New Zealand's pastoral ecosystems: challenges, solutions, and the protective role of *Epichloë* endophytes

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Abstract

New Zealand's pastoral ecosystems heavily rely on introduced grass species like perennial ryegrass, hybrid and Italian ryegrasses (*Lolium* spp.) and fescues (*Festuca* spp.), which can form mutualistic relationships with *Epichloë* endophytes. These endophytes protect grasses from insect herbivory by producing alkaloids that deter insect pests. However, while they benefit the plant, these alkaloids can also negatively affect grazing livestock. Unlike many other temperate grassland systems, New Zealand's pastures have low plant diversity, with most sown species originating from Europe. This lack of diversity, combined with a historically limited suite of natural enemies, has contributed to a unique pasture insect pest burden. Pests such as Argentine stem weevil (*Listronotus bonariensis*), black beetle (*Heteronychus arator*), and root aphid (*Aploneura lentisci*) cause significant economic losses, threatening pasture persistence and productivity. To mitigate these challenges, many of New Zealand's dominant pasture grasses are artificially associated with selected *Epichloë* endophytes that provide insect protection against key insect pests while minimising impacts on grazing livestock. These endophytes produce alkaloids that act as feeding deterrents and/or reduce the fitness of herbivorous insects, providing a natural bio-protection mechanism. This review explores the unique ecological characteristics of New Zealand's pasture systems, including the impact of invasive and native insect pests and the role of *Epichloë* endophytes in pasture protection. Emerging challenges include climate change-driven shifts in pest populations and the need for sustainable pasture management strategies. Integrating ecological principles with advanced endophyte technologies can improve pasture resilience while minimising environmental trade-offs.

Keywords: Plant-insect interactions, integrated pest management, perennial ryegrass

Background

New Zealand is a primary industry-based economy, heavily reliant on agriculture for economic prosperity. The most significant contributor is pastoral agriculture, including the dairy, beef, sheep, and deer sectors. As of 2021, the agriculture sector contributed approximately 5.78% to New Zealand's gross domestic product (GDP), which generated over NZ $14.4 billion (Ōhanga 2016). Unlike many nations that depend on feedlot systems or supplementary grain feeding, New Zealand's livestock industry thrives on extensive grazing, leveraging the country's temperate climate, high rainfall, and fertile soils to support year-round pasture growth. It is not unexpected that New Zealand's pastoral agriculture ranks among the world's most energy-efficient and low-emission systems (Mazzetto et al. 2022). However, New Zealand's reliance on stable environmental conditions makes the pastoral sector increasingly vulnerable to climate change, shifting soil dynamics, and the emergence or spread of insect pests. The combination of introduced grass species and the extensive, pasture-based farming system has created conditions that support the proliferation of specific insect pests, many of which are not found in other parts of the world. This makes pest management in New Zealand particularly challenging and crucial to maintaining the health and productivity of its agricultural systems. This strong dependence on pastoral farming highlights the importance of ongoing innovation in pasture management, environmental sustainability, and adaptation to global market demands. Fungal symbiotic *Epichloë* endophytes are an integral part of technology development aimed at improving pastures (Caradus 2024b). These naturally occurring fungi form beneficial

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symbiotic relationships with cool-season grasses such as perennial ryegrass, enhancing their resilience to pests, diseases, and environmental stressors (Card et al. 2021; Hewitt et al. 2021; Caradus 2024b).

This review discusses the uniqueness of New Zealand's pastoral systems and the challenges posed by insect pests. It also provides an overview of the critical role of *Epichloë* endophytes in maintaining pasture production and providing solutions for insect pest resistance.

New Zealand's pasture ecology: then and now

New Zealand's pastures may appear similar to those of other pasture-based nations due to the widespread use of grazing systems for livestock production. However, New Zealand's pastures are ecologically distinct, shaped by 55 million years of geographic isolation and a unique human settlement history (Bunce et al. 2009; Goldson et al. 2020). The absence of grazing mammals in ancient New Zealand played a crucial role in the evolution of these ecosystems. The development of the dominant pasture systems in New Zealand began with European settlement in the late 19th century. European settlers cleared large areas of indigenous bushland, swamplands, and tussock to establish modern pastures using exotic forage species, introducing livestock such as sheep and cattle (Lancashire 2006; Perry et al. 2014). With the conversion of land use, European settlers introduced grass species such as perennial ryegrass (*Lolium perenne* L.), annual ryegrass (*Lolium multiflorum* Lam.), cocksfoot (*Dactylis glomerata* L.), browntop (*Agrostis capillaris* L.) and white clover (*Trifolium repens* L.), which are well adapted to New Zealand's climate (Craig 2016). By 1950, intensive pasture farming had expanded significantly, driven by the growing demand for wool and meat. By 2021, over 13 million hectares of the country's total land area of 26.8 million hectares were devoted to grassland farming (Beef and Lamb 2022). Of this, around 7 million hectares were intensively managed pastures. Therefore, ryegrass and clover are critical to New Zealand's agricultural economy, contributing to an export gross output value of over NZ $14 billion and NZ $2 billion per annum, respectively (Nixon 2016). Their widespread use has resulted in highly productive yet modified landscapes with pastures dominated by introduced species and having an overall low grass species diversity.

