The importance of endophyte in agricultural systems - changing plant and animal productivity

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Abstract

Infection of tall fescue and ryegrass pastures with *Neotyphodium* endophytes are of much greater interest in New World pastures than in Europe where they have been present as long as agriculture itself. This paper presents an overview of the importance of endophyte infection in pastures, enhancing the productivity and persistence of their hosts, both directly and through protection from invertebrate pressure, the biological factors behind this importance and the measures available to profit from the advantages of endophyte infection while palliating the negative effects.

Keywords: tall fescue, ryegrass, livestock, edaphic stress, invertebrate pests

Introduction

The initial interest in *Neotyphodium* endophytes in grasses focused on intensively managed pastures of tall fescue (*Festuca arundinacea*) and perennial ryegrass (*Lolium perenne*). Study of meadow fescue (*F. pratensis*) (Gams *et al.* 1990) and Italian ryegrass (*L. multiflorum*) (Latch *et al.* 1988) came later, while research on adventitious grasses has intensified in parallel to the interest in agricultural species (Faeth *et al.* 2004; Pan & Clay 2002). It is immediately interesting that the intense interest in ryegrass and tall fescue began (and largely remains) in the New World, where these species are relatively recent introductions.

Perennial ryegrass is identified as a grass that has specifically evolved as adapted to the intensive grazing associated with domesticated livestock, and spread across Europe with farmers and their animals (Balfourier *et al.* 2000). Tall fescue is closely related to it (Darbyshire & Warwick 1992; Jenkin 1933), and their respective endophyte symbionts are regarded as more recently evolved than those of the annual ryegrasses (Moon *et al.* 2000).

Tall Fescue and Perennial Ryegrass in Intensive Livestock Agriculture

The establishment of a widespread tall fescue grazing resource in USA is credited to the development of the cultivar ‘Kentucky 31’ (Ball *et al.* 1993). This one source accounts for the tall fescue that spread in the second quarter of C20th across huge areas in south-east and central west USA, much of which had soils severely degraded by intensive row cropping. These pastures were (are) intensively infected with endophyte, accounting for the toxicosis that became a growing concern (Bush & Buckner 1973; Yates 1962) and probably also for the difficulty faced by plant breeders in producing improved cultivars that could match ‘Kentucky 31’ in robustness and persistence.

With the identification of endophyte (*N. coenophialum*) as the source of the toxins responsible for fescue toxicosis (Bacon *et al.* 1977), “Fungus-free Fescue” was promoted as a safe forage and the answer to the limitations of livestock productivity on fescue pastures. This soon proved to be a false hope as farmer experience and research results (Read & Camp 1986) established that the robustness and persistence that were the hallmarks of fescue pasture had been lost (Ball *et al.* 1993).

Perennial ryegrass pastures have been widespread in New Zealand (NZ) since the last quarter of C19th and cannot be traced to any one source. Grass seed from the British Isles, including perennial ryegrass, was first sown in early C19th (Stewart 2006) and significant seed imports continued for the rest of that century, from both the British Isles and Australia. Grass seed harvested in the drier regions of Canterbury and Hawkes Bay became a significant source for new pastures from the 1880s. A certified seed system became operative from 1929, after superior locally grown sources were identified (Levy & Davies 1929), and an improved bred strain of perennial ryegrass became available from 1930. This was continually reselected and improved, accounted for a large proportion of seed used in NZ for the next four decades, and was infected with endophyte. Most old ryegrass pastures in NZ are intensively infected with endophyte (Latch & Christensen 1982; Widdup & Ryan 1992).

As for tall fescue, when *N. lolii* was identified as responsible for ryegrass staggers (Fletcher & Harvey 1981), it was proposed that endophyte-free ryegrass would end the problem. This was not tried on-farm, as within months it was shown (Prestidge & Gallagher 1988; Prestidge *et al.* 1982) that endophyte provided protection against Argentine stem weevil (*Listronotus bonariensis*), which at the time was probably the highest profile pasture pest in NZ.

