

Plant breeding for resilient pastures

John R. CARADUS^{1*}, Joseph H. BOUTON², E. Charles BRUMMER³, Marty J. FAVILLE⁴, Richard M. GEORGE⁵, David E. HUME⁴, Courtney INCH⁶, Graham A. KERR⁶, Stephane MONTEL⁷, Alan V. STEWART⁸ and Derek R. WOODFIELD⁹

¹Grasslanz Technology Ltd, PB 11008, Palmerston North 4442, New Zealand

²Professor Emeritus, University of Georgia and Bouton Consulting Group, LLC, Athens, Georgia, USA

³Plant Breeding Center, University of California-Davis, Davis, California, USA

⁴AgResearch Ltd, PB 11008, Palmerston North 4442, New Zealand

⁵PGG Wrightson Seeds Ltd, 10 Bisley Road, Hamilton 3214, New Zealand

⁶Barenbrug NZ Ltd, 2547 Old West Coast Road, RD1, Christchurch 7671, New Zealand

⁷Cropmark Seeds Ltd, 49 Manion Road, Rolleston 7677, New Zealand

⁸PGG Wrightson Seeds Ltd, PO Box 69175, Lincoln, Christchurch 7640, New Zealand

⁹PGG Wrightson Seeds Ltd, PB11008, Palmerston North 4442, New Zealand

*Corresponding author: john.caradus@grasslanz.com

Highlights

Plant breeding has had, and continues to have, an important role in providing farmers with resilient pastures. Early breeding relied on improvement of ecotype populations and this was accelerated by crossing with selected introduced germplasm. The primary traits under selection have targeted speed of establishment, total and/or seasonal dry matter (DM) yield, nutritive value or feed quality, flowering time and reduced aftermath heading, disease resistance, persistence and seed yield. Continued improvement through plant breeding to meet environmental concerns and tolerances to both biotic and abiotic stresses will be achieved through ongoing plant introductions, exploiting heterosis, speed breeding, genomic selection, improvements in phenotyping, metabolomics, improved compatibility with beneficial microbes, and potentially the use of transgenic and gene editing technologies.

Keywords: forage, genetic improvement, heritability, selection, traits

Background

Animal protein production in New Zealand continues to be largely reliant on utilising pasture through *in situ* grazing. This relatively low-cost farming system is a competitive advantage (Caradus 2007) but it is now threatened by the increased use of supplements and nitrogen (N) fertiliser particularly by the dairy industry (Penno et al. 1996; Rogers & Putt 1997). Increased production and profitability have been the main drivers for higher input and although they typically increase production, their associated costs may reduce on-farm profitability. New Zealand has about 27 million sheep of which about 18 million are breeding ewes; 3.7 million cattle of which 1 million are breeding cows or heifers; and 6.4 million dairy cattle of which 5 million are cows or heifers (<https://beeflambnz.com/data-tools/>

[industry-production-trends](#)). Further increases in total milksolids produced will likely occur through increased milk production per cow (<https://www.dairyglobal.net/Market-trends/Articles/2020/2/Why-NZ-farmers-favour-efficiency-539524E/>). Improved cow genetics, better pasture management (increasing feed utilisation), increased feed on offer which might result from either supplementation, increased fertiliser N application, improved plant genetics, or a combination of all of these, are options to increase milk production. Significantly, pasture harvested or eaten can explain the majority of variation in milksolids yield per hectare between farms (Figure 1, Newman & Savage 2009). This reinforces the importance of providing farmers with high performing and resilient pastures through plant breeding. Resilient is defined in this paper as the capacity to survive and recover quickly from periods of stress, or simply “toughness”.

Maintaining New Zealand’s competitive advantage for dairy production is reliant on valuing seven components of the farm system: the inclusion of white clover and other legumes in pastures; the negative impact of grass endophyte alkaloids; the dilemma of feeding pasture to high breeding worth cows; the niche positioning of alternative forage species; the tactical use of fertiliser N; the economic importance of extending days in-milk; and the benefits accrued from feed budgeting and astute pasture management (Caradus & Clark 2001). Some of these also apply to improving the competitiveness of sheep and beef farming operations, where improved profitability in recent years has been due to increased animal growth rates and lambing rates rather than higher stock numbers (<https://beeflambnz.com/sites/default/files/data/files/Compendium%202019.pdf>). Much of this improvement is due to providing more and better quality feed (Fraser & Rowarth 1996).

Improving pasture resilience to maintain long

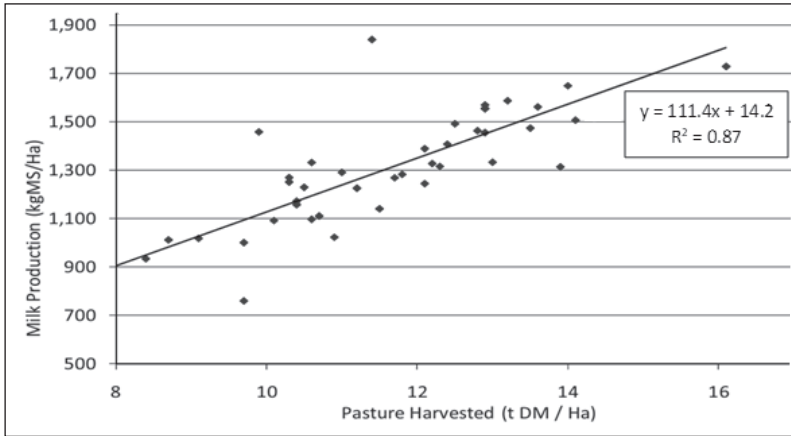


Figure 1 Milk solids production (kg MS/ha) and pasture harvested/eaten (t DM/ha) – from Newman & Savage (2009).

term pasture yield and persistence will improve New Zealand's international competitiveness. Challenges include the observation that the yield of sown species typically declines over time (Parsons et al. 2011), driven by environment and management (Tozer et al. 2011), and physiological changes in plants as they age (Ong et al. 1978; Donaghy & Fulkerson 1998), such as white clover as it transitions from its seedling tap-rooted state to a perennating plant with stolon roots (Brock & Hay 2001).

The forage species used on New Zealand's 6 million hectares of farmed, high-producing grassland are all introduced, predominantly from Europe (Ministry for the Environment 2010). Along with these grasses a number of insect pests have been introduced, but without their natural biocontrol agents, resulting in a vulnerable pasture ecosystem (Goldson et al. 2020) that is now highly reliant on *Epichloë* endophytes for ensuring some persistence. There are a further 8 million ha of less productive exotic and indigenous grassland vegetation. Perennial ryegrass (*Lolium perenne*) is deemed to be the most valuable plant species in New Zealand, *Pinus radiata* second, with white clover (*Trifolium repens*) the third (Nixon 2016). It is likely that perennial ryegrass and white clover will remain the dominant constituents of improved pasture for the foreseeable future, but there are opportunities for inclusion of other species such as chicory (*Cichorium intybus*) to increase nutritive value and animal growth rates, and plantain (*Plantago lanceolata*) to mitigate N leaching (Cranston et al. 2015; Carlton et al. 2019). These species need to be understood in terms of the value they bring and their role in grazed pastures. If the climate changes as predicted, inducing longer summer soil moisture deficits in parts of the country, alternative forage species like lucerne (aka alfalfa, *Medicago sativa*) and tall fescue

(*Lolium arundinaceum*) will find a larger niche than previously, especially for cultivars with high nutritional value adapted to grazing environments. Annual pasture renewal rates vary from about 3% for sheep and beef farms to about 8% for dairy farms, averaging about 4% across all farming types (Thomas et al. 2014). The benefits of pasture renewal need to be clearly enunciated and discussed with farmers. Recent work indicates that farmers who do renew pasture have a

better understanding about the availability of improved cultivars and the likely financial returns of growing them, as well as access to relevant information, than those who did not renew their pastures (Rijswijk & Brazendale 2016).

Traditionally, plant breeding has sought to improve on-farm productivity, primarily through increased DM yield, improved feed quality (e.g., reduced aftermath heading), improved persistence, or a combination of these. While these aims remain, they are now overlaid with additional requirements of a triple-bottom line that New Zealand's international customers of its pastoral produce are demanding, resulting in additional complexity for plant breeding. These include increasing environmental regulations imposed on farming operations such as limits of N fertiliser use, protection of waterways, slope restrictions on winter cropping, and social licence requirements such as limits to inductions and bobby calves, and limits on mud when grazing winter crops. Plant breeders will also need to identify plant material that will be adapted to predicted climate change, and the effect this will have on plant performance, species requirements, and the resulting changes that will happen in farm systems (e.g., autumn calving and lambing, increased cropping).

Examining the future demands of forage plants in New Zealand to provide resilient pastures, what this will mean for the plant breeding industry, and whether the current industry can deliver to these demands are important questions. It is important to understand what has worked well and not so well for plant genetics and breeding in delivering species and cultivars with the appropriate traits for the environment and management systems in which they are to perform. Additionally, it is now understood that improved pastures are more than just plants; they are also reliant on microbes, such

as *Epichloë* endophytes for resistance against insect pests, *Rhizobium* for biological N-fixation (Shi et al. 2019), mycorrhiza for nutrient and water uptake, and other organisms in the soil such as worms for nutrient cycling.

Plant breeding must balance these opportunities and challenges to improve the performance of farm systems. The value being delivered to farmers from plant breeding endeavours needs quantification and re-evaluation due to a static trend in pasture eaten per hectare on New Zealand dairy farms (Figure 2, Chapman et al. 2020), again acknowledging the importance of pasture eaten on production of milk (Figure 1). These data contradict evidence of genetic gain in DM yield from plant breeding (Woodfield 1999; Harmer et al. 2016). Some of the observed increase in DM/ha eaten, from 1990 to 2014, could be accounted for by increased N fertiliser application (150 kg N/ha over the same period), and dairy expansion in the South Island with the use of irrigation. Thus, the role of plant breeding may not have been to increase yield *per se* so much as to provide cultivars that respond well to applied N and that are adapted to different environments and managements.