Challenges for New Zealand farmers

As pastureland expanded across the country, insect damage became apparent, particularly through the impact of indigenous species such as the New Zealand grass grub (*Costelytra giveni* White) and the porina moth (*Wiseana* spp. Walker). These native pests, which had not previously encountered large-scale pasture systems, became significant contributors to the degradation of the pasture, creating challenges for pasture management and pest control (Cockayne 1920). Control methods included mass-trapping of flying adults, various forms of cultivation, tillage management, changes to sward composition, and crop rotations, including cropping (Dumbleton 1943). Despite these efforts, none have provided complete or long-term control. Effective control of soil-dwelling pasture pests was not achieved until the introduction of organochlorine insecticides, such as DDT, which showed high efficacy against these pests (Kelsey & Hoy 1950). However, organochlorine insecticides were banned in the early 1970s due to their highly toxic nature to both the environment and non-target organisms, including beneficial insects, birds, and mammals (Boul et al. 1994). To date, no safe alternative chemical control with the same efficacy has been found as a replacement.

As New Zealand became more connected to global trade and human movement, new pasture insect pests were inadvertently introduced, presenting significant challenges to the country's pasture-based agricultural system. One of the earliest documented arrivals was the Argentine stem weevil (*Listronotus bonariensis* Kuschel; ASW), likely introduced through trade and the movement of plant material from South America in 1916, although it likely arrived before that (Stewart et al. 2023). The weevil rapidly established itself, becoming a major pest of ryegrass and other key forage species. This weevil is of relatively minor significance to grasslands in its native range but causes major damage to New Zealand pastures (Barker et al. 1984a). Similarly, the African black beetle (*Heteronychus arator* Fabricius) was originally described from South Africa and was first recorded in New Zealand in the late 1930s (Fabricius 1775; Todd 1959). The success of these insect pests in New Zealand is largely due to the country's low diversity of pasture grass species and the absence of naturally evolved predators. New Zealand's pasture ecosystems provide limited habitat for native predator insects (Ewers & Didham 2006; Brockerhoff et al. 2010). Furthermore, New Zealand's ecosystems did not evolve alongside the predators typically found in other regions, which play a important role in controlling pest populations. As a result, most indigenous natural enemies have little impact on suppressing invasive pests in pastures (Ewers & Didham 2008), creating an environment where introduced insect pests can flourish, causing significant damage to crops and pastures.

Further challenges for New Zealand farmers include poor pasture persistence, which leads to weed encroachment and reduced productivity (Tozer et al. 2011b; Tozer et al. 2011a). This issue is further compounded by climate change, which brings more extreme weather conditions, such as prolonged droughts, heavy rainfall, and increased climate variability. Perennial ryegrass is especially vulnerable to these stresses, which could have significant long-term impacts on its viability and productivity in the future (Beukes et al. 2021; McCahon et al. 2021).

The big six

The most damaging pasture insect pests in New Zealand, here referred to as the 'Big Six', include the grass grub, Argentine stem weevil, root aphid (*Aploneura lentisci* Passerini), porina, African black beetle, and pasture mealybug (*Balanococcus poae* Maskell). In New Zealand, these pasture insect pests are estimated to cause annual economic damage ranging from NZ $1.7 billion to $2.3 billion (Ferguson et al. 2019). These insects have become the primary invaders of New Zealand's pastures and are the main contributors to damage in modern pasture systems.

Argentine stem weevil

The Argentine stem weevil is a significant pest in New Zealand ryegrass pastures, estimated to cause up to $200 million in damage every year (Ferguson et al. 2019). First recorded in 1916 (Stewart et al. 2023), ASW was accidentally introduced from South America and has become a major threat to pasture health. The adult weevil feeds on the leaves of grasses, while the larvae burrow into the stems, weakening the plant. Argentine stem weevils are found throughout New Zealand, with densities reaching up to 723 adults/m^2 in some areas (Barker & Addison 1993). This damage compromises pasture growth and productivity and, in severe cases, results in the complete loss of pastures (Barker et al. 1984b). However, in its native habitat, the ASW causes significantly less damage, demonstrating its remarkable adaptability and resilience in its new environment (Lloyd 1966). One of the most notable traits of the ASW is its ability to rapidly evolve in response to natural enemies, such as parasitic wasps introduced for biological control. Over time, the ASW has developed evasive behaviours, reducing its vulnerability to parasitoids like *Microctonus hyperodae*, which were initially highly effective in managing its population (Goldson & Tomasetto 2016; Tomasetto et al. 2018). This adaptive behaviour highlights the ability of ASW to avoid predation but also to exploit ecological conditions to thrive in new environments, posing ongoing challenges for pest management strategies in modern pasture systems.

