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Genetic origins of perennial ryegrass (*Lolium perenne*) for New Zealand pastures

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Abstract. New Zealand perennial ryegrass germplasm originated largely from seed introduced from the UK during the 1800s. Modern breeding began in the 1930s and soon utilised selections from the best ecotypes as "mother" seed for the seed industry and after numerous reselections this resulted in the release of Grasslands Ruanui 1955. Winter growth was improved by hybridising with Italian ryegrass to produce the "short rotation hybrid" cultivar Grasslands Manawa, released in 1943. Further introgression to perennial ryegrass led to the development of Grasslands Ariki "long rotation hybrid", functionally a perennial, released in 1965.

The identification of a valuable ecotype from the Mangere district in Northern New Zealand in the late 1960s had a substantial impact on ryegrass breeding in New Zealand and has subsequently been widely used in all Australasian ryegrass breeding programs. Germplasm from mild oceanic regions of North West Spain, collected in the 1980s, has provided a valuable combination of winter growth with late flowering behaviour. This has been used in many recent breeding programs.

Considerable research has gone into endophytes of ryegrass to develop safe and persistent pastures. The lack of chemical diversity within endophytes of New Zealand ecotypes has required considerable sourcing of overseas germplasm for endophyte discovery. In recent years breeders have introgressed a wider range of germplasm, including winter active Mediterranean material, cold tolerant Northern European material, as well as Italian ryegrass and meadow fescue. Tetraploid perennial ryegrass cultivars have been released in the last 20 years, based largely on New Zealand diploid cultivars but also using some European tetraploids. Today a full range of cultivars from early flowering diploids to late flowering tetraploids is available to the farming industry.

The use of a wider range of germplasm is discussed in relation to advances in our knowledge of genetic origins of perennial ryegrass. Genetic advances should be achievable from more diverse germplasm by using a combination of traditional breeding techniques and new technologies, such as marker assisted selection. However, lifting overall pasture performance still remains a challenge as ryegrass cultivars are used in mixtures with white clover and any increase in the ryegrass yield is often partially cancelled by decreased clover yields.

Initial Introductions and Strain Identification

British immigrants first introduced perennial ryegrass, along with other pasture species, to New Zealand before 1820. Seed for pasture establishment continued to be introduced as part of the general trade with Britain for 60 or more years until sufficient seed began to be harvested locally. Most seed imported from Britain is likely to have originated from those areas where commercial harvesting of seed was common such as Ireland, Ayrshire and Devon, although small quantities of seed may have also originated from the Netherlands, Denmark and France. Trade with Australia and other colonies would have resulted in grass seed of similar origins.

Much of this material was likely to have been early free-flowering types typical of the numerous naturalised ecotypes (Forde & Suckling 1980, Burgess & Easton 1986) although it is likely that some later flowering material was also imported.

By the 1880s New Zealand had developed a local trade and even a small export trade of ryegrass seed. Imports decreased in importance such that by 1912 most seed used in New Zealand was locally produced (Cockayne 1912).

Although it had been recognised that strains of ryegrass differed in performance, few experiments were carried out before 1896. Over the next 30 years a number of experiments showed that local ecotypes that had developed in the permanent pasture regions of New Zealand were superior to British and European commercial lines and to “false perennials” commonly sown and harvested in the cropping districts (as outlined in the reviews by Corkill 1958, Rumball 1983, Easton 1983 and Burgess & Easton 1986). Further experiments over the next 60 years have continued to note the poor performance of overseas cultivars in New Zealand (McLeod 1974, Rumball & Armstrong 1975, Lancashire *et al*. 1979).

As a result of the recognition that seed harvested from older perennial pasture resulted in persistent perennial ryegrass Government Seed Certification Scheme was introduced in the 1920s to certify seed originating from older pastures. This scheme was one of the first in the world and later extended to include cultivars originating from plant breeding programs. This not only ensured that farmers had a reliable source of persistent ryegrass genetics but it would also have maximised the chance for seed containing viable endophyte.