Brief history of forage plant breeding in New Zealand

Improvement of pasture and forage plants in New Zealand through plant breeding is a 95-year legacy (Wratt & Smith 1983; Easton et al. 2002). In the 1930s, the Government introduced pasture plant breeding initiatives through the creation of DSIR Grasslands, headquartered at Palmerston North (Levy 1932). Equally important was the establishment of seed testing laboratories and the development of seed certification systems in the 1920s.

Plant Breeders Rights, allowing intellectual property protection of bred cultivars, was passed into law as The Plant Variety Rights Act in 1975 (Wynn-Williams 1987). It was later upgraded in 1985 and 1991, and was again under review in 2020/21 to bring it into line with the 1991 version of the International Convention on the Protection of New Varieties of Plants (UPOV Convention). Protection of plant breeders' rights, and the internationalisation of the seed industry, was the beginning of plant breeding capability moving from Government-managed and funded facilities to the private sector, and eventually into proprietary seed companies. This transfer of pasture and forage breeding capability was completed in 2016 when AgResearch no longer supported applied plant breeding and restricted its efforts to pre-breeding and genomics.

The promise of plant gene transformation (namely, genetic engineering), defined here as any technology associated with gene modification or transfer, was

heralded in the 1980s (White 1988), but has not been part of forage and pasture cultivar commercial development despite considerable investment over the last 30 years. This is largely due to four reasons: the paucity of inherited traits controlled by one or few genes of sufficient value to warrant targeting with transformation technologies; the technical difficulties associated with introducing a gene or genes into polyploid out-crossing forage species; freedom to operate on many underlying patents; and New Zealand's uncompromising regulatory system. Even if a regulatory process becomes a reality, it will greatly increase trait deployment costs.

National Forage Variety Trials (NFVT), managed under the auspices of the New Zealand Plant Breeding and Research Association (NZPBRA) were commenced in 1991 (<https://www.nzpbra.org/forage-trials/>) and provided a co-operative industry-run system of evaluating cultivar performance (Easton et al. 1997). Yield data from these trials have been used since 2012 by DairyNZ in co-operation with the NZPBRA for establishing the Forage Value Index (FVI) for ryegrass cultivars marketed in New Zealand (<https://www.dairynz.co.nz/feed/pasture-renewal/select-pasture-species/about-fvi/>; Bryant et al. 2013; Ludemann et al. 2017). Pastures based on superior ryegrass genetics are estimated in the 2020 FVI to be worth up to an additional \$576/ha p.a. on a typical dairy farm, over the \$0/ha genetic base figure for ryegrass cultivars released before 1996 (DairyNZ 2020). The FVI provides a Cultivar Selector Tool to allow farmers to make more informed, confident, and profitable decisions when choosing ryegrass cultivars for their pasture renewal programme. Relative herbage accumulation and nutritive value rankings of ryegrass cultivars do not differ significantly when ryegrass is grown in monoculture or in mixtures with white clover (Cosgrove et al. 2018). Nevertheless, cultivar testing systems should reflect management practices used on-farm, and with most cultivar trials undertaken as monocultures, evaluating ryegrass in mixtures with various clovers and herbs as occurs on-farm needs consideration (Harmer et al. 2016). In addition, most varietal agronomic trials use a common management across all cultivars irrespective of their differing maturities and seasonal growth patterns.

The benefits from mixed species swards and especially the incorporation of legumes and herbs into diets should not be underestimated (Waghorn & Clark 2004). Plant breeding of minor legumes and herbs has been a feature of plant breeding in New Zealand, largely initiated by government plant breeders. A number of these are now species of significant interest with private plant breeding companies, including grazing-tolerant red clovers (Ford & Barrett 2011), plantain (Stewart 1996), chicory (Rumball 1986; Hare et al.

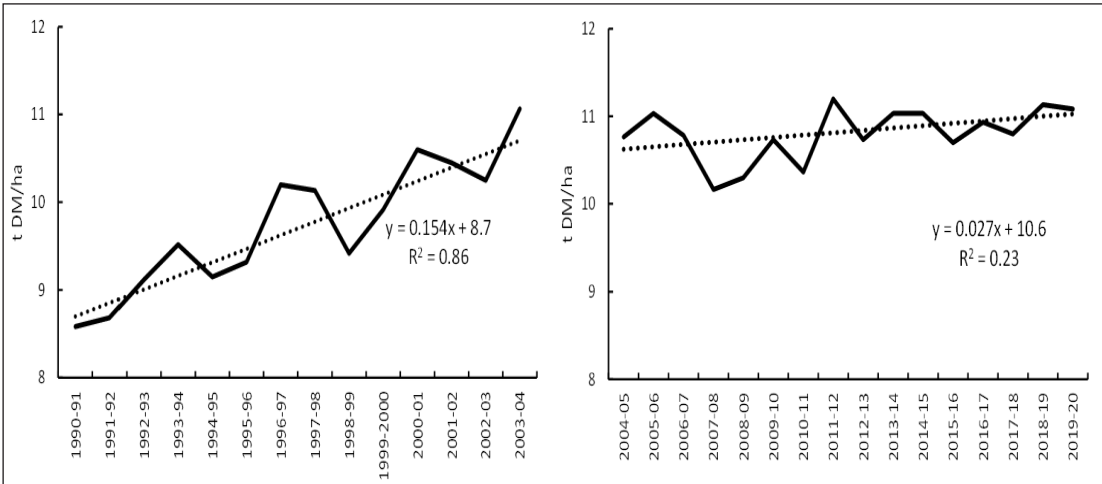


Figure 2 Mean pasture eaten (t DM/ha) on New Zealand dairy farms from 1990 to 2004 and from 2004 to 2020 (from Chapman et al. 2020).

1987), lucerne (Dunbier 1983), tall fescue (Easton & Pennell 1993; Easton et al. 1994; Minneé et al. 2010), cocksfoot (*Dactylis glomerata*, Lolicato & Rumball 1994), grazing bromes (*Bromus stamineus*, Stewart 1992), prairie grass (*Bromus willdenowii*, Baars & Cranston 1977; Rys et al. 1977), meadow fescue (*Festuca pratensis*, Popay et al. 2009), and forage brassica species (Lindsay et al. 2007; Dumbleton et al. 2012). However, there are many other forage species that fit minor ecological niches across New Zealand adding to resilience of pastures. These include annual legumes (Monk et al. 2016) and lotus species (Bologna et al. 1996) but for most of these there has been little recent breeding activity.

Increased levels of fibre, dead matter and fungal toxins can lower the nutritive value of pasture (Waghorn & Clark 2004). Temperate grasses in most regions of New Zealand are infected with *Epichloë* endophytes that can produce animal-toxic alkaloids which vary among different endophyte strains. The development of grass cultivars containing non-toxic *Epichloë* endophytes, or endophytes of greatly reduced potential toxicity, increases perennial ryegrass, tall fescue and meadow fescue persistence through protection against insect pests, but reduces or eliminates animal health and welfare problems evident in older pastures (Caradus et al. 2021).

The targets of plant breeding – what are breeders seeking to achieve?

The primary traits targeted include speed of establishment, total and/or seasonal DM yield, nutritive value or feed quality, flowering time and reduced aftermath heading, disease resistance, persistence, and seed yield (to ensure delivery of an economically

viable product). The Pastoral Industry Forage Strategy (Pastoral Industry Forage Discussion Document 2017) identified additional traits of importance:

- Overall feeding value
- Nitrogen concentration
- Drought tolerance
- Heat stress tolerance
- Tolerance/resistance to insect pests, leaf rusts, and soil pathogen pressure
- Tolerance to grazing pressure
- Aluminium tolerance (especially of legumes)
- Response to increasing carbon dioxide levels

Some of these are related to yield and persistence (e.g., pest resistances and stress tolerances) while others relate to feed quality (e.g., feeding value), with all ultimately contributing to resilient pastures. It is likely that improving forage feed quality also requires breeders to target multiple traits to ensure consistent improvements in on-farm performance (Stewart & Hayes 2011). Some are related to potential changes in climate where the risk is partly mitigated through most plant breeding companies having an international focus and/or ownership, with germplasm often already evaluated in warmer, drier climates to provide an understanding of adaptation.

Determining the heritability (Allard 1966) of traits is important to provide a guide to the likely gains from plant breeding initiatives. Heritability can be expressed either in the broad sense as the ratio of the total genetic variance to the phenotypic variance, or narrow-sense as the ratio of the additive genetic variance to the phenotypic variance. The latter is more pertinent as only the additive variance is captured in most out-crossing forages. A wide range of heritability estimates are reported for a diverse array of traits across forage

species in Table 1. Heritability estimates need to be considered carefully as the specific experimental design and the germplasm being evaluated can dramatically affect the estimates obtained. In fact, breeders should focus on improving methods used to measure phenotypes that would serve to decrease experimental error, thereby increasing heritability.

Most heritability estimates for forage species are low to moderate. The value of heritability estimates may be an unreliable predictor of genetic improvement if the performance of plants in the selection environment

(e.g., spaced plants) is not positively correlated to their performance in the production environment (e.g., mixed species sward); a positive gain in one could lead to a negative selection response in the other (Falconer 1989; Rowe & Brink 1993; Sykes et al. 2017). A lucerne grazing tolerance heritability estimate is not reported (Table 1) but there is a standard test that allows claims for grazing tolerance (Bouton & Smith 1998). This test was validated in several temperate geographies (Bouton 2012), most recently tropical Brazil (Pedreira et al. 2020). The test uses repeatable checks to assess

Table 1 Examples of heritability estimates and specific traits (included in column for some) for important traits targeted in forage plant breeding programmes.