The interest in Argentine stem weevil had been heightened by farmer experience and research that closely-related ryegrass cultivars differed radically in their tolerance of this pest (Kain *et al.* 1982). It was soon shown that while nucleus seed of both cultivars was infected with endophyte, the percentage infection of seed found in commerce differed significantly, reflecting their commercialisation history. Hindsight then showed there had been a history of new cultivars carrying a high frequency of infection, and remaining that way while demand ran ahead of seed supply, so that seed was cleaned and sold within weeks of harvest. Once initial demand was satisfied, seed began to be held over at least a year, and endophyte infection declined. Infrequent multiplication of high-grade seed and use of old high-grade seed exacerbated the problem (M.P. Rolston, pers. comm.). Subsequent new cultivars, with high levels of infection, were then compared with controls carrying lower levels, and appeared artificially good.

Later studies have identified several other invertebrate herbivores that can severely affect endophyte-free ryegrass in NZ, but which are deterred by endophyte-infection (Pennell *et al.* 2005; Popay & Bonos 2005; Prestidge *et al.* 1994). Further, endophyte toxins deter grazing ruminants (the toxicoses regarded as the down-side of endophyte-infection), so that infected grass is grazed less intensively (less frequently and not as close to the ground and the leaf meristems) than infected swards (Edwards *et al.* 1993). Infected swards are thus protected from debilitating over-grazing.

Endophyte and Ecological History

Tall fescue pastures in USA and ryegrass pastures in NZ are probably typical of the situation elsewhere in the New World. In

Australia, endophyte infection is widespread in ryegrass pastures (Cunningham *et al.* 1993; Reed *et al.* 2005), although there is not usually the immediate pest-driven collapse of endophyte-free pastures sometimes seen in NZ.

Results from Europe are different. Some studies have found little endophyte, and when endophyte is reported as significantly present (Oliveira & Castro 1997), frequency is typically lower than found in NZ (Widdup & Ryan 1992). Some studies have found no advantage to endophyte-infected plants or swards while others have found modest advantages (Lewis *et al.* 1997; Ravel *et al.* 1995).

The situation of perennial ryegrass in Europe is a long-established equilibrium, as old as agriculture in that continent (Balfourier *et al.* 2000), in climate and soil zones to which it is adapted, and with buffered impact of invertebrate pests. In temperate northern Europe, where ryegrass monocultures are established, the climate and management regimes are very non-stressful for ryegrass, and in regions where climate is more stressful, the swards tend to be more complex mixtures. Frequency of endophyte infection in old European perennial ryegrass swards has been related to edaphic stress (Lewis *et al.* 1997; Ravel *et al.* 1997a), but not to the extent that infected swards persist while newly-sown endophyte-free swards collapse within 2 years. In NZ, there is, in many situations, a near mono-culture of ryegrass and an invertebrate fauna in which some pests enjoy little natural control so that they can quickly destroy an endophyte-free sward. Endophyte, present in perennial ryegrass seed imported from Europe, has greatly increased in infection frequency under these selective pressures. Where the biological control agent against Argentine stem weevil (*Microctonus hyperodae*) has successfully established, the advantage of endophyte-infected ryegrass has become less obvious (Barker & Addison 2006; Goldson *et al.* 1995).

Some pasture pests have been identified as deterred by endophyte in tall fescue, but most authors attribute the greater persistence and productivity of infected swards in USA to enhanced tolerance of edaphic stress (Malinowski *et al.* 2005; Read & Camp 1986). Different experiments have associated tolerance of water stress with a number of mechanisms such as leaf rolling, stomatal closure, osmotic adjustment, accumulation of sugar alcohols and phyto-hormone status (Bacon 1993; Elbersen & West 1996; Richardson *et al.* 1992; Richardson *et al.* 1993; West *et al.* 1993). Greater tolerance of sub-optimal soil nutrient status has also been documented (Malinowski *et al.* 2000). There has been less European work on tall fescue endophyte than for ryegrass, but it is clear that endophyte-free tall fescue is widely regarded as robust in pastures. Perhaps summer-active tall fescue is being used in USA in zones with greater summer temperatures and drought stress than are encountered in non-Mediterranean Europe. In the Mediterranean region, grasses in old swards are summer-dormant.

