <i>lolii</i>, or <i>E. festucae</i>				
Nil endophyte	No chemistry	No insect pest protection	Excellent	[74,81,143,144]
AR1	Peramine	Argentine stem weevil (larva), pasture mealybug (<i>Balanococcus poae</i>)	Excellent	[81]

Table 4. Cont.

<i>Epichloë</i> Brand (or Strain)	Known Chemistry	Insect Pest Affects Significantly Reduced	Animal Performance	References
AR37	Epoxyjanthitrems	Argentine stem weevil (adult), pasture mealybug, porina, African black beetle, root aphid	Excellent, but minor staggers can occur with sheep/lambs	[145]
NEA (NEA2)	Low ergovaline and peramine, very low lolitrem B	Pasture mealybug, African black beetle	Excellent	[146,147]
NEA2 (mix of NEA2 and NEA6)	Medium ergovaline, medium-low peramine, very low lolitrem B	Argentine stem weevil, pasture mealybug, African black beetle, root aphid	Excellent, but lamb live weight gain could be reduced in extreme circumstances	[147–151]
NEA4 (mix of NEA2 and NEA3)	Medium ergovaline, medium-low peramine, very low lolitrem B	Argentine stem weevil, pasture mealybug, African black beetle	Excellent, but lamb live weight gain could be reduced in extreme circumstances	[147]
Standard endophyte	High ergovaline, peramine and lolitrem B	Argentine stem weevil, pasture mealybug, African black beetle; root aphid	Can cause ryegrass staggers in sheep and lambs, and significantly decrease lamb growth rates in summer and autumn, and significantly increase dags. In dairy cows, it has been shown to depress milksolids production through summer and autumn.	[74,81,143,144,149,151]
<i>Festulolium</i>; endophyte is <i>E. uncinatum</i>				
U2	Loline compounds NFL, NAL, and NANL	African black beetle, Argentine stem weevil, pasture mealybug, root aphid, grass grub, field crickets	Excellent	[124,152,153]
Tall fescue; endophytes are <i>E. coenophiala</i>				
Nil endophyte	No chemistry	No insect protection	Excellent	[154]
MaxQ II (USA); MaxP (NZ, Australia) (AR584)	Peramine, loline compounds NFL, NAL, and NANL	African black beetle, Argentine stem weevil, pasture mealybug, grass grub, root aphid, fall armyworm, corn flea beetle (<i>Chaetocnema pulicaria</i>), bird cherry-oat aphid (<i>Rhopalosiphum padi</i>), field crickets	Excellent	[155,156]
E34	Low ergovaline	Not tested	Excellent; lowered blood serum prolactin levels	[156]

The economic benefit of some of the more widely commercialised strains has been estimated. For example, the value to the New Zealand economy from AR37 has been calculated to be NZ\$3.6 billion over the 20-year life of its patent [157]. In the USA, the positive financial benefits of MaxQ tall fescue have been demonstrated for beef cows, calves, and feeder cattle farming systems [158,159] and sheep farming systems [160].

3. *Epichloë* Endophytes—Applications Outside the Pastoral Industry

3.1. Application to the Turf Industry

For grassed areas such as airports, children's playgrounds, sports turf, and parks, which exclude domesticated grazing animals, *Epichloë* endophytes that produce deterrent secondary metabolites such as ergot alkaloids, lolitrem B, and lolines have been deliberately used to discourage herbivores such as rabbits, granivorous birds, and rodents [161–165].

3.2. Application to Cereals

While *Epichloë* endophytes are not naturally found in modern cereals such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), oats (*Avena sativa*), or rye (*Secale cereale*), they are found in wild grasses related to these species, namely from the genera *Elymus* and *Hordeum* [166]. Research has set out to determine whether *Epichloë* can provide the same benefits to cereals as they do to temperate grasses. Artificial inoculation of *Epichloë* strains from wild grasses into wheat and rye can result in stunted or dwarf phenotypes due to compatibility issues [167]. However, in outbreeding rye, the range of phenotypes can result in normal phenotypes, which, in the field, provide the host plant with increased fungal pathogen resistance and improved yields under some managements [168], and reduce damage from a range of insect pests [169,170]. In wheat, inoculations have been possible through using Chinese spring wheat addition lines [171].

4. Conclusions and Prospects

The mutualistic relationship between asexual *Epichloë* spp. and cool-season grasses is critical for the maintenance of temperate grass based pastoral agriculture in several countries. While it remains more of a biological curiosity in Europe, where this mutualistic association evolved between *Epichloë* and the host species of *Lolium* and *Festuca*, it is essential in many countries where these grasses were introduced due to the prevalence of both introduced and endemic insect pests and pathogens, and the compounding effect of drought and heat [72,103]. Changes in climate, management, and further pest incursions will continue to challenge the persistence of cool-season grasses making the reliance on the mutualism with *Epichloë* even more important. The ongoing search for novel endophytes with beneficial chemistry continues, but can now be supplemented with the use of new techniques such as gene editing to design endophyte strains for specific biotic and abiotic challenges [172,173]. The ultimate outcome will be the delivery of natural biocontrol options to protect grasses from pest and disease challenges, without the use of synthetic chemistry, and improve yield in drought conditions.

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