Trait	Species and specific traits	Heritability	Reference
Herbage yield	White clover	0.35 – 0.72 (N)	Rowe & Brink 1993
	Perennial ryegrass	0.13 – 0.30 (N)	Fè et al. 2015
	Perennial ryegrass, tall fescue, cocksfoot	0.10 – 0.20 (N)	Frandsen 1986
	Tall fescue	0.37 – 0.78 (B)	Burton & DeVane 1953
	Wheatgrasses, canarygrass	0.71 – 0.95 (B)	Barker et al. 1989
Nutritive value	Perennial ryegrass – fibre, crude fat, metabolisable energy, crude protein	0.27 – 0.48 (N)	Aroju et al. 2020
	Perennial ryegrass, tall fescue, cocksfoot – digestibility	0.40 – 0.60 (N)	Frandsen 1986
Canopy structure	Ryegrass – tiller number, tiller angle, leaf length, leaf angle, leaf rigidity	0.53 – 0.94 (N)	Rhodes 1973
Persistence traits	White clover – stolon branching frequency	0.16 – 0.45 (N)	Caradus & Chapman 1996
	White clover – internode length	0.26 – 0.56 (N)	
Seed yield	Perennial ryegrass – seed yield per plant	0.42 – 0.86 (B) 0 – 0.80 (N)	Elgersma 1990
	Tall fescue – seed yield per plant	0.34 – 0.76 (B)	Burton & DeVane 1953
Nitrogen concentration	Perennial ryegrass	0.63 (N)	Cooper 1973
		0.22 (N)	Aroju et al. 2020
Drought tolerance	Wheatgrasses, canarygrass – water use efficiency	0.69 – 0.94 (B)	Barker et al. 1989
	White clover root traits – taproot diameter, number large nodal roots, root/shoot ratio	0.08 – 0.54 (N)	Woodfield & Caradus 1990
Disease and pest resistance	Tall fescue	0.59 – 0.90 (B)	Burton & DeVane 1953
	White clover – nematode resistance	0.17-0.61 (B)	van den Bosch & Mercer 1996; van den Bosch et al. 1997
Grazing/defoliation tolerance	Lucerne (alfalfa)	Not determined, but successfully selected	Bouton & Smith 1998
Aluminium tolerance	Perennial ryegrass	0.24 – 0.33 (B)	Wheeler et al. 1992
	White clover	0.20 – 0.53 (N)	Caradus et al. 1991
Frost tolerance	White clover	0.93(N)	Caradus et al. 1990

B: broad sense heritability estimate; N: narrow sense heritability estimate.

performance across trials and diverse locations, and its use when comparing populations selected from grazed pastures to the original populations has clearly indicated that selection for lucerne grazing tolerance is “heritable”.

Contrasting drivers of natural selection and selective breeding

Forage and pasture species are recent domestications compared to major crops such as maize, wheat, and rice (McCouch 2004). Modern cultivars of pasture species are either selected directly from ecotype wild populations (Bouton et al. 2005a) or from crosses between cultivars which themselves were only a few generations removed from wild populations (Bouton et al. 2005b). Drivers of natural selection are primarily adaptation, persistence, and/or reproduction to ensure ongoing survival of the species. These are at odds with the drivers of plant breeding such as high yield and high feed quality while maintaining multi-year persistence. For example, the traits for increased persistence of white clover under grazing are high stolon branching, short internode length, narrow stolon diameter, and small leaf size which are all associated with low DM yield (Rhodes & Harris 1979; Woodfield & Caradus 1996). High hydrogen cyanide content in leaves is also related to higher persistence of white clover (Caradus & William 1989), but in some situations this could be construed as an anti-quality factor (Gutzwiller 1993).

Reseeding types of ryegrass are common in older unimproved pastures, while modern ryegrasses are often later flowering with less aftermath seedhead development and therefore, less prone to seed drop under grazing (Burgess & Easton 1986). Although fine leaved perennial ryegrasses derived from Hawke’s Bay ecotypes such as ‘Grasslands Ruanui’ were persistent, they were also low yielding; other successful cultivars such as ‘Grasslands Nui’ and ‘Ellett’, derived from open crowned, large-tillered populations of ‘Mangere’, showed that other germplasm sources with persistence could also have higher production. However, some of that success was likely due to *Epichloë* endophyte

infection, which provided tolerances to biotic and abiotic stresses. More recently, the incorporation of ryegrass germplasm from north-west Spain into breeding programmes has further improved cultivar performance (Stewart 2006).

Impact of the Forage Value Index (FVI) on plant breeding selection targets

The perennial ryegrass FVI is managed by DairyNZ and calculates the economic value for cultivars (as operating profit per hectare) in a dairy farm model using the seasonal DM yield from NZPBRA National Forage Variety Trials and trait information on seasonal metabolisable energy content and persistence (DairyNZ 2020). The values are region-specific for both short-term and perennial ryegrass cultivars. For perennial ryegrass, the FVI is intended to assist farmers when choosing cultivars for pasture renewal. Economic values predict how well a cultivar will perform on-farm compared to the \$0/ha ‘genetic base’ figure for perennial ryegrass cultivars released before 1996 (DairyNZ 2020). In addition, performance values (1-5 rating) for perennial ryegrass are provided for seasonal DM yield for winter, early spring, late spring, summer and autumn.

The FVI performance values for short-term ryegrass cultivars (those grown for 12 months or for winter feed) are provided for speed of establishment and seasonal DM yield for winter, early spring, late spring and summer (late spring and summer do not apply to winter feed cultivars). Like perennial ryegrass, the economic values for 12 months and winter feed are the predicted differences in operating profit over a period relative to the \$0/ha genetic base figure for cultivars released before 1996 (DairyNZ 2020). Table 2 shows the estimates of economic values for perennial ryegrass across the four regions and demonstrates the high value of early spring growth in dairy farm systems, in cultivars.

Production traits

Consistent annual and seasonal DM yields are the

Table 2 Economic values (EV in \$/kg DM change in trait, the predicted change in operating profit for a dairy farm) for perennial ryegrass seasonal dry matter yield traits used in the calculation of the 2020 Forage Value Index (taken from DairyNZ 2020).

Season EV	Upper North Island	Lower North Island	Upper South Island	Lower South Island
Winter	0.29	0.40	0.49	0.42
Early spring	0.52	0.51	0.44	0.48
Late spring	0.17	0.12	0.34	0.19
Summer	0.37	0.29	0.15	0.07
Autumn	0.36	0.28	0.28	0.24

predominant production traits sought by forage breeders for ongoing genetic improvement. The methods used to select these are critical to ensuring successful genetic progress. A balance is often required between evaluations of plants in well-managed and controlled environments compared to those in more complex, real-world environments. For example, do production traits of plants grown as grazed spaced plants, where plant phenotype is clearly apparent, compare well to those grown in mixed grazed swards? Similar issues arise when comparing mowing and grazing trials of elite germplasm. For white clover, the variation in cultivar yield in a grazed grass sward explained by growth as spaced plants decreased from 45% in Year 1 to 10% in Year 3 (Caradus et al. 1989). Nevertheless, some agreement was observed between spaced plant and sward performance rankings, particularly for the best performing lines.

Quality traits

Feeding value of forage/pasture is a combination of feed nutritive value and voluntary intake (Waghorn & Clark 2004) and it is highly related to maturity. To improve nutritive value, plant breeders have delayed the flowering date of grasses, reduced aftermath heading (i.e., the propensity for plants to produce a second generation of seeding), and reduced lignification within the plant (Chapman et al. 2014). Increasing clover content of pastures is well known to improve animal production (Harris et al. 1997; McClearn et al. 2020) and some grasses such as tall fescue have been shown to be more amenable to white clover growth and persistence than perennial ryegrass (Hyslop et al. 2000). Where tetraploid ryegrass cultivars have similar yield and persistence to diploids, stocking rates can be improved by up to 8% with an increased animal DM intake of 3-5%, with at least a similar improvement in animal production (Hageman et al. 1993; Vipond et al. 1993). Another means to improving pasture quality eaten is to include other legumes such as red clover or leafy herbs such as chicory and plantain in the pasture (Moorhead et al. 2002; Waghorn & Clark 2004; Judson et al. 2009; Moorhead & Piggot 2009; Cranston et al. 2015).

Environmental adaptation and mitigation

Traditionally breeders have taken a simple, pragmatic approach by growing germplasm in the field and selecting those lines and genotypes that survive and have high yield. This 'simple approach' is driven partly by cost and flexibility (several species and/or populations are screened cheaply and together in the same paddock) but also because field conditions combine the impact of multiple stresses simultaneously. The alternative approach to isolate and test each stress individually is

expensive and time consuming but counterproductive if some stresses are negatively correlated. However, field testing only reflects the conditions at particular sites and in particular years, which may or may not present sufficient levels of the various stresses of interest to enable useful selection. At least some in-field selection trials should include few/no stress situations, so resilient plants utilise the favourable conditions and demonstrate their full genetic potential. Finally, we may need to accept that resilient plants may have disadvantages in some situations, for example, where the benefits of highly productive but short-term cultivars outweigh the extra renewal costs.

While considering productivity, plant breeding endeavours should aim to reduce the environmental footprint associated with pasture and supplementary crops (Woodfield & Judson 2018). Two approaches are required: firstly, to reduce negative impacts on water quality, and secondly, to seek traits that will reduce or at least mitigate against further exacerbating climate change (e.g., lower greenhouse gas emissions).

Reducing negative effects on water quality requires less nutrient leaching in the case of N, or sediment loss in the case of phosphorus (P), and loss of soil and nutrients to waterways. This can be achieved by modifying rooting depth and architecture ensuring plants effectively retain water thereby preventing runoff (Macleod et al. 2013), or absorb excess nutrients through intercepting sub-surface nutrient flows to waterways. Including plants which inhibit biological nitrification in the sward, such as plantain, is also valuable by reducing the release of the more soluble nitrate from urine patches allowing plants time to absorb it before it is leached from the system (Dietz et al. 2012; Bowatte et al. 2018; Carlton et al. 2018).