The pastures of the New World thus expose tall fescue and perennial ryegrass to edaphic stress and pest attack at greater intensity than typically encountered in the longer-established situations in Europe. In many respects, the incidence and impact of endophyte in tall fescue and perennial ryegrass pastures in Europe is more similar to that of natural ecosystems, where ecological advantage is less immediately evident (Faeth 2002), than to the managed pastures of the New World.

Growth and Productivity of Pastures

As noted above, endophyte-infected swards in NZ and USA have been shown to sometimes offer radically greater persistence and productivity than endophyte-free controls. In NZ ryegrass swards this is usually associated with invertebrate pest activity. Endophyte-free swards sometimes collapse under pest pressure (Barker *et al.* 1984), and even without total death, productivity is affected. In a network of trials over six sites, herbage yield of endophyte-infected ryegrass was greater than that of endophyte-free controls. In summer and autumn the mean difference over 3 years was 20 and 30% respectively (Popay *et al.* 1999). The usual outcome of insect pressure is that the sward component that is endophyte-infected, even if initially small, increases and becomes dominant (Francis & Baird 1989; Hume & Brock 1997). The instability of endophyte-free pastures, contaminated and then moving quickly to infected status, is a feature of both ryegrass and tall fescue (Hume & Barker 2005).

Direct enhancement of ryegrass growth and tolerance of edaphic stress has been documented (Latch *et al.* 1985; Ravel *et al.* 1997b), but while frequency of endophyte infection in ryegrass has been related to edaphic stress in France (Lewis *et al.* 1997), the effect of invertebrate pests is the over-riding effect in New Zealand, and is difficult to eliminate from experiments. There have been reports that in the absence of any invertebrate pest pressure, endophyte-infection may impose a cost on the host plant (Keogh & Lawrence 1987), but there is no evidence that such a cost is ever a factor in a field situation. There is evidence of poor clover performance associated with high endophyte frequency in the ryegrass component of a sward, with some data suggesting a direct effect not accounted for by grass vigour (Sutherland & Hoglund 1989). If such an effect could be substantiated, farmers in mild regions with minimal invertebrate pest pressure (such as in the south of NZ) might be better using endophyte-free swards. However, this proposed advantage to endophyte-free swards has not been substantiated on a field scale (Eerens *et al.* 1998).

In NZ, endophyte-free tall fescue usually persists, but does sometimes succumb, particularly under pressure from African black beetle (*Heteronychus arator*), and research has shown significant persistence and yield advantages associated with infection (Cooper *et al.* 2002; Easton & Cooper 1997). Tall fescue pastures in USA have usually proved non-viable without endophyte infection (Read & Camp 1986), particularly in the South. Where milder temperatures or very careful management succeeds in maintaining persistence, yield is affected. Endophyte infection makes a large positive contribution to herbage available to livestock from tall fescue pastures.

Toxicoses

Tall fescue has long been known to be toxic (Cunningham 1948) and the physiology of toxicosis has been intensively researched (Oliver 1997; Oliver 2005; Spiers *et al.* 2005). The most evident physiological effect is the disruption of the animals' thermo-regulatory control, and most health and productivity effects can be ascribed to this. Ergopeptine alkaloids are the active factors responsible (Yates *et al.* 1985), but whether the primary products present in herbage or derivatives of them are directly involved is not yet clear (Hill *et al.* 2001). Minor components present in herbage may specifically contribute (Gadberry *et al.* 1997).

Productivity losses associated with tall fescue toxicosis have been well documented (Thompson *et al.* 1993). A summary of ten trials in different states of USA showed a mean 37.5% loss in liveweight gain on endophyte-infected tall fescue (Schmidt & Osborn 1993). Grazing intake is depressed in affected animals, and in some trials this effect is enough to account for productivity impacts (Schmidt & Osborn 1993).

Research has documented more than 40% impairment in fertility (Gay *et al.* 1988), and 60% in milk production (Hemken *et al.* 1979). Animals occasionally die. "Fescue foot" is a severe effect, requiring the immediate slaughter of affected animals. The effects on pregnant mares (Cross 1997) can be appalling.