Grass grub

New Zealand grass grub is an endemic insect with larvae that feed intensively on the roots of ryegrass and white clover. As a consequence, this species is ranked as the most costly insect pest in New Zealand, causing pasture production losses of NZ$75–380M per year (Ferguson et al. 2019). Damage initially appears as yellowing patches in pasture swards, which later result in areas of dead plants where larval numbers are high. Such patches can be rolled back like carpet. Grass grub can be found throughout New Zealand, although they are uncommon in the subtropical northern North Island of New Zealand. Numbers ≥ 150 larvae/m^2 are considered damaging to pastures (Ferguson et al. 2019) and population densities of more than 500 larvae/m^2 are common, with numbers of over 1000 larvae/m^2 recorded (East et al. 1979).

Porina

Porina caterpillars, comprising seven species (*W. cervinata, W. copularis, W. jocosa, W. mimica, W. fuliginea, W. signata,* and *W. umbraculata*), are recognised as the second most damaging native pasture pest in New Zealand, causing financial loss up to $88 M per year (Ferguson et al. 2019). Larvae tunnel into the soil of grasslands and emerge at night to feed (Barlow et al. 1986; Barratt et al. 1990). They typically sever leaves and drag the excised foliage back to their burrows, where they can feed safely for several days (Dugdale 1994). Porina caterpillars thrive and cause significant damage in the cooler regions of New Zealand, ranging from alpine areas to lowland plains in the central North Island and throughout the South Island.

Root aphid

Root aphids are endemic to the Middle East and Mediterranean regions and have been present in New Zealand since at least the 1930s (Cottier 1953). These aphids occur year-round and prefer feeding on young grass roots, into which they initially probe several times before inserting their stylets into the phloem sieve (Van Emden & Harrington 2017). Aphids can be found throughout the root system, to at least 100mm soil depth (Pennell et al. 2005). In New Zealand, aphids reproduce parthenogenically and will continue to do so for several generations (Rasmussen et al. 2008). The damage in the field and the economic impact of root aphids are difficult to assess because of the inherent difficulties of studying below-ground insects, as well as their small size and fragile nature (Ferguson et al. 2019). In a pot trial, the foliage and root biomass of perennial ryegrass were reduced by up to 27% and 49%, respectively (Popay & Cox 2016; Hewitt et al. 2023b).

African black beetle

African black beetle (ABB) is a soil-dwelling, shiny-black scarab beetle, predominantly found in grasslands (Matthiesse & Learmonth 1998; Bell et al. 2011). Native to Africa, the ABB was accidentally introduced to New Zealand and Australia, with the first observations in New Zealand recorded in the late 1930s (Todd 1959). The ABB is a significant pest in agricultural systems due to its capacity for extensive plant damage per individual (Bulinski & Matthiessen 2002). Grasses, including perennial ryegrass, are the preferred host for both larval and adult ABB (King et al. 1981). While ABB larvae cause the most damage to the root structure (Bell et al. 2011), adult beetles feed on the base of plants, often destroying entire tillers and causing significant plant damage (Karpyn Esqueda et al. 2017). Densities of over 100 larvae/m^2 can significantly damage turf grasses (Ford et al. 2001).

Pasture mealybug

Pasture mealybugs are endemic to New Zealand and are known to damage cool-season grasses, particularly in the Canterbury, Nelson, and Manawatū regions (Pearson 1988). Similar to root aphids, pasture mealybugs feed by sucking sap from phloem tissue, that can impact grass survival (Pennell et al. 2005). They often reside under leaf sheaths near the crown, close to the meristem, and are typically surrounded by white, waxy secretions. Pasture mealybugs have two generations per year during the spring-autumn period (Pennell & Ball 1999). The economic impact of pasture mealybug infestations has not yet been documented.