Breeding for regional adaptation

Regional climate variability poses the option to identify pasture species better adapted to some of these environments than the predominantly used temperate species of perennial ryegrass and white clover. For example, some Northland farmers are seeking to move away from ryegrass/white clover, which have been sown largely for winter-spring production, and are looking to substitute these for C₄ grasses and subtropical legumes. This trend may strengthen and migrate further south through the North Island with predicted climate change. The substantial work undertaken evaluating C₄ grasses in New Zealand in 1970-1990 (Forde et al. 1976a, b; Field & Forde 1990; Crush & Rowarth 2007) has never been capitalized upon but may have relevance to current and future pasture resilience in warmer parts of New Zealand. However, for this to be commercially viable, seed companies will need to be reassured of a significant benefit to pastoral farmers so that market

size is sufficiently large to warrant investment and a reliable seed production system has been developed, which is often not the case for subtropical grasses and legumes.

Breeding cultivars for specific regions has often been requested. However, meta-analysis of National Forage Variety Testing results have shown that for perennial ryegrass at least there are only two climatic zones – the upper North Island and the remainder of New Zealand (Pers. comm. D. Baird, VSN NZ Ltd.). Plant breeders also test their selections regionally and from this provide expectations of cultivar performance. Plant breeders also seek wide adaptation through not just selecting for best performance in one region, but rather for better yield and persistence across a range of regions. Future use of what are considered minor species that are adapted to regional climates may be limited by market size that would ensure an acceptable return on investment. Alternatively, there is the option of importing seed of minor forage species that are permitted, do not breach the HSNO Act, and are deemed not new to New Zealand. However, although this could have already occurred, to date it has not been on any significant scale.

Persistence

Understanding the key drivers of persistence for the major forage species enables breeding to more effectively select for the traits in specific controlled tests, which in turn provides a means to developing more precise molecular markers for these traits. However, heritability of traits related to persistence is low to moderate (Table 1), which will constrain progress. Developing phenotyping methodologies to accurately select for persistence and for other traits will enhance genetic gain.

The processes of plant breeding – the means to an end

Effective pasture and forage plant breeding requires systems that can manage heterozygous and heterogeneous populations, varying impacts of environment, competition in mixed species swards, defoliation variation due to differing managements and animal classes, perennialism, and interactions with microbiological communities (e.g., *Epichloë* in the case of some grasses). In addition, most forage and pasture species of importance are out-crossing and cultivars released are a heterogeneous mixture, or population, of heterozygous genotypes. Previous publications highlight key potential advances in pasture plant breeding such as using exotic germplasm and secondary gene-pools, genomics, marker-assisted selection, genetic modification, exploiting grass-endophyte associations, breeding for specific environments,

and the successful adoption of international breeding programmes (Williams et al. 2007).

Plant breeding's purpose is to create new or improved variation that is different to or better than current cultivars and is predominantly driven by the commercial seed industry (Figure 3).

Germplasm collection

New Zealand pastoral agriculture is solely reliant on introduced species and as a result is highly dependent on overseas germplasm collections to ensure new genetics are available for continued pasture breeding improvement (Corkill et al. 1981). Few introduced lines performed as well as ecotypes and almost all the original breeding of perennial cultivars before the 1950s was based on locally adapted ecotype populations, which had developed over years of natural selection from original introductions largely from the United Kingdom. Ecotypes continued to play a role in breeding with the 'Mangere' perennial ryegrass ecotype forming the basis of several bred cultivars including 'Grasslands Nui', 'Ellett', 'Yatsyn1' (Kerr 1987), and 'Bronsyn'. In white clover, ecotype collections from New Zealand hill country resulted in the commercialisation of 'Grasslands Tahora', 'Nomad' and 'Prop', and another from Northland collections 'Grasslands Prestige' (Caradus et al. 1996). After this phase, introduced germplasm from the Mediterranean was used in crosses with the local material to improve winter growth in many species. In recent years, perennial ryegrass germplasm from north-west Spain has played a key role in breeding within New Zealand (Stewart 2006).

The germplasm base of most pasture species in New Zealand is relatively narrow, when compared to the available global genetic variation of the species, as demonstrated recently for perennial ryegrass and white clover (Faville et al. 2020b), and it requires continued efforts to locate and import new and diverse material (Williams et al. 2007). This is particularly the case if breeders are needing to identify and exploit genetic variation for novel traits such as resilience to water deficits. However, this is becoming more difficult with borders increasingly becoming closed to germplasm collection and transfer (Williams et al. 2007; Lightbourne 2009). In New Zealand, the impact of the Hazardous Substances and New Organisms regulatory environment restricts field-based research in new species. For example, the New Organisms regulations have prevented the use of wild relatives to improve perennial or Italian ryegrass (only 2 of 8 wild relatives are permitted for importation into New Zealand). Contrastingly for white clover, most of its wild relatives can be imported and used (New Zealand Biosecurity Index; <https://www1.maf.govt.nz/cgi-bin/bioindex/bioindex.pl>).

Heterosis

Heterosis, or hybrid vigour, is the genetic phenomenon whereby progeny yields can be significantly higher than those of either parent (Stuber 1994). This is achieved through the selective and controlled breeding of two inbred parent lines, which upon crossing delivers heterosis. This breeding strategy is used in self-pollinating inbred species and with the use of male-sterility genes, in out-crossing species such as maize (Sprague 1983) and rye (Geiger & Miedaner 1999). After selecting parental lines with the desired traits, one line is converted to be male sterile (the female line, which as a result produces no pollen), which is then fertilised by the pollen of the other, male-fertile line when the two lines are grown together under carefully managed conditions. This is an expensive exercise and while successful on high value vegetable crops, it is still to be effectively used with pasture species.

A number of systems have been explored to produce hybrid grasses with increased heterotic vigour (Herridge et al. 2019):

1. Semi-hybrids: In many out-crossing species such as perennial ryegrass, severe inbreeding depression occurs when developing inbred lines and so hybrid vigour is better captured by crossing populations with very different genetic backgrounds (Foster 1971; Brummer 1999). The production of a semi-hybrid ryegrass as first-generation certified seed is achieved by sowing a mixture of basic seed of two cultivars (Barrett et al. 2010; O'Connor et al. 2015). In both cases it was found that seasonality affected progeny growth relative to the better parent, and that the best semi-hybrids did not out yield the commercial controls. Specifically breeding complementary populations that combine well when crossed could conceivably make this method more successful.
2. True hybrids, which involve the use of cytoplasmic male sterility systems, which result in failure to produce functional pollen (Havey 2004), are used successfully in field crop breeding (Bohra et al. 2016). Use in perennial out-crossing forage crops is theoretically possible but is not yet a commercial reality (Wit 1974; Connolly & Wright-Turner 1984; Kiang et al. 1993; Kiang & Kavanagh 1996; McDermott 2008; Islam et al. 2014). Finding adequate heterosis is difficult (Liu 2015).

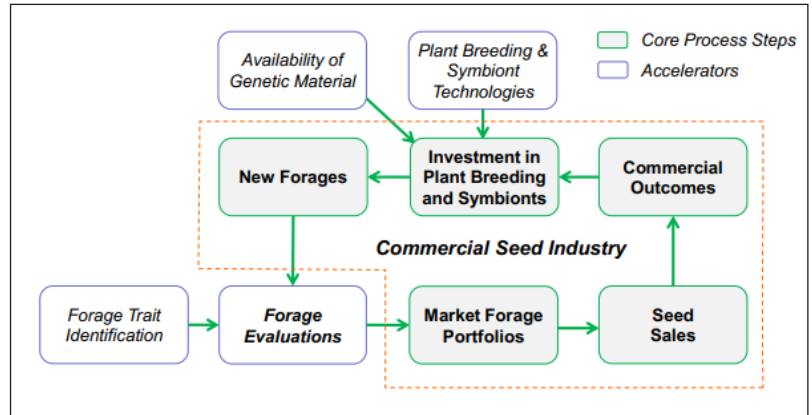


Figure 3 The forage improvement process in New Zealand (Pastoral Industry Forage Discussion Document 2017).

3. Partial F_1 hybrids based on self-incompatible genes are recorded where up to 83% hybrids develop in perennial ryegrass (Pembleton et al. 2015). These are still in the experimental stage and sufficient heterosis has yet to be demonstrated.

In all these cases, the careful development and breeding of complementary heterotic groups has not yet been conducted; consequently, to maximise the value of hybrids, breeders need to focus on how germplasm resources are deployed in the breeding programme.

In addition to breeding hybrid cultivars of one species, interspecific hybridization between ryegrass types and/or between ryegrasses and fescues has also been explored. In this case, hybrids are initially produced under very controlled conditions and the resulting plants represent a new, hybrid species, which can then be bred further. Hybrid ryegrasses (*Lolium* × *boucheanum*) created by crossing Italian or annual ryegrass (*L. multiflorum*) with perennial ryegrass are the most common interspecific hybrids used in New Zealand pastures. These provide better winter production than true perennials and in summer-moist environments persist for up to 5 years or more.

Speed breeding

Speed breeding (Watson et al. 2018) can circumvent long generation times. This is carried out in fully enclosed, controlled-environment growth chambers for annual crops, including subterranean clover (*Trifolium subterraneum*, Pazos-Navarro et al. 2017). Its application to perennial pasture and forage species is yet to be demonstrated. Computer simulations have shown that additional genetic gains can be achieved from speed breeding, but for optimal outcomes methods to mitigate inbreeding are required (Jighly et al. 2019). If inbreeding becomes a routine step in breeding programmes seeking to make hybrids, then

speed breeding would be very desirable to decrease the time to produce inbred lines.

Genetic introgression of wild relatives

Genetic resources outside of the target species can be very valuable as a source of traits not available in but needed for the target species, for example, drought tolerance, root structure, or salt tolerance. While presenting more risk, coupled with increased time and investment compared with conventional approaches, several major crops have benefitted greatly from crossing with wild species (Tanksley & McCouch 1997). Expanding gene diversity within species using secondary and tertiary gene pools may provide future options to breed for better adapted and more resilient pastures for marginal areas. For example ‘Grasslands Kara’ cocksfoot was bred from hybrids between ‘Grasslands Apanui’ cocksfoot and two Portuguese populations of the diploid subspecies *lusitanica* that had vigorous winter growth (Rumball 1982).