Ryegrass staggers, first observed in the 1880s, has been clinically described, and a quantitative scale developed for research comparisons (Keogh 1973). An early suggestion associating ryegrass staggers (and tall fescue toxicosis) with *Neotyphodium* endophyte was discounted (Cunningham 1958). After the association with ryegrass endophyte was established (Fletcher 1982; Fletcher & Harvey 1981), the primary active factor, lolitrem B, was described (Gallagher *et al.* 1984).

Further research showed that clinical ryegrass staggers were not the only negative effect on livestock. Liveweight gain, herbage intake, body temperatures, respiration rate, faecal moisture content and, in sheep, the accumulation of faecal contamination (and associated fly-strike) are all affected (Easton & Couchman 1999; Fletcher *et al.* 1999; Reed *et al.* 2005; Watson *et al.* 1999). There has been one report of severe effects on lamb survival (Cunningham *et al.* 1993). Ergovaline was shown to be present in infected ryegrass herbage, not at the concentrations documented for tall fescue, but in the range to be physiologically active (Easton *et al.* 1993; Rowan & Shaw 1987).

Dairy cows are less often visibly affected by ryegrass staggers than sheep, and in several short-term comparisons (Thom *et al.* 1999) there was little evidence of impaired milk production. However, studies through whole seasons have shown effects up to 15% over a full lactation, and of 20% or more in late summer and autumn (Bluett *et al.* 2005; Bluett *et al.* 2003; Ussher 2003). A recent intensive trial with controlled feeding has also shown impairment of milk production (Thom 2007).

A number of veterinary reports from northern NZ (Brookbanks *et al.* 1985) describe heat stress in cattle similar to fescue toxicosis. This did not appear to be associated with the presence on farms of adventitious tall fescue (Kearns 1986), and it was argued that ergovaline in ryegrass pastures could account for the symptoms (Easton *et al.* 1996). However, endophyte status of ryegrass has not affected body temperatures or incidence of heat stress in controlled experiments with cattle (Bluett *et al.* 2005; Easton & Couchman 1999).

On farms, ryegrass staggers can vary from an irritant, impeding efficient movement of animals, to catastrophic episodes making normal farm operations impossible (Milne *et al.* 1999). In Australia there have been documented episodes of widespread livestock death from ryegrass endophyte toxicosis (Cunningham *et al.* 1993; Reed *et al.* 2005).

While most research and experience is with herbage grazed *in situ*, there have been many documented cases of ryegrass and fescue toxicosis arising from the consumption of hay made from endophyte-infected herbage. Ergovaline and lolitrem persist in dried and ensiled herbage (Clark *et al.* 1996; Fletcher 2005; Hume *et al.* 2007; Roberts *et al.* 2002). However, activity does decay with time, particularly for ergovaline, so that hay can be stock-piled if necessary. Hay is used away from farms, and expensive horses and zoo animals (Bluett *et al.* 2004; Essen *et al.* 1995) have been affected with ryegrass staggers.

Concentrations of toxins in infected herbage varies through the season (Fletcher *et al.* 2000b; Reed *et al.* 2001), with the part of the plant and thus in the pasture profile (Keogh & Tapper 1993; Musgrave 1984), and with the genetics of the host (Agee & Hill 1994; Easton *et al.* 2002). Plant status of nitrogen and other nutrients also affects toxin concentrations. Controlled experiments have documented depression of toxin concentrations at higher levels of nitrogen nutrition (Hunt *et al.* 2005; Rasmussen *et al.* 2007) that could not be accounted for by dilution effects, but increased concentrations with application have also been reported (Lane *et al.* 1997), and higher concentrations of mycelium in leaf were associated with urine patches (Keogh 1986), which were also more intensively grazed. This multi-dimensional variation makes toxin levels and toxicosis outbreaks difficult to predict. Toxin intake by livestock can not be tightly controlled, but grazing management that avoids sustained grazing into old tissue close to the ground, and encourages fresh regrowth without excessive nitrogen peaks will reduce the risk of exposure (Fletcher 2005).