Although the effects of endophyte (*Neotyphodium lolii*) were not known at that time, it is likely that its presence in ryegrass was as important for persistence then as it is today. Argentine stem weevil (*Listronotus bonariensis*) was documented in New Zealand as early as 1927 (Marshall 1937) and its presence would have ensured that the persistent ecotypes contained endophyte (Burgess and Easton 1986). However, Argentine stem weevil was probably in New Zealand much earlier as molecular evidence suggests that it came from Uruguay, probably as a result of the practice of purchasing hay to feed horses during earlier shipping voyages from Britain (Williams *et al*. 1994).

Early Plant Breeding prior to 1960

By 1930 it was recognised that considerable variation existed in material collected from old pastures and that it was possible to select superior types. The first perennial ryegrass cultivar was based on selections among the best ecotypes which had developed in old pastures in Hawke's Bay and Poverty Bay (Levy 1932). The breeders then released this “mother” seed as the basis of Seed Certification. By the late 1930s most seed was “New Zealand pedigree”, early flowering, leafy and persistent. Although modified and reselected repeatedly over many years this material eventually formed the basis of Grasslands Ruanui in 1955.

<u>Improved Seasonal Growth</u>

In an innovative bid to improve winter growth beyond that of the original introductions, Corkill (1945) developed hybrids of the best local *Lolium perenne* and the more winter active but shorter lived *Lolium multiflorum* to create a “short rotation” cultivar known as “H1”, released in 1943 and later renamed Grasslands Manawa. This resulted in useful amounts of winter growth and a cultivar that persisted for 2-4 years. Later Corkill backcrossed H1 to *L. perenne* to develop the long rotation ryegrass cultivar Grasslands Ariki released in 1965. This exhibited improved winter growth over *L. perenne* but also exhibited a persistence approaching that of *L. perenne* (Barclay 1963). Although certified as a "hybrid ryegrass" (*Lolium boucheanum*) it was functionally used as a perennial.

These so called "hybrid" cultivars were the first attempt to increase cool season growth of New Zealand cultivars to a level compatible with New Zealand's mid latitude mild oceanic climate.

Germplasm Introduction

Considerable germplasm has been introduced since the early colonial introductions, mainly of commercial material, and the results generally confirm the observations of Saxby (1934), Rumball & Armstrong (1974) and Lancashire *et al*. (1979). They conclude that imported northern European germplasm is not well adapted to New Zealand, lacking winter growth and often exhibiting susceptibility to crown or stem rust (*Puccinia coronata* and *P. graminis*). Similarly, Mediterranean germplasm often exhibits high winter growth potential but is usually not well adapted to New Zealand's mild moist climates. However, the genetic potential of many introduced lines has potentially been unfairly biased by lack of endophytes.

Overseas germplasm may potentially possess useful genes for crossing with local material. Mediterranean material has been crossed with local germplasm to capture this improved winter growth in a range of pasture species (Barclay 1959), although it is only since the 1980s that breeders have used this approach with *L. perenne.*

Breeding from 1960-1980

The 1960s saw the identification of a valuable new ecotype from the T. R. Ellett's farm in Mangere, Auckland. This resulted in the cultivars Grassland Nui (Armstrong 1977) and Ellett perennial ryegrass. Although endophyte effects may have been complicated early comparisons this ecotype has formed the basis of many cultivars well adapted to the North Island. The Mangere ecotype features suggest introgression from *L. multiflorum* consistent with a derivation from old "colonial" pastures based on mixtures of perennial and Italian ryegrasses.

The Mangere material differs from the previous Ruanui type material by having more winter growth, a higher proportion of reproductive tillers (Bahmani *et al*. 2002, 2003), greater crown rust resistance but often a greater susceptibility to stem rust. Occasionally during this period the cultivars S23 and Vigor (Melle) were introduced from Europe, to fill the then small niche for late flowering varieties. However, their performance was compromised due to lack of endophyte and poor winter growth.

Breeding from 1980-2005

Since the 1980s ryegrass breeding has expanded as commercial breeders have become involved. Although endophyte presence may have slowed breeding progress breeders have explored a wider range of germplasm and now have access to more international germplasm.