Provided the wild relative of the target species is an authorised species in New Zealand, wide hybridisation provides the potential to bring new traits into breeding pools without the regulatory constraints currently impeding the use of genetic modification and gene editing techniques. Undesirable genetics coupled with pre- and post-fertilisation barriers are some of the disadvantages that need overcoming to make exotic introgression viable and ensure the benefits can be transferred to pasture species at the commercial scale.

Genomic selection

Genomic selection (GS) uses genome-wide molecular markers to estimate the breeding worth of selection candidates without phenotyping them directly. Estimates are calculated using a prediction model generated from a reference population of individuals with both known genotypes and phenotypes. In forages, and more importantly in perennial forages, GS enables the breeder to apply selection without growing the plants through an entire life cycle (Li et al. 2015; Barrett et al. 2018). The advantage of GS in perennial forage species is therefore the reduction in selection cycle time and possibly evaluation costs per cultivar produced (Resende et al. 2014). For longevity traits such as vegetative persistence and biomass accumulation over time, GS offers considerably shorter generation intervals.

In addition to reduced selection cycle time, increased genetic gain could be further achieved through increased selection accuracy. While GS accuracy in perennial ryegrass is unlikely to be higher than progeny testing alone for biomass yield (Hayes et al. 2013), it is likely to be significantly higher than breeding methods that rely on mass selection of plants in spaced-plant

nurseries, where the correlation between spaced-plants and plot productivity traits is near zero. Substituting selection of spaced-plant nurseries from mass selection to GS (trained from a reference population of plots) is essentially the equivalent of having a significantly positive genetic correlation between spaced-plants and plot productivity traits (Lin et al. 2016).

There is no doubt that forage plant breeding could benefit from GS because many of the key traits are difficult to measure, take considerable time to determine (e.g., persistence), are expensive to evaluate, or are dependent on appropriate field conditions (e.g., in wet seasons selection for persistence associated with drought is not possible). Various genomic breeding schemes are proposed (Hayes et al. 2013; Resende et al. 2014; Faville et al. 2018) but this methodology is only recently being investigated in forages and has yet to deliver commercial outputs. Nevertheless, divergent selection for DM yield and heading date in perennial ryegrass demonstrated a positive impact of GS on trait improvement, as well as highlighting the importance of target environment selection for training models, and the influence of relatedness between the training set and selection populations (Faville et al. 2020a).

Phenotyping

Genomic selection is highly dependent on accurate phenotypic data for field performance of the large plant populations needed to train genomic prediction models (Easton et al. 2015). Characterisation of economically important agro-climatic zones and the evaluation of breeding material in these zones is a minimum requirement for future trait assessment in perennial ryegrass GS. This means using mini-swards for evaluating perennial ryegrass and planting rows into established grass swards for species like white clover, while ensuring that evaluations occur over multiple years particularly if persistence is the trait of interest. Phenomics tools, such as LiDAR (light detection and ranging, Ghamkhar et al. 2019), which enable rapid, accurate and non-destructive measurement of herbage biomass in large field populations, are also critical for GS to be conducted at a commercial scale.

Pasture and forage species typically are perennial, grown in mixed species swards, and defoliated to variable levels due to differing intensity, accompanying companion species, relative palatability, and type of grazing. This provides significant challenges to the breeder when selecting for traits such as yield and persistence, let alone nutritive value. Spaced-plant trials used to phenotype plants are not necessarily predictive of performance in mixed species swards (Waldron et al. 2008). They showed that while heritability of yield of tall fescue families was similar for measurements made of spaced plants and swards, there was an inconsistency

of family ranking between the two environments ($r=0.30$, not significant). When measuring crude protein concentration, there was no genetic correlation between the two systems ($r= -0.13$, not significant). Similarly, Riday & Brummer (2014) demonstrated that selecting birdsfoot trefoil (*Lotus corniculatus*) with a cocksfoot companion leads to more persistent birdsfoot trefoil varieties for use in grass mixtures than birdsfoot trefoil bred without a grass companion.

LiDAR has been tested in perennial ryegrass breeding trials and calibrated against both fresh and dry matter yields (George et al. 2019; Ghamkhar et al. 2019). It has demonstrated reasonably accurate estimates of DM yield within seasons for the paired-row breeding plots, although it was sensitive to large changes in DM content (%) among seasons. LiDAR-derived measures of winter, spring, summer and autumn growth explained a significant amount of the variation in fresh weight yield ($R^2 = 0.81, 0.92, 0.94$ and 0.90 , respectively) and DM yield ($R^2 = 0.87, 0.73, 0.87$ and 0.79 , respectively).

Genetic marker analyses of various types, including GS, have all run up against the issue of having either poor phenotypic data or no data at all for traits of significant importance, such as biomass production. Developing methods to robustly phenotype yield, nutritive value, and persistence in the field on progeny plots growing under production conditions is essential to improving forage crops (Brummer & Casler 2014), yet in many breeding programmes, the ability to collect data on large numbers of progenies and populations is not feasible. If nothing else, genomics will force programmes to collect better phenotypic data, which will improve genetic gain, regardless of whether marker assisted selection or GS models become routinely used.

Metabolomics

The study of metabolites, or small molecules, found in cells and tissues of plants provides an approach to better understand the chemistry that links biotic and abiotic stress tolerance in plants. Integrating metabolomics with quantitative genetics, transcriptomics and genetic modification has the potential to improve the outcomes from plant breeding. These methods can elucidate biological mechanisms underpinning critical traits, enabling identification of functional gene variants and, subsequently improvement of trait-specific DNA markers, biomarkers or gene edits to improve important traits (Cao et al. 2017; Kumar et al. 2017; Subbaraj et al. 2019).

Transgenic technologies

While an option since the 1980s (White 1988) there are few examples of commercial transgenic cultivars, largely due to the high regulatory costs associated with release from containment. Examples of success are

limited to lucerne in the USA where two traits have been commercialised, Roundup Ready® herbicide resistance and reduced lignin (marketed under the brand HarvXtra®). The latter, deregulated in 2014, was for a genetically engineered event to express reduced levels of guaiacyl lignin, a major subunit component of total lignin that slows the digestion of cellulose in livestock, as compared to conventional lucerne at the same stage of growth (Shea 2014).

In New Zealand, there are two significant investments for improved traits in perennial ryegrass and white clover using transgenic technologies. In perennial ryegrass, the aim is to produce high metabolisable energy germplasm which when expressed in the leaves of perennial ryegrass, increases leaf lipids up to about 7% of dry weight (approximately double 'normal' levels, Winichayakul et al. 2008; Beechey-Gradwell et al. 2018). In legumes, the aim to deliver condensed tannin expression in leaves of white clover and lucerne has been achieved through using a single gene transformation (Hancock et al. 2012, 2014). Condensed tannins in forages, through binding protein, can significantly reduce N leaching and also methane emissions (Woodfield et al. 2019). A scenario for achieving co-existence of genetically modified (GM) and non-GM crops and pastures has been proposed to stimulate discussion (Rolleston 2016). However, there is no doubt that introducing GM organisms (GMOs) into the New Zealand market is challenging, not just with regard to the political will and regulatory requirements, but also balancing the high costs of development with benefits, acknowledging that it is the large international agricultural markets that drives the development of this technology (Willocks 1999). The regulatory process needs to assess the risk associated with a trait rather than the process of delivering that trait; the consequences of transgene flow; and whether the transgene will even enter the food chain (Wang & Brummer 2012). A possible approach for New Zealand is the new USDA SECURE Rule for their Biotechnology Regulatory Service (BRS) (https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/biotech-rule-revision/secure-rule/secure-about/340_2017_perdue_biotechreg) – “The SECURE rule differs from the previous regulatory framework by focusing on an organism’s properties or traits and not on the method used to produce it”.

Gene editing

Gene editing is a controlled process allowing precise changes to DNA that alter a gene or the expression of a gene. This is used to turn known genes 'on' or 'off', or to enhance a particular trait (Dronov & Howard 2017). Gene editing has the potential to revolutionise breeding programmes in New Zealand of economically important perennial species such as ryegrass and

tree crops where conventional breeding methods show little potential (Fritsche et al. 2018). The most versatile gene editing process is the CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)-Cas9 (CRISPR-associated protein 9) system (Doudna & Charpentier 2014; Chilcoat et al. 2017; Brooks & Gaj 2018). Currently, New Zealand manages all products of gene editing as GMOs. The government is taking a cautious approach being mindful of market perceptions as well as the science (The New Zealand Government 2016). However, the three largest importers of New Zealand primary products, China, Australia and USA, all currently grow GM crops, and both Australia and USA do not regulate single (or few) base pair deletions using targeted gene editing.

The successes/achievements of plant breeding

Twenty years ago Woodfield (1999), Easton et al. (2002), and Woodfield & Easton (2004) summarised the genetic gain for annual DM yield due to plant breeding in a range of pasture species. This showed gains of 0.21 to 1.49% per year, variable even within species, with perennial ryegrass breeding achieving 0.3 to 0.6% per year (Easton et al. 2002). These genetic gains compared favourably with major crops such as maize that enjoy considerably greater research investment (Russell 1991), and unlike grazed forages, have only a single harvest where the harvested part of the plant is well defined. More recently Harmer et al. (2016) showed through an analysis of 46 Australian and New Zealand perennial ryegrass field trials that there are two distinct periods of genetic gain. Firstly, before 1990, where genetic gain for total annual DM yield was limited, and secondly, after 1990 where consistent genetic gains of approximately 0.76% per year or 105 kg DM/ha/yr occurred, with rates higher than this especially in winter, summer and autumn. Reasons for this post-1990 improvement are not clear but it does coincide with the transition from largely public funded breeding to private commercially funded breeding initiatives. The increase in DM production attributed to genetic gain in perennial ryegrass has been estimated to contribute an additional \$15 to \$20/ha in farm profitability compounded each year since 1990 (Chapman et al. 2017). In addition, during that time non-toxic *Epichloë* endophytes for improving perennial ryegrass persistence and palatability were widely deployed. Indeed, the successful integration of selected beneficial *Epichloë* endophytes into a range of perennial ryegrass cultivars is one of the more significant breeding achievements of the past decade resulting in improved persistence under drought, grazing, and insect pressure (Johnson et al. 2019). Increased yields from breeding have not led to reduced persistence of perennial ryegrass (Chapman et al. 2015; Harmer et al. 2016)

Improving ryegrass nutritive value was achieved

through creating tetraploids (Easton et al. 2011) and later flowering germplasm with less aftermath heading (Lee et al. 2012). Changes in seasonal yield distribution of perennial ryegrass have been largely driven by the calculated economic values of the predicted change in operating profit on farm (Table 2). Economic benefits have been estimated to be in the range of \$54/ha/year (late-heading diploids compared with mid-heading diploids) to \$232/ha/yr (tetraploids compared with mid-heading diploids) to New Zealand dairy farmers (Wims et al. 2017).

Increasing both white clover yield and persistence, which are largely negatively correlated (Caradus & Williams 1989), was pursued through selecting for high stolon growing point densities while maintaining or increasing leaf size (Caradus et al. 1997). This selection strategy resulted in the development of cultivars such as 'Grasslands Demand' and 'Grasslands Sustain' (Brock & Hay 1996). Comparison of white clover cultivars bred in New Zealand or overseas demonstrated that New Zealand bred cultivars were better adapted than overseas cultivars in terms of yield and persistence (Widdup et al. 2015). However, overseas cultivars containing Mediterranean germplasm exhibited beneficial features in the trials, which coincides with the fact that many recently bred New Zealand cultivars contain germplasm from these origins. The importance of evaluating and selecting under local conditions, in competition with grass, under grazing, over multiple environments and years cannot be underestimated in white clover.

The increasing importance of non-traditional species such as plantain and chicory in pasture mixes has been driven by the realisation that they add value through mitigating some environmental issues (Judson et al. 2018), improving tolerance of droughts through more taprooted root systems, and improved nutritive traits (Li & Kemp 2005).

Integrating host and microbial selection - *Epichloë*, rhizobium, mycorrhiza

The importance of key microbes in determining plant performance is now recognised and utilised in pastoral agriculture (Lugtenberg et al. 2013). Integrating them into high-performing managed pastures however, requires plant breeders to be cognisant of the genetic factors impacting host plant and microbe compatibility and therefore effectiveness of the symbiosis in delivering benefit. *Rhizobium* bacteria that colonise roots of legumes provide a free source of N for pasture growth. Nitrogen is a key limiting nutrient for pasture growth (Field & Ball 1978; Sun et al. 2008). Ryegrass, tall fescue and meadow fescue are protected from a range of insect pests through *Epichloë* fungi that grow within these host grasses (Johnson et al. 2013). Most plants also form symbiotic associations with

mycorrhiza aiding water and nutrient uptake (Begum et al. 2019). As these bacteria and fungi live within the plant in a mutualistic symbiotic relationship, they can be highly influenced by the genetics of the host plant. Genetic compatibility between host and microbe is therefore often critical for a successful and improved outcome, and as such, can require special consideration from the breeder.

Rhizobia in association with the host legumes such as clovers and lucerne are able to capture ('fix') atmospheric N within root nodules – a process called biological N fixation. This is a natural process, which is less energy intensive and results in less greenhouse gas emissions than for the manufacture and application of artificial N fertilisers (Gibbs 2019). Ways to enhance the N-fixation process will provide economic benefits for the pastoral industry and New Zealand. Recent research has identified strains of rhizobia that are more competitive and produce higher levels of fixed N than the current commercial strain TA1 (Shi et al. 2019). Further work has demonstrated that the genetics of the host white clover plant can influence the mutualistic relationship so there is an opportunity to select the best genetics of white clover to deliver better N-fixation and overall pasture performance. The heritability of this trait is still to be fully determined but there is variation which breeders may be able to exploit using conventional and GS methodologies for cost-effective development of hosts supporting improved N fixation traits (Pers. comm. S. Weith, Lincoln University).

Epichloë fungal endophytes are common in old perennial ryegrass pastures and sown cultivars (Johnson et al. 2013; Hume et al. 2020). New Zealand has led the world in identifying, commercialising and achieving higher farmer uptake of selected endophyte strains that provide protection against pasture insect pests but reduce and minimise the detrimental impacts on animal health, welfare and production (Caradus et al. 2021). However, as a mutualistic association the genetics of both the host and fungus are important and often the commercialisation of selected endophyte strains can be hindered by poor compatibility between the host and endophyte. Breeding for improved grass-endophyte compatibility has helped overcome some of these obstacles. Emerging genetic tools, such as genome editing and GS that improve manipulation and selection of both host and endophyte genomes are expected to improve breeding efficiency for endophyte compatibility traits (Johnson et al. 2019). This challenge has been a major reason why transferring fescue endophyte strains that express loline compounds, which have widespread pesticidal effects and no animal toxicity effects, into perennial ryegrass hosts while a

desirable objective (Easton et al. 2009), has not yet been successfully commercialised.

Root arbuscular mycorrhizal species are known to benefit the growth of plants, including grasses, in P-deficient soils (Crush 1973, 1995; Berthelot et al. 2018). However, these will only have a place where soil P levels are low (Powell 1976). Arbuscular mycorrhiza are beneficial for legume establishment and growth (Crush 1978; Crush & Caradus 1980), and stimulate nodulation and N-fixation (Kucey & Paul 1982). They may also interact with *Epichloë* endophytes (Guo et al. 1992; Muller 2003; Mack & Rudgers 2008; Buyer et al. 2011), but not always (Novas et al. 2005; Popay & Jensen 2005). There are few studies seeking practical applications from this symbiotic association in New Zealand mixed species pastures, but selection for host plants with a propensity to form more effective mycorrhizal associations is plausible (Crush & Caradus 1980) and should be a priority in lower fertility soils.

Essentially all forage plant breeding has ignored symbionts while developing improved cultivars, with the recent exception focusing on grass-endophyte associations. We believe that to improve agricultural output and sustainability, breeding methods to better optimise symbiotic outcomes in crop and pasture species need to be developed (Caradus & Johnson 2019; Porter & Sachs 2020).

Conclusions/future implications

The future of forage plant breeding in delivering resilient pastures

Pasture and forage plant breeding is the process of manipulating important traits through plant genetics to deliver new products that benefit pastoral farmers by improving productivity, reducing negative environmental impacts, and enhancing product quality that meets consumer demand. The challenge is to achieve these gains under different managements and environments, which constrain the genetic potential of cultivars. Most forage species used in New Zealand are outbreeding and therefore cultivars are populations of different but closely related genotypes. Breeders will continue to use well established selection strategies of recurrent selection both within existing high performing families and through introgression of genes from new germplasm, while taking into account interactions with beneficial microbes. Integration of recently developed genomic selection techniques may in time aid more accurate and timely selection for traits that are either expensive to measure or take long timeframes. The strict regulation of gene editing and transgenic technologies will reduce opportunities for New Zealand. However, the complexity and flexibility at which most current commercial forage breeding

companies operates are often taken for granted by genomicists and biotechnologists; multiple species with many populations and traits are screened simultaneously over multiple locations at a modest cost. It is therefore important to determine how new technology will fit into existing commercial forage breeding operations, given their high costs (most technologies are initially costly in money and personnel, yet commercial breeding budgets are “zero sum”) and typical lack of flexibility across multiple species and breeding populations.

The current challenge is different to the one outlined by Easton et al. (2002) where modest but steady productivity gains were expected from pasture plant breeding. We are now facing both environmental constraints limiting inputs, the increasing impact of a changing climate, and the continued threat from invasive pests to pasture resilience. Plant breeding has an important role to play in improving pastoral agricultural productivity in New Zealand, whilst reducing its environmental footprint, in a more variable climate, and continuing to sequester carbon. Breeding for DM yield with reduced N fertiliser inputs, while understanding that N supply greatly impacts yield, will require balancing yield and N use efficiency.

Breeding for resilience needs to be undertaken in the field where germplasms are affected by a wide range of factors and the interactions among them, not in controlled environments, and this can provide significant challenges in complexity. Can we continue to improve currently-bred species for DM yield, resilience, and rate of recovery from drought (which implicates both insects and *Epichloë* endophyte effects), or is it a better strategy to breed more drought- and heat-tolerant species and learn how to manage them more effectively? We also need to anticipate the potential impacts on pasture resilience of so-called “sleepers pests”, such as tropical armyworm, that may become a significant issue as their range expands with projected climate change.

Plant breeding faces the complex challenge of improving farm productivity, in a more erratic climate, with greater environmental, public and consumer influence. Historically, plant breeders have added significant value to New Zealand’s pastoral industry, and we firmly believe they will continue to do so. While the basic objectives of plant breeding have not changed, the knowledge and tools available have moved rapidly in recent years, with genomic selection allowing for quicker and more accurate breeding, the development of tools such as LiDAR for assessing pasture traits better, metabolomics for providing better understanding linking plant function with genetics, and more accurate gene manipulation options through gene editing technologies.

REFERENCES

- Allard RW. 1966. *Principles of plant breeding*. John Wiley and Sons, Inc., New York, United States of America. 485 p.
- Arojju SK, Cao M, Jahufer MZZ, Barrett BA, Faville MJ. 2020. Genomic predictive ability for foliar nutritive traits in perennial ryegrass. *Genes, Genomes, Genetics* 10: 695-708. <https://doi.org/10.1534/g3.119.400880>
- Baars JA, Cranston A. 1977. Performance of ‘Grasslands Matua’ prairie grass under close mowing in the central North Island. *Proceedings of the New Zealand Grassland Association* 39: 139-147. <https://doi.org/10.33584/jnzc.1977.39.1497>
- Barker RE, Frank AB, Berdahl JD. 1989. Cultivar and clonal differences for water-use efficiency and yield in four forage grasses. *Crop Science* 29: 58-61. <https://doi.org/10.2135/cropsci1989.0011183X002900010013x>
- Barrett BA, Faville MJ, Ghamkhar K, Carena MJ. 2018. Developing new tools for pasture plant breeding. *Journal of New Zealand Grasslands* 80: 255-262. <https://doi.org/10.33584/jnzc.2018.80.343>
- Barrett BA, Turner MA, Lyons TB, Rolston MP, Easton HS. 2010. Evaluation of semi-hybrid perennial ryegrass populations. *Proceedings of the New Zealand Grassland Association* 72: 11-16. <https://doi.org/10.33584/jnzc.2010.72.2810>
- Beechey-Gradwell ZD, Winichayakul S, Roberts NJ. 2018. High lipid perennial ryegrass growth under variable nitrogen, water and carbon dioxide supply. *Journal of New Zealand Grasslands* 80: 219-224. <https://doi.org/10.33584/jnzc.2018.80.349>
- Begum N, Qin C, Ahanger MA, Raza S, Khan MI, Ashraf M, Ahmed N, Zhang L. 2019. Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. *Frontiers in Plant Science* 10: Article 1068. doi: 10.3389/fpls.2019.01068
- Berthelot C, Blaudez D, Beguiristain T, Chalot M, Leyval C. 2018. Co-inoculation of *Lolium perenne* with *Funneliformis mosseae* and the dark septate endophyte *Cadophora* sp. in a trace element-polluted soil. *Mycorrhiza* 28: 301-314. <https://doi.org/10.1007/s00572-018-0826-z>
- Bohra A, Jha UC, Adhimoalam P, Bisht D, Singh NP. 2016. Cytoplasmic male sterility (CMS) in hybrid breeding in field crops. *Plant Cell Reports* 35: 967-993. doi:10.1007/s00299-016-1949-3
- Bologna JJ, Rowarth JS, Fraser TJ, Hill GD. 1996. Management of birdsfoot trefoil (*Lotus corniculatus* L.) pastures for productivity and persistence. *Proceedings Agronomy Society of New Zealand* 26: 17-21.

- Bouton J. 2012. Breeding lucerne for persistence. *Crop and Pasture Science* 63: 95-106. <https://doi.org/10.1071/CP12009>
- Bouton JH, Smith Jr SR. 1998. Standard test to characterize alfalfa cultivar tolerance to intensive grazing with continuous stocking. In: *North American Alfalfa Improvement Conference. Standard Tests to Characterize Alfalfa Cultivars. Third Edition* (Amended 2004) [Online] Available at <http://www.naaic.org/stdtests/Grazing.html>
- Bouton JH, Woodfield DR, Caradus JR, Wood DT. 2005a. Registration of 'Durana' white clover. *Crop Science* 45: 797. <https://doi.org/10.2135/cropsci2005.0797>
- Bouton JH, Woodfield DR, Caradus JR, Wood DT. 2005b. Registration of 'Patriot' white clover. *Crop Science* 45: 797-798. <https://doi.org/10.2135/cropsci2005.0797a>
- Bowatte S, Hoogendoorn CJ, Newton PCD, Liu Y, Brock SC, Theobald PW. 2018. Grassland plant species and cultivar effects on nitrous oxide emissions after urine application. *Geoderma* 323: 74-82. <https://doi.org/10.1016/j.geoderma.2018.03.001>
- Brock JL, Hay MJM. 1996. A review of the role of grazing management on the growth and performance of white clover cultivars in lowland New Zealand pastures. In: Woodfield DR. Ed. *White clover: New Zealand's Competitive Edge. Agronomy Society of New Zealand Special Publication No. 11/ Grassland Research and Practice Series 6*: Dunedin, New Zealand: New Zealand Grassland Association, pp. 65-70. <https://doi.org/10.33584/rps.6.1995.3379>
- Brock JL, Hay MJM. 2001. White clover performance in sown pastures: A biological/ecological perspective. *Proceedings of the New Zealand Grassland Association* 63: 73-83. <https://doi.org/10.33584/jnzg.2001.63.2434>
- Brooks AK, Gaj T. 2018. Innovations in CRISPR technology. *Current Opinions in Biotechnology* 52: 95-101. <https://doi.org/10.1016/j.copbio.2018.03.007>
- Brummer EC. 1999. Capturing heterosis in forage crop cultivar development. *Crop Science* 39: 943-954. <https://doi.org/10.2135/cropsci1999.0011183X003900040001x>
- Brummer EC, Casler MD. 2014. Cool-season forages. In: Smith S, Diers B, Specht J & Carver B. Eds. *Genetic gain in major U.S. field crops*. CSSA Spec. Publ. 33. Madison, Wisconsin, United States of America: ASA, CSSA, and SSSA, pp. 33-51. <https://doi.org/10.2135/cssaspecpub33.c3>
- Bryant JR, Chapman DF, Leonard E, McMillan WH, Kerr GA, Judson G, Cookson T, Edwards GR. 2013. Development of a forage evaluation system for perennial ryegrass cultivar and endophyte combinations in New Zealand dairy systems. *Proceedings of the 22nd International Grassland Congress*, 15-19 September 2013, Sydney, Australia. pp. 1854-1855.
- Burgess RE, Easton HS. 1986. Old pasture populations of ryegrass in New Zealand and their use in plant breeding. DSIR Plant Breeding Symposium. *New Zealand Agronomy Society Special Publication 5*: 295-300.
- Burton GW, DeVane EH. 1953. Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. *Agronomy Journal* 45: 478-481. <https://doi.org/10.2134/agronj1953.00021962004501000005x>
- Buyer JS, Zuberer DA, Nichols KA, Franzluebbers AJ. 2011. Soil microbial community function, structure, and glomalin in response to tall fescue endophyte infection. *Plant and Soil* 339: 401-412. <https://doi.org/10.1007/s11104-010-0592-y>
- Cao M, Fraser K, Jones C, Stewart A, Lyons T, Faville M, Barrett B. 2017. Untargeted metabotyping *Lolium perenne* reveals population-level variation in plant flavonoids and alkaloids. *Frontiers in Plant Science* 8: <https://doi.org/10.3389/fpls.2017.00133>
- Caradus JR. 2007. Pastoral agriculture – New Zealand's competitive advantage. *Proceedings of the New Zealand Grassland Association* 69: 1-10.
- Caradus JR, Chapman DF, Cookson T, Cotching B, Donnelly L, Ferguson J, Finch SC, Gard S, Hume DE, Johnson LJ, Kerr GA, Norriss MG, Peddie K, Popay AJ. 2021. *Epichloë* endophytes – new perspectives on a key ingredient for resilient perennial grass pastures. In: Douglas GB. Ed. *Resilient Pastures Symposium. Grassland Research and Practice Series 17*. Dunedin, New Zealand: New Zealand Grassland Association, pp. 347-360. <https://doi.org/10.33584/rps.17.2021.3435>
- Caradus JR, Clark DA. 2001. Advancing dairy farming profitability through research. *Proceedings of the New Zealand Grassland Association* 63: 17-22. <https://doi.org/10.33584/jnzg.2001.63.2427>
- Caradus JR, Chapman DF. 1996. Selection for heritability of stolon characteristics in two cultivars of white clover. *Crop Science* 36: 900-904. <https://doi.org/10.2135/cropsci1996.0011183X0036000400014x>
- Caradus JR, Clifford PTP, Chapman DF, Cousins GR, Williams WM, Miller JE. 1997. Breeding and description of 'Grasslands Sustain', a medium-large leaved white clover (*Trifolium repens* L.) cultivar. *New Zealand Journal of Agricultural Research* 40: 1-7. <https://doi.org/10.1080/00288233.1997.9513224>
- Caradus JR, Hay RJM, Woodfield DR. 1996. The positioning of white clover cultivars in New Zealand. In: Woodfield DR. Ed. *White clover: New Zealand's Competitive Edge. Agronomy Society of New Zealand Special Publication No. 11. Grassland Research and*