Endophyte and the Seed Industry

The discovery of the importance of endophyte, and then of the influence of seed harvest and management practice on endophyte viability (Hare *et al.* 1990; Rolston *et al.* 1986; Welty *et al.* 1987) had immediate implications for the seed industry. An early response was to add value to inventory by delivering seed to defined specification, with either high or very low incidence of endophyte infection according to the need of a market niche. Seed industry partners have been essential contributors in delivering to market selected endophyte strains with known properties, and have upgraded seed stand agronomy, harvest and cleaning practice and inventory management (Green & McKenzie 1999; Rolston & Agee 2007). In USA, one company has been primarily responsible, but in NZ, all proprietary herbage seed companies have been involved.

An associated industry handles and markets straw from ryegrass and tall fescue seed stands (including straw from turf grass cultivars). Ergovaline and lolitrem B persist in straw, and their presence negatively affects the value of this by-product (Miyazaki *et al.* 2001; Stamm *et al.* 1994; Welty *et al.* 1994).

Selected Endophyte

Development of endophyte strains that do not produce alkaloids toxic to livestock was first proposed by Latch (Latch 1989; Latch 1994), and identification of selected strains and their release to livestock farmers through the seed industry have been discussed at earlier Symposia (Bouton & Easton 2005; Fletcher & Easton 1997; Fletcher & Easton 2000). The advantages in health and productivity of livestock grazing herbage infected with selected endophyte in research trials have been well documented (Bouton *et al.* 2000; Bouton *et al.* 2002; Fletcher 1999; Fletcher *et al.* 2000a; Fribourg *et al.* 2002; Parish *et al.* 2003a; Parish *et al.* 2003b; Watson *et al.* 2004). These strains have also proved to be good research tools, allowing determination of the negative effects accumulated over time of the toxic strains typically present in pastures. Such longer term studies were difficult to achieve using endophyte-free controls.

On farm, results have been excellent. Use of Max-Q® in USA has been constrained by the small size of many herds and the fact that many farmers rely on off-farm income, so that they are risk-averse. Nevertheless, many thousands of acres of toxic tall fescue have been converted to Max-Q pastures, with regular repeat orders as areas on individual farms are extended. All this contributes to profitability. In NZ and Australia, sown tall fescue pastures have historically been endophyte-free (Easton *et al.* 1994), but the persistence and yield advantages of infection with selected endophyte are already attracting farmers and are expected to greatly extend the value of tall fescue in these markets (Cooper *et al.* 2002; Wheatley *et al.* 2003).

AR1 endophyte (producing peramine but not ergovaline or lolitrem B) accounts for most endophyte-infected proprietary perennial and hybrid ryegrass cultivars sold in NZ. Any displacement of AR1 is by alternative selected endophyte strains that are more recently available (Hume *et al.* 2004). AR1 provides less robust protection against black beetle than commonly occurring toxic endophyte in northern NZ (Popay & Baltus 2001), so that options for improvement are actively sought. In fact, AR1 pastures have proved to be more robust on farm than was expected, and uptake has been comprehensive, even in the north of the country where insect pressure might have compromised its success. In Australia too, uptake of ryegrass infected with selected endophyte has been excellent and continues to grow (Evans 2007).

Just as the seed industry has adapted practice to deliver selected endophyte to specification (see above), livestock farmers have had to adapt their practice. Seed can not be stored for months on farm, delivery needs to be immediately prior to sowing. Protocols for preparing fields for sowing, and managing young pastures to properly kill the old sward and avoid contamination with infected plants have been developed (Bluett *et al.* 2001; Hume 1999) and actively promoted. Care needs to be taken not to feed out hay from another source onto pasture infected with selected endophyte. Livestock free of the effects of toxicosis will graze closer to the ground (Edwards *et al.* 1993) so that farmers need to exercise care to avoid over-grazing.

However, the evidence suggests that while AR1 has successfully displaced toxic endophyte from new pastures sown, its availability has not persuaded farmers to replace old pastures if they were not going to do that as part of normal farm practice. It is estimated that only 5% of NZ pasture is replaced per year. Ryegrass pastures that can be readily cultivated are only a part of the remaining 95% (Field 1989), but even allowing for that, the NZ farming industry is well short of achieving the readily available potential gains from freeing livestock from the pernicious effects of endophyte toxins.

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