Well adapted New Zealand pasture ecotypes continue to provide the basis for many new cultivars (Burgess and Easton 1986, Widdup & Ryan 1992). Indeed the plants surviving after a number of years in pastures sown with newer cultivars will continue to provide a valuable source of adapted material for breeding in the future.
A valuable source of germplasm from North West Spain was recognised during the late 1970s. This region has mild winters, similar to parts of the North Island of New Zealand and moist summers. The material from this region exhibits the unusual combination of winter activity, late flowering, low vernalisation response and excellent crown and stem

rust resistance. Initially this material was used, along with selections from Grasslands Nui, in the cultivar Grasslands Impact.

In 1986 a collection expedition to Spain, France and Italy was carried out to expand the genetic resources available to New Zealand (Forde & Easton 1986) and many breeders have used germplasm collected from North West Spain in recent breeding programs. For example, Tolosa, Arrow and the tetraploid Banquet derived from Grasslands Impact.

Although direct introductions of germplasm can seldom be used as cultivars in their own right the introgression of germplasm into cultivars can be valuable. Spain has provided a valuable source of aluminium tolerance utilised in the cultivar Kingston (Bennet & Stewart 1999). Meridian has utilised Australian material from naturalised Kangaroo Valley ecotypes. The cultivar Pacific utilised material from Spain and Italy along with some from Ruanui. *Festuca pratensis* has been introgressed into the cultivar Matrix.

The cultivar Aberdart bred for high water soluble carbohydrate in the UK has recently been imported. Its seasonal growth pattern is typical of UK and European material in having minimal winter growth in New Zealand. Although higher water soluble carbohydrate are exhibited in the UK, its inconsistent expression in the warmer conditions of New Zealand and Australia fail to compensate for its lower winter yields and lack of endophyte (Smith *et al*. 1998, Parsons *et al*. 2004). However, the presence of this cultivar has stimulated research on breeding of adapted cultivars aimed at improving nutritional benefits to New Zealand farming systems, but as yet it remains unclear whether the factors required are higher water soluble carbohydrates or some other parameter.

<u>Endophyte</u>

In the early 1980s, much of the understanding about perennial ryegrass improvement was challenged by the discovery of the crucial role played by the endophyte (*N. lolii*) in the persistence and pest tolerance of perennial ryegrass (Easton *et al*. 2001). The complicating factor of differing endophyte levels in seed lots is likely to have been a significant complicating factor in reducing genetic progress in ryegrass breeding (Woodfield 1999).

A sheep performance experiment comparing selections from the cultivar Ariki made for high and low cellulose resulted in the unexpected finding that the high cellulose selection outperformed the low (Lancashire & Ulyatt 1975). Many years later when the seed was tested it became clear this was the result of endophyte differences.

Cultivar performance experiments can easily be confounded by endophyte effects and one of the first published indications where endophyte effects were monitored was by Kerr (1987). As a result of these confounding effects all cultivar comparisons today monitor endophyte levels to ensure results are not confounded by uncontrolled plant – endophyte interactions.

The dilemma with the naturally occurring endophyte in perennial ryegrass in New Zealand is that although it conveys resistance to some important insect pests (Easton *et al.* 2001), it also causes the debilitating stock disease 'ryegrass staggers' as well as other problems such as reduced animal liveweight gain and milk production (Fletcher *et al*. 1999). These effects were due to a range of alkaloids produced by the plant-endophyte association. Over 20 years of research has resulted in an endophyte strain AR1 that lack the alkaloids responsible for animal health problems but which contain the insect deterrent alkaloid peramine. This alkaloid is capable of providing the plant with significant resistance to at least two important insect pests, Argentine stem weevil and pasture mealy bug (*Balanococcus poae*), which can reduce plant persistence throughout most of New Zealand. However, some insects such as black beetle (*Heteronychus arator*) and root aphid (*Aploneura lentisci*) are not controlled by the AR1 endophyte. Other endophytes, such as AR37, are likely to be commercialised in the future to control these pests (Popay & Bonos 2004).

The search for endophytes with useful alkaloid profiles, such as AR1 and AR37, required a examination of European ryegrass collections as endophytes from local pasture collections exhibited little chemical variation (Tapper pers. comm.). Local endophytes group together strongly with British strains in relationships studies (van Zijll de Jong *et al*. 2005). This limited variation in endophytes reflects the historical practice of importing seed from Britain rather than from more diverse European sources. It also implies a limited genetic diversity in ryegrass naturalised within New Zealand. Indeed, Casler (1995) found New Zealand ryegrass accessions to be less variable than many European accessions and considerably less variable than those from the Eastern Mediterranean.

<u>Tetraploids</u>

Tetraploids were first explored in both perennial and annual ryegrass in New Zealand by Corkill (pers. comm.) in the late 1950s. This resulted in the release of the tetraploid annual Grasslands Tama in 1968 but it was not until the 1980s that the “long rotation hybrid” cultivar Grasslands Greenstone, based on the diploid Grasslands Ariki, was commercially released. Since then a number of perennial and “hybrid” cultivars have been released such as Nevis, Horizon, Banquet, Quartet and Sterling but it is only in the last 10 years that these have become used to any extent on farms. Almost all are based on adapted New Zealand diploid material although European material has also been used in the cultivar Sterling. The cultivar Quartet is derived from a late flowering diploid ecotype discovered in old pastures in the North Island (Norriss pers. comm.).

Genetic Progress and Breeding

Advances in perennial ryegrass breeding within New Zealand have taken place on many fronts, including yield, seasonal growth, disease resistance, endophytes, flowering behaviour and development of tetraploids. Estimates of the genetic progress for annual yield are between 0.25 and 1.5% per year (Easton *et al*. 1997, 2001, 2002, Woodfield & Easton 2004), a rate comparable with white clover and other crops. However, in practice cultivars are used in mixtures with white clover and any genetic increase in the ryegrass component may partially suppress clovers to limit increases in overall pasture yields.

The development of endophytes safe for animal consumption but which enhance pasture persistence has been of valuable to the New Zealand pastoral industry with benefits estimated to be greater than $74 million per year. Similarly, the combined value of exotic pasture germplasm, largely perennial ryegrass and white clover, used in pasture breeding programs over the last 30 years is estimated to be worth over $735 million a year to the $14 billion pastoral export industries (Lancashire 2005).

Breeders continue to enhance resistance to foliar diseases such as crown and stem rust, despite races continually evolving to overcome such efforts. Increased knowledge of rust races would assist breeding for resistance but molecular studies to clarify rust races are in their infancy (Dracatos *et al*. 2005).

The development of later flowering ryegrasses, such as Grasslands Impact and Quartet, allowing pastures to remain leafy and of higher quality later into the spring has been of value, as have ryegrasses with reduced aftermath heading providing high quality leafy pasture in summer (Woodfield & Easton 2004).

The introduction and increased use of tetraploids has allowed higher animal intakes potentially leading to improved animal performance (Easton *et al*. 2002).

Today a wider range of cultivars and types are on the market allowing astute farmers more management options than previously (Stewart & Charlton 2003).

Potential Germplasm Exploitation

Genetic studies on isozyme variation by Balfourier *et al.* (1998) show that the genetic diversity of *L. perenne* decreases from the Middle-East to the North West part of its range in Ireland and UK. Chloroplast markers suggest that *L. perenne* originated in the Middle East and migrated to Western Europe along both the Danubian and Mediterranean routes (Balfourier *et al*. 2000), most probably with the spread of agriculture in the last 10,000 years.

The patterns of diversity in *L. perenne* in Europe contrasts with those species of non-agricultural origin such as tree species, and other grasses, where migration north from a southern glacial refuge has maximum diversity in southern Europe (Hewitt 1999). A typical example of expansion from glacial refugia is that of *F. pratensis* (Fjellheim *et al*. 2005).

New Zealand has almost exclusively used germplasm from Western European origins, notably UK and Spain. Viewed in light of the migration patterns of perennial ryegrass within Europe it would be expected that the diversity of *L. perenne* naturalised in New Zealand is even lower than that in UK and Western Europe. This expectation is supported by the germplasm study of Casler (1995) and by the limited alkaloid variation in New Zealand perennial ryegrass endophytes.

It is likely that New Zealand can exploit more genetic variation from ryegrasses nearer to the Middle-East. However, capitalising on this new source of variation requires introgression of often poorly adapted germplasm into well adapted material.
In order to incorporate this additional genetic variation from the eastern Mediterranean and Middle-East it will be necessary to obtain further germplasm. Searches of genebank seed collections of perennial ryegrass in Europe, USA, Australia and New Zealand suggest that there are approximately 12000 accessions, although often with considerable duplication. However, a detailed search of these lines suggests that there are less than 50 from the Middle East with perhaps a further 150 from the eastern Mediterranean.

To increase the number of accessions from the eastern Mediterranean, New Zealand public and private ryegrass breeders organised a collection expedition in 2000 to one of the few oceanic climate zones in the region, the south east coast of the Black Sea in Turkey. The seed collected is only now going though quarantine clearance protocols before it can be explored by breeders. Even then it is likely to be at least 10 years before cultivars emerge that incorporate this material.

The use of genes from underutilised *L. perenne* in the eastern Mediterranean and Middle East and introgression from other closely related species should provide New Zealand ryegrass breeders with a valuable pool of new genetics for exploitation in the future. In addition to this germplasm, there should also be considerable potential to introgress genes from *L. multiflorum, L. rigidum, F. pratensis, F. arundinacea* and other closely related species. Introgression of new quantitative trait loci (QTL) alleles from wild relatives could follow the Marker Assisted Selection approach of Fulton *et al*.

(2000) in tomato and Xiao *et al*. (1998) in rice where new and valuable alleles were discovered and introgressed.

Molecular studies should reveal more details on cultivar relationships (Guthridge *et al*. 2001), genetic diversity available in collections and allow more appropriate introgressions into adapted material to enable better utilisation of genetic resources for improving New Zealand ryegrass pastures.

Table 1 Origin of New Zealand diploid cultivars

Diploid Cultivar	**Period of release**	**Hawkes Bay ecotypes**	**Mangere ecotype**	**NW Spain collections**	**comment**
Grasslands Ruanui	1930s	****			reselected ecotype material
Grasslands Ariki	1960s	***			"hybrid" cultivar with 25% introgression from *Lolium multiflorum*
S23	1970s				imported from UK
Vigor	1970s				imported from Belgium
Grasslands Nui	1970s		****		
Ellett	1980s		****		
Droughtmaster	1980s	***			old pasture, possibly Ruanui or Ariki origin
Grasslands Marsden	1980s	***			Selection from Ariki for low leaf strength
Ceres Marathon	1980s	****			old Canterbury pasture, possibly Ruanui origin
Takapau Persistor	1980s	***			old pasture
Endeavour	1980s	**	**		Ellett cross old pasture
Embassy	1990s	*	*		50% Uruguay, 50% NZ old pasture material
Grasslands Pacific	1990s	**		*	25% central Italy
Yatsyn	1990s		****		
Aires HD	1990s				old pasture, possibly Ruanui and/or Nui origin
Banks	1990s				Embassy and NZ material
Bronsyn	1990s		***		
Dobson	1990s		*		
Grasslands Samson	1990s	*	**		old pasture, possibly Nui origin
Grasslands Impact	1990s		**	**	based on Nui and NW Spain
Ceres Kingston	1990s	*	**		25% Mediterranean Spain
Meridian	1990s		**		half Australian Kangaroo Valley material
Vedette	1990s		***		
Ceres Cannon	2000s		***		
Grasslands Supreme	2000s	**			old pastures and "hybrid" types
Matrix	2000s	*	*	*	Aires and Impact with maximum 8% introgression *F. pratense*
Tolosa	2000s			***	
Aberdart	2000s				UK and European material, imported from UK,
Commando	2000s				collection from old NZ pasture
Extreme	2000s		****		
Hillary	2000s	****			
Revolution	2000s	*	*	*	Similar to Matrix
Arrow	2000s		**	**	

(* represents approximately 25% genetic origin)

Table 2 Origin of New Zealand tetraploid cultivars

Tetraploid Cultivar	Period of release	Hawkes Bay ecotypes	Mangere ecotype	NW Spain collections	comment
Grasslands Greenstone	1980s	***			Tetraploid of Ariki
Nevis	1990s		****		Tetraploid of Mangere material
Quartet	1990s				Tetraploid from a diploid late flowering NZ collection
Ceres Horizon	1990s	*	**		Tetraploid based on old NZ pastures
Bealey	2000s			***	
Banquet	2000s		**	**	Tetraploid based on Impact
Grasslands Sterling	2000s	**			Greenstone and European tetraploids

(* represents approximately 25% genetic origin)

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