Epichloë endophytes

In addition to insect challenges, farmers also began noticing unexplained health issues in their grazing animals, including reduced feed intake, poor weight gain, lameness, and in some cases, reproductive issues like infertility or abortion. Furthermore, ryegrass staggers is a neurological disorder that affects livestock, particularly cattle and sheep, grazing on perennial ryegrass pastures. Similarly, fescue toxicosis was observed in cattle grazing tall fescue (Festuca arundinacea) pastures in the United States. Investigations into livestock health issues led to the discovery of *Epichloë* endophytes, which live in intercellular spaces of above-ground plant tissue. These are transmitted through the host seed and form beneficial associations with some Pooideae grasses, such as perennial ryegrass. These endophytes were unintentionally introduced to New Zealand via imported pasture seed and were later identified as the primary cause of livestock disorders (Bacon et al. 1977; Fletcher & Harvey 1981). The toxic alkaloids produced by *Epichloë* endophytes are responsible for these health conditions. For example, the endophyte commonly found in New Zealand ryegrass, *Epichloë* var. *lolii* (also known as New Zealand Common Toxic, NZ_{CT}, Standard endophyte SE) is known to cause ryegrass staggers and heat stress in grazing livestock (Gallagher et al. 1981; Fletcher 1993). Initially, it was thought that removing the endophyte from pastures would alleviate these animal health issues and improve productivity. However, it was soon discovered that endophyte-free pastures were highly susceptible to damage from insect pests (Rowan et al. 1990). This led to the recognition that the production of fungal alkaloids by *Epichloë* endophytes was linked to insect deterrence as well as animal toxicosis (Gallagher et al. 1981; Prestidge et al. 1982; Popay & Lane 2000).

Epichloë endophytes enhance the resilience of their grass host largely through the production of alkaloids. Four compound classes have been the focus of most research (reviewed by Lane et al. (2000)): indole diterpenes (lolitrems and epoxyjanthitrems), ergot alkaloids (clavines, lysergic acid, and derivative alkaloids), pyrrolopyrazine (peramine), and pyrrolizidines (lolines). Tall fescue endophytes can produce lolines, peramine, and ergot alkaloids (Christensen et al. 1993; Porter 1995; Schardl et al. 2012). In comparison, perennial ryegrass endophytes can produce lolitrems, epoxyjanthitrems, ergot alkaloids, and peramine (Johnson et al. 2013). The endophyte is confined to the plant shoots, where alkaloids like peramine, lolitrem B, and ergovaline are measurable; however, only loline compounds are found in significant concentrations in the roots (Patchett et al. 2008a; Hewitt et al. 2024). All four classes of alkaloids have negative effects on insects (Table 1) but ergovaline, lolitrem B and epoxyjanthitrems are also toxic to grazing livestock (Fletcher & Harvey 1981; Easton et al. 1996). The combination of alkaloids produced by the endophyte is a characteristic of each endophyte strain (Lane et al. 2000). The variation in alkaloid production among *Epichloë* strains allows for the selection of strains that can balance animal health and welfare while still providing effective protection against insect pests.

Harnessing *Epichloë* endophyte technology

Due to the economic and environmental drawbacks of synthetic insecticides, including organochlorine, organophosphate, carbamate, pyrethroid, benzoyl phenyl urea, and neonicotinoids (Barlow & Goldson 2002), researchers have explored the use of *Epichloë* endophytes as a natural alternative for insect management. To evaluate the effects of different alkaloid groups on insect pests, scientists commonly conduct both controlled diet experiments and pot trials. These studies involve extracting specific compounds or classes of compounds from plant tissues and incorporating them into synthetic or semi-synthetic diets, which are then fed to insects at varying concentrations. An overview of how known alkaloid compounds affect New Zealand's most damaging pasture insect pests is outlined in Table 1. This knowledge has guided the search for optimal alkaloid profiles, which are then commercialised as seed products for farmers. The presence of more than one *Epichloë* strain within a single grass genotype is considered unlikely (Christensen et al. 2000). However, some commercial brands include more than one endophyte strain in the seed mixtures (Table 2). Over the past twenty years, multiple endophyte strains and brands have been marketed in New Zealand and internationally, including AR1, AR37, NEA2, Happe,

Table 1 The impact of *Epichloë*-derived compounds against New Zealand's most damaging pasture insect pests.

Insect pest	Compound class	Alkaloid compound	Description	Reference
Argentine stem weevil	Pyrrolopyrazine	Peramine	deters adult oviposition and hence reduced larval damage	(Rowan et al. 1990)
	Ergot	Ergovaline	feeding deterrence for adults	(Popay et al. 1990)
	Indole-diterpenes	Lolitrem B	feeding deterrence/ toxic against larvae	(Popay et al. 2003b)
		Paxilline	feeding deterrence against larvae	(Rowan 1993)
	Pyrrolizidine	Lolines (not defined)	feeding deterrence and larval death, reduced oviposition	(Patchett et al. 2008b; Jensen et al. 2009; Barker et al. 2015a)
		N-formyl loline (NFL)	increased larval mortality	(Jensen et al. 2009)
		N-acetylnorloline (NANL)	increased larval mortality	(Jensen et al. 2009)
Grass grub	Ergot	Clavines	feeding deterrence	(Popay & Tapper 2007)
	Pyrrolizidine	Lolines (not defined)	reduced root feeding and larval weight gain, deterrence	(Popay & Lane 2000; Popay et al. 2003a; Patchett et al. 2008a; Patchett et al. 2011)
		N-acetyl loline (NAL)	strong deterrence	(Popay & Tapper 2007)
		N-formyl loline (NFL)	strong deterrence	(Popay & Lane 2000; Popay & Tapper 2007)
		N-acetylnorloline (NANL)	weak deterrence	(Popay & Tapper 2007)
Porina	Indole-diterpenes	Epoxyjanthitrems	reduced feeding and survival	(Popay et al. 2012; Hennessy et al. 2016; Babu et al. 2018; Finch et al. 2020)
	Pyrrolizidine	Lolines (not defined)	reduced feeding and weight gain	(Popay & Lane 2000)
Root aphid	Pyrrolopyrazine	Peramine	no effect	(Popay & Gerard 2007)
	Pyrrolizidine	Lolines (not defined)	reduced population	(Schmidt 1993)
African black beetle	Pyrrolopyrazine	Peramine	no effect	(Ball et al. 1997)
	Ergot	Ergovaline	antifeedant	(Popay & Ball 1998)
		Chanoclavine	no effect	(Hudson et al. 2021)
	Indole-diterpenes	Lolitrem B	no effect on adults	(Ball et al. 1997)
		Paxilline	no effect on adults	(Ball et al. 1997)
		Lolines (not defined)	Antifeedant for larval and adult	(Bryant et al. 2010; Barker et al. 2015b)

Edge, and Avanex® for ryegrass (Figure 1); MaxP (also known as MaxQ) and Protek for tall fescue; and GrubOUT® U2 for meadow fescue (Lolium pratense) and fescue hybrids (Johnson et al. 2013; Young et al. 2013). In New Zealand, the AR37 endophyte has delivered an estimated economic benefit of $3.6 billion over two decades (ACIL Allen Consulting 2017). The New Zealand Plant Breeders Research Association (NZPBRA) produces official ratings that enable the direct comparison of different endophyte strains (Caradus et al. 2021). The results are presented using a standardised rating system, providing a clear and practical tool for farmers, researchers, and industry partners to select the most appropriate endophyte strain, balancing animal safety with insect resistance (Hewitt et al. 2021; New Zealand Plant Breeding & Research Association 2025). Each strain and plant cultivar offers benefits depending on environmental conditions and insect pressure, yet no single animal-safe endophyte has been found that effectively protects against all major pasture pests.

An important factor in successfully utilising *Epichloë* endophyte technology is maintaining endophyte viability during seed storage. These symbiotic fungi are sensitive to environmental conditions, with their survival significantly reduced by high temperatures and humidity (Tian et al. 2013). Even under standard ambient storage, viability can decline sharply within six months. To preserve endophyte integrity, seeds must be stored in cool, dry conditions, ideally below 5°C and at relative humidity levels under 60% (Rolston et al. 1986).

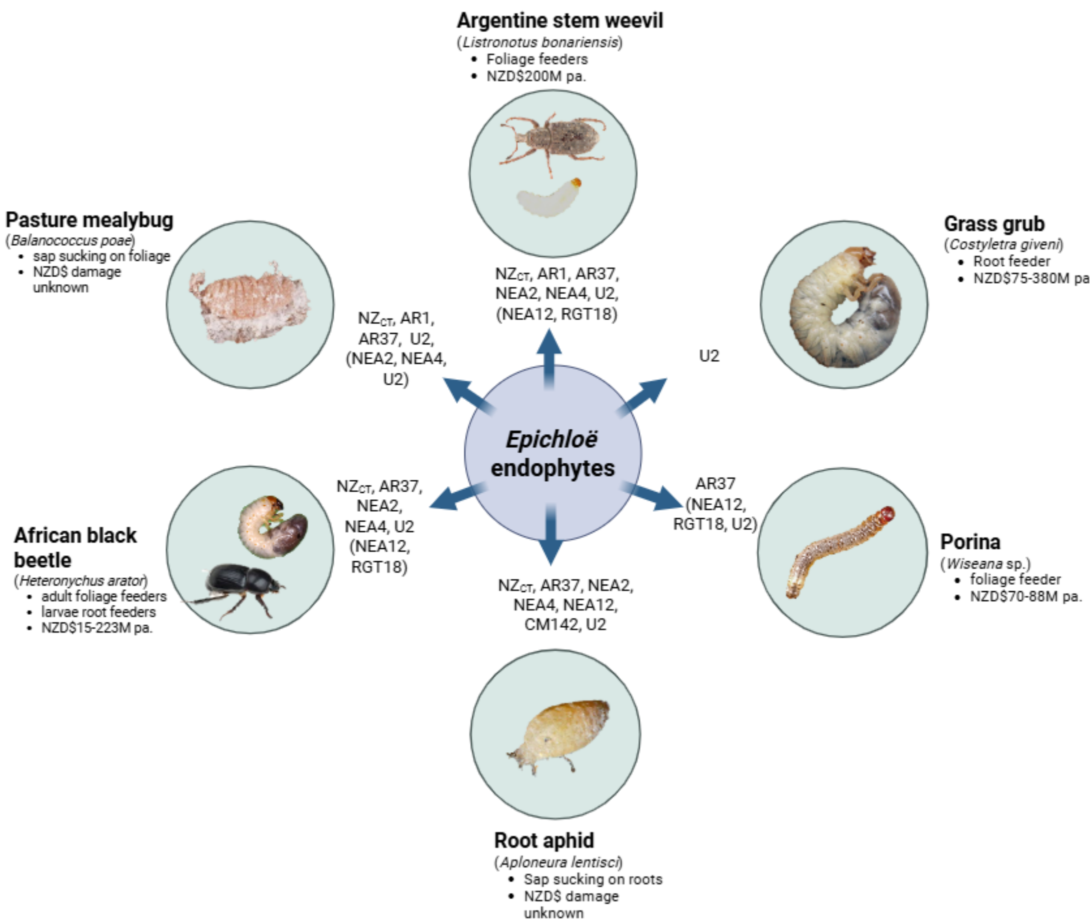

Figure 1 Description of the six major insect pests of perennial ryegrass in New Zealand, their impacts, and the commercial *Epichloë* endophytes in perennial ryegrass (NZ_{CT}, AR1, AR37, NEA2, NEA4, NEA12, RGT18, CM142) and Festulolium (U2) that mitigate these pests. Endophyte strains in brackets are provisional results and require further testing to support rating according to the protocols of the New Zealand Plant Breeding & Research Association (2025).

Table 2 Known alkaloid profiles of commercialised *Epichloë* endophytes in perennial ryegrass and Festulolium hybrids.

Alkaloid group	Alkaloid	*Epichloë* strains								
		NZ_{CT}	AR1	AR37	NEA	NEA2*	NEA4	Edge	Happe	U2
Pyrrolopyrazine	Peramine	high	high	-	low	low/me-dium	medium/low	medium	-	-
Indole diterpenes	Lolitrem B	high	-	-	very low	medium	very low	-	-	-
	Epoxyjanthitrems	-	-	high/medium	-	-	-	-	-	-
Ergot alkaloids	Ergovaline	high	-	-	low	medium	medium	-	-	-
Lolines	NFL, NAL, and NANL	-	-	-	-	-	-	-	medium	medium

*NEA2 is a mix of multiple endophyte strains (Eady 2021)
NZ_{CT} is the New Zealand common-toxic strain

Endophytes in a changing environment

As New Zealand faces the increasing challenges of climate change, such as more frequent droughts, extreme weather events, and shifts in insect pest dynamics, the relationship between pasture grasses and *Epichloë* endophytes is inevitably impacted. Adapting endophyte technologies to perform reliably under changing environmental conditions is essential for the sustainability of New Zealand's pasture-based systems.

Environmental conditions directly affect both the host grass and the *Epichloë* endophytes, influencing their interactions with insect pests and overall performance, and competitive ability. In New Zealand, the primary challenge for *Epichloë*-infected perennial ryegrass pastures is the increasing severity and frequency of drought (Reisinger et al. 2010; Macinnis-Ng et al. 2021). This is because perennial ryegrass is particularly sensitive to drought (Matthew et al. 2012). Anecdotally, *Epichloë*-infected perennial ryegrass and fescues tend to perform better in harsh environments and extreme weather events than endophyte-free varieties (Richardson et al. 1992; Thom et al. 2013). Endophyte infection can improve drought tolerance, especially in tall fescue (Swarthout et al. 2009; Nagabhyru et al. 2013), but results in ryegrass are mixed (Hahn et al. 2008; Kane 2011). Endophytes may benefit the grass host by altering root structure, water retention, and biomass, which improves water and nutrient uptake (Richardson et al. 1992; Wäli et al. 2006; Zhang et al. 2011; Nagabhyru et al. 2013; Yin et al. 2014). However, the greatest benefit of *Epichloë* infection to environmental limitations, such as drought, occurs when plants face simultaneous stress from both drought and insect predation. This is because insects can exploit the already weakened state of drought-affected plants. For example, drought conditions lead to increased root aphid populations in both *Epichloë*-infected and endophyte-free perennial ryegrass plants (Hewitt et al. 2023b). Intermittent drought, common in farming environments, raised amino acid concentrations, which in turn increased root aphid populations, adding additional stress to the already weakened plant (Hewitt et al. 2023b). Similarly, ABB feeding intensifies on drought-stressed foliage due to higher nitrogen (N) levels (Hewitt et al. 2023a). However, the severity and duration of drought significantly influence the interactions between grasses, endophytes, and insect herbivores. In the case of sap-sucking insects like root aphids, fitness is expected to decline under prolonged and severe drought conditions. These insects rely on positive plant turgor pressure to extract N-rich phloem sap (Archer et al. 1995), and population growth requires intermittent recovery of turgor, enabling the insects to access these nutrients (Huberty & Denno 2004). Similarly, the feeding intensity of ABB is likely to diminish as extreme drought reduces host plant availability and quality (Hewitt et al. 2023a). In such conditions, plant dieback limits insect feeding and reproduction, thereby reducing pest pressure (He & Dijkstra 2014). However, in drought-stressed plants subjected to ABB and root aphid feeding, *Epichloë* endophyte infection reduced plant damage under combined resource limitation and herbivory (Hewitt et al. 2023b; Hewitt et al. 2023a). These dynamics highlight the critical role of drought severity in shaping herbivore impacts within grass-endophyte systems.

Extreme weather events, including intense rainfall leading to waterlogging, are anticipated to increase due to climate change, which can significantly impact agricultural systems (McFarlane et al. 1989; Frame et al. 2020). *Epichloë* endophytes enhance host plant resistance to waterlogging by actively adjusting the plant's osmotic potential and oxidative balance (Song et al. 2015; Wang et al. 2017). It is to be expected that prolonged flooding and waterlogging will also affect plant-insect interactions. In general, the flooding of grassland reduces invertebrate diversity, abundance, and biomass (Plum 2005). While it is logical to assume that the reduction in invertebrate populations caused by waterlogging would result in less plant damage, the interaction of prolonged waterlogging in *Epichloë* endophyte-infected pastures has yet to be investigated.

Nutrient availability, such as with N and phosphorus (P), will be a growing challenge for future pasture systems. The application of P fertiliser, a finite resource but vital for pasture productivity, is questioned as we face increasing pressure to reduce our environmental impacts and manage costs (Bindraban et al. 2020). Given the established link between P availability and plant growth, it is expected that P also impacts *Epichloë* endophytes and herbivorous insect pests. Increases in P availability can reduce foliar ergovaline concentrations in grasses (Malinowski & Belesky 2000; Graff et al. 2020) and affect other alkaloids, such as epoxyjanthitrems and lolines in root tissue, with total loline levels decreasing as P increases (Hewitt et al. 2024). Conversely, foliar loline concentrations rise with higher P fertiliser input (Hewitt et al. 2025). These changes in alkaloid concentrations appear to be independent of fungal biomass and likely result from shifts in alkaloid synthesis and translocation (Hewitt et al. 2024). Similar to the reduction in P fertiliser input, New Zealand pastures are now subject to a cap of 190 kg N per hectare, as mandated by new legislation on N input. Nitrogen, another essential macronutrient for plant growth, reduces endophyte DNA in perennial ryegrass by stimulating tillering, which leads to the growth of additional tillers that lack endophytes (Rasmussen et al. 2007). A reduction in fungal biomass, as indicated by a reduction in fungal DNA detected, dilutes the concentration of alkaloids, a process further amplified by the increased plant growth induced by N application (Rasmussen et al. 2007). This suggests that farmers may inadvertently be reducing the effectiveness of endophyte cultivars they invested in when applying high levels of N.

Environmental stressors such as nutrient limitation and drought significantly influence plant-insect interactions and the role of *Epichloë* endophytes in grassland systems (Faeth & Fagan 2002; Newman et al. 2003; Ryan et al. 2014; Graff et al. 2020; Hewitt et al. 2023b). Despite changes in nutrient availability or water stress, *Epichloë* endophytes consistently enhance plant resilience under simultaneous biotic and abiotic pressures by supporting herbivore defence, often through the modulation of alkaloid production. Their ability to maintain protective functions under suboptimal conditions underscores their ecological and agricultural value, playing an increasingly important role in sustaining pasture health, productivity, and long-term grassland viability.

The hunt for the 'holy grail'

Theoretically speaking, one of the most desirable host–endophyte combinations is a perennial ryegrass cultivar with high drought resistance that is infected with an *Epichloë* endophyte strain that produces both peramine and lolines. Peramine protects against foliar-feeding pests such as ASW. Meanwhile, lolines are translocated into the root system, providing defence against root-feeding insect pests such as the grass grub, root aphid, and ABB larvae, an advantage that addresses the limitations of other endophyte strains in perennial ryegrass, which typically lack effective root-level protection. This dual-alkaloid strategy would ensure broad-spectrum insect resistance, enhancing pasture productivity while maintaining livestock safety, as both peramine and lolines have no toxicity to grazing animals. While individual endophyte strains are capable of producing either peramine or lolines, no known strain simultaneously expresses both alkaloids at levels sufficient to confer robust protection against both foliar and root-feeding insect pests in perennial ryegrass. Furthermore, introducing loline-producing *Epichloë* strains into perennial ryegrass, typically from fescue species, is complicated by the need for genetic compatibility between host and endophyte (Christensen et al. 1997). While cross-species transfers are possible, they often result in poor transmission and reduced seed viability, limiting their success in commercial breeding programmes (Caradus & Johnson 2020).

Given the absence of a naturally occurring endophyte that produces both peramine and lolines at effective levels, there is growing interest in the potential of genetically modified (GM) *Epichloë*-host associations. Through targeted genetic engineering, it may be possible to introduce or enhance the biosynthetic pathways required for the simultaneous production of multiple protective alkaloids. This approach could enable the development of tailor-made endophyte strains that offer dual protection against both foliar and root-feeding insect pests while eliminating or reducing the risks to livestock and ensuring compatibility with elite ryegrass cultivars. Although still in its early stages, GM endophyte technology may represent a promising frontier in the effort to safeguard New Zealand's pasture ecosystems in the face of increasing pest pressure and climate variability. This technique involves altering an organism's genes by introducing, eliminating, or rearranging specific genes using molecular biology methods. One of the key advantages of gene editing is its ability to introduce new traits and genetic variation that would not be present in the unmodified genome, offering the potential for more precise and beneficial modifications to the host-endophyte relationship. In the case of *Epichloë* endophytes, it may enhance beneficial traits such as insect resistance, drought tolerance, pathogen resistance and alkaloid production, ultimately improving pasture health and livestock welfare. Gene editing technologies, including CRISPR (Clustered Regularly Interspaced Palindromic Repeats), Zinc Finger Nucleases, and TALENs (Transcription Activator-Like Effector Nucleases), provide advanced precision in modifying specific genes (Lee et al. 2019). These methods allow for a fast, efficient and targeted disruption or alteration of genes without incorporating foreign DNA (Veillet et al. 2019; Wolter et al. 2019). Although, the use of gene editing technologies outside of a laboratory setting is currently not available in New Zealand (Ministry of Business, Innovation and Employment 2024), the manipulation of genetic traits has been a common practice over the past decades mainly for horticulture, vegetable and cereal crops (Zhang et al. 2018; Brummer & Wang 2020). Efforts to apply gene editing technology to forage plant improvement have gained momentum in the last decade (Khoshhal Sarmast 2019; Bilal et al. 2025). A comprehensive review of the application of this technology to forage plants, including those for New Zealand pastures, is presented in Caradus (2024a). Gene editing may offer the potential to create tailored endophyte strains that address specific challenges in agriculture, making it a valuable tool for future developments in pasture management. However, its wider use and practical application will depend on overcoming technical, regulatory, and societal challenges, as well as the outcome of the New Zealand 2024 Gene Technology Bill (Pers. Comm. John Caradus, Grasslandz Technology Ltd.).

Conclusion

New Zealand's pastoral ecosystems are highly vulnerable to introduced insect pests due to their simplified grass-dominant pastures with limited natural enemies. The arrival of new pest species can have devastating consequences on pasture productivity and, ultimately, the national economy. In this context, *Epichloë* fungal endophytes are not just a valuable tool but an essential component of current and future pasture systems. Their ability to enhance plant resilience against insect herbivory and environmental stress makes them a cornerstone of sustainable pasture management. For New Zealand to maintain a productive, resilient, and economically viable pastoral sector, the integration of *Epichloë* endophytes must be prioritised in both breeding programs and farm management strategies. This is especially important as climate change and environmental resource limitations continue to challenge New Zealand pasture systems. Gene editing may offer a tool to develop tailored grass-*Epichloë* associations with improved pest resistance and reduced livestock toxicity, potentially addressing the limitations of current strains. Its future use in New Zealand agriculture will likely depend on regulatory developments and broader societal acceptance.

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