- Practice Series 6. Dunedin, New Zealand: New Zealand Grassland Association, pp. 1-6. <https://doi.org/10.33584/rps.6.1995.3376>
- Caradus JR, Johnson LJ. 2019. Improved adaptation of temperate grasses through mutualism with fungal endophytes. In: Schouten A. Ed. *Endophyte biotechnology: promise for agriculture and pharmacology*. Wallingford, United Kingdom: CAB International., pp. 85-108. <https://doi.org/10.1079/9781786399427.0085>
- Caradus JR, Mackay AC, van den Bosch J, Wewala S, Greer DH. 1990. Heritability of frost tolerance in white clover (*Trifolium repens*). *Journal of Agricultural Science, Cambridge* 114: 151-155. <https://doi.org/10.1017/S0021859600072130>
- Caradus JR, Mackay AC, van den Bosch J, Woodfield DR. 1989. Comparative evaluation of white clover cultivars in spaced pant and small mixed species plot trials. *New Zealand Journal of Agricultural Research* 32: 433-436. <https://doi.org/10.1080/00288233.1989.10421763>
- Caradus JR, Mackay AC, Wewala S. 1991. Selection for tolerance and susceptibility to aluminium within white clover (*Trifolium repens* L.). In: Wright RJ, Baligar VC & Murrmann RP. Eds. *Proceedings 2nd International Symposium "Plant-Soil Interactions at low pH"*. Pipestream State Park, Pipestream, West Virginia, USA. June 24-29, 1990, pp. 1029-1036. https://doi.org/10.1007/978-94-011-3438-5_115
- Caradus JR, Williams WM. 1989. Breeding for legume persistence in New Zealand. In: Marten GC, Matches AG, Barnes RF, Brougham RW, Clements RJ & Sheath GW. Eds. *Persistence of forage legumes*. Proceedings of a Trilateral Workshop, Honolulu, Hawaii, 17-22 July 1988. Madison, Wisconsin, USA: American Society of Agronomy, pp. 523-539. <https://doi.org/10.2134/1989.persistanceofforagelegumes.c37>
- Carlton AJ, Cameron KC, Di HJ, Edwards GR, Clough TJ. 2019. Nitrate leaching losses are lower from ryegrass/white clover pastures containing plantain than from ryegrass/white clover forages under irrigation. *New Zealand Journal of Agricultural Research* 62: 150-172. <https://doi.org/10.1080/00288233.2018.1461659>
- Chapman DF, Bryant JR, Olayemi ME, Edwards GR, Thorrold BS, McMillan WH, Kerr GA, Judson G, Cookson T, Moorhead A, Norris M. 2017. An economically based evaluation index for perennial and short-term ryegrasses in New Zealand dairy farm systems. *Grass and Forage Science* 72: 1-21. <https://doi.org/10.1111/gfs.12213>
- Chapman DF, Lee JM, Waghorn GC. 2014. Interaction between plant physiology and pasture feeding value: a review. *Crop and Pasture Science* 65: 721-734. <https://doi.org/10.1071/CP13379>
- Chapman DF, Muir PD, Faville MJ. 2015. Persistence of dry matter yield among New Zealand perennial ryegrass (*Lolium perenne* L.) cultivars: insights from a long-term data set. *Journal of New Zealand Grasslands* 77: 177-184. <https://doi.org/10.33584/jnzc.2015.77.463>
- Chapman DF, William I, Lewis C. 2020. Productivity of New Zealand dairy pastures – recent trends and future prospects. *New Zealand Institute of Primary Industry Management, The Journal* 24: 25-32.
- Chilcoat D, Liu Z-B, Sander J. 2017. Use of CRISPR/Cas9 for crop improvement in maize and soybean. In: Weeks DP & Yang B. Eds. *Progress in molecular biology and translational science*. San Diego, California, USA: Elsevier, pp. 27-46. <https://doi.org/10.1016/bs.pmbts.2017.04.005>
- Connolly V, Wright-Turner R. 1984. Induction of cytoplasmic male-sterility into ryegrass (*Lolium perenne*). *Theoretical and Applied Genetics* 68: 449-453. <https://doi.org/10.1007/BF00254817>
- Cooper JP. 1973. Genetic variation in herbage constituents. In: Butler GW & Bailey RW. Eds. *Chemistry and biochemistry of herbage*. Volume 2. London: Academic Press, pp. 379-417.
- Corkill L, Williams WM, Lancashire JA. 1981. Pasture species and cultivars for regions. *Proceedings of the New Zealand Grassland Association* 42: 100-122. <https://doi.org/10.33584/jnzc.1981.42.1568>
- Cosgrove GP, Popay AJ, Taylor PS, Wilson DJ, Aalders LT, Bell NL. 2018. Implications of grass-clover interactions in dairy pastures for forage indexing systems. 3. Manawatu. *New Zealand Journal of Agricultural Research* 61: 174-203. <https://doi.org/10.1080/00288233.2018.1430591>
- Cranston LM, Kenyon PR, Morris ST, Kemp PD. 2015. A review of the use of chicory, plantain, red clover and white clover in a sward mix for increased sheep and beef production. *Journal of New Zealand Grasslands* 77: 89-94. <https://doi.org/10.33584/jnzc.2015.77.475>
- Crush JR. 1973. The effect of *Rhizophagus tenuis* mycorrhizas on ryegrass, cocksfoot and sweet vernal. *New Phytologist* 72: 965-973. <https://doi.org/10.1111/j.1469-8137.1973.tb02073.x>
- Crush JR. 1978. Changes in effectiveness of soil endomycorrhizal fungal populations during pasture development. *New Zealand Journal of Agricultural Research* 21: 683-685. <https://doi.org/10.1080/00288233.1978.10427466>
- Crush JR. 1995. Effect of VA mycorrhizas on phosphorus uptake and growth of white clover (*Trifolium repens* L.) growing in association with ryegrass (*Lolium perenne* L.). *New Zealand Journal of Agricultural Research* 38: 303-306. <https://doi.org/10.1080/00288233.1995.9513131>

- Crush JR, Caradus JR. 1980. Effect of mycorrhizas on growth of some white clovers. *New Zealand Journal of Agricultural Research* 23: 233-237. <https://doi.org/10.1080/00288233.1980.10430791>
- Crush JR, Rowarth JS. 2007. The role of C₄ grasses in New Zealand pastoral systems. *New Zealand Journal of Agricultural Research* 50: 125-137. <https://doi.org/10.1080/00288230709510287>
- DairyNZ. 2020. Forage Value Index. *The DairyNZ FVI Handbook* 2020 edition. 47 p.
- Dietz M, Machill S, Hoffmann HC, Schmidtke K. 2012. Inhibitory effects of *Plantago lanceolata* L. on soil N mineralization. *Plant and Soil* 368: 445-458. <https://doi.org/10.1007/s11104-012-1524-9>
- Donaghy DJ, Fulkerson WJ. 1998. Priority for allocation of water-soluble carbohydrate reserves during regrowth of *Lolium perenne*. *Grass and Forage Science* 53: 211-218. <https://doi.org/10.1046/j.1365-2494.1998.00129.x>
- Doudna JA, Charpentier E. 2014. Genome editing. The new frontier of genome engineering with CRISPR-Cas9. *Science* 346: 1258096. <https://doi.org/10.1126/science.1258096>
- Dronov R, Howard W. 2017. Gene editing and CRISPR. Occasional papers. *Office of the Chief Scientist Issue* 14: 1-5.
- Dumbleton A, Gowers S, Conner A, Christie M, Kenny P, Mulcock H, Charteris B. 2012. Cleancrop™ Brassica System: The development of herbicide resistant brassica crops for New Zealand farming systems. *Proceedings of the New Zealand Grassland Association* 74: 25-30. <https://doi.org/10.33584/jnzg.2012.74.2880>
- Dunbier MW. 1983. Lucerne. In: Wratt GS & Smith HC. Eds. *Plant breeding in New Zealand*. Wellington, New Zealand: Butterworths, DSIR, pp. 243-252. <https://doi.org/10.1016/B978-0-409-70137-1.50037-3>
- Easton HS, Amyes JM, Cameron NE, Green RB, Kerr GA, Norriss MG, Stewart AV. 2002. Pasture plant breeding in New Zealand: where to from here? *Proceedings of the New Zealand Grassland Association* 64: 173-179. <https://doi.org/10.33584/jnzg.2002.64.2455>
- Easton HS, Bair, D, Baxter G, Cameron N, Hainsworth R, Johnston C, Kerr G, Lyons T, McCabe R, Nichol W, Norriss M, Stewart A, Thom E. 1997. Annual and hybrid ryegrass cultivars in New Zealand. *Proceedings of the New Zealand Grassland Association* 59: 239-244. <https://doi.org/10.33584/jnzg.1997.59.2248>
- Easton HS, Jahufer MZZ, Flay C, Schmidt J, Rolston MP, Trethewey JAK, Ryan DL, Faville MJ. 2015. Environment and ryegrass genetics – multisite trial of advanced breeding populations. *Journal of New Zealand Grasslands* 77: 233-238. <https://doi.org/10.33584/jnzg.2015.77.455>
- Easton HS, Lee CK, Fitzgerald RD. 1994. Tall fescue in Australia and New Zealand. *New Zealand Journal of Agricultural Research* 37: 405-417. <https://doi.org/10.1080/00288233.1994.9513078>
- Easton HS, Lyons TB, Cooper BM, Mace WJ. 2009. Loline alkaloids for better protection of pastures from insect pests. *Proceedings of the New Zealand Grassland Association* 71: 151-154. <https://doi.org/10.33584/jnzg.2009.71.2743>
- Easton HS, Pennell CG. 1993. Breeding tall fescue for establishment vigour. *Proceedings of the New Zealand Grassland Association* 55: 151-154. <https://doi.org/10.33584/jnzg.1993.55.2094>
- Easton H, Stewart A, Kerr G. 2011. Ryegrass in pastures – breeding for resilience. In: Mercer CF. Ed. *Pasture Persistence Symposium. Grassland Research and Practice Series 15*. Dunedin, New Zealand: New Zealand Grassland Association, pp. 139-148. <https://doi.org/10.33584/rps.15.2011.3208>
- Elgersma A. 1990. Heritability estimates of spaced-plant traits in three perennial ryegrass (*Lolium perenne* L.) cultivars. *Euphytica* 51: 163-171. <https://doi.org/10.1007/BF00022447>
- Falconer DS. 1989. *Introduction to quantitative genetics*. 3rd edition. Longman Scientific and Technical, Hong Kong. 438 p.
- Faville MJ, Cao M, Schmidt J, Ryan DL, Ganesh S, Jahufer MZZ, Hong SW, George R, Barrett BA. 2020a. Divergent genomic selection for herbage accumulation and days-to-heading in perennial ryegrass. *Agronomy* 10: 340. <https://doi.org/10.3390/agronomy10030340>
- Faville MJ, Ganesh S, Cao M, Jahufer MZZ, Bilton TP, Easton HS, Ryan DL, Trethewey JAK, Rolston PM, Griffiths AG, Moraga R, Flay C, Schmidt J, Tan R, Barrett BA. 2018. Predictive ability of genomic selection models in a multi-population perennial ryegrass training set using genotyping-by-sequencing. *Theoretical and Applied Genetics* 131: 703-720. <https://doi.org/10.1007/s00122-017-3030-1>
- Faville MJ, Griffiths AG, Baten A, Cao M, Ashby R, Ghamkhar K, Hong W, Larking A, Williamson M, Webber Z. 2020b. Genomic assessment of white clover and perennial ryegrass genetic resources. *Journal of New Zealand Grasslands* 82: 27-34. <https://doi.org/10.33584/jnzg.2020.82.437>
- Fè D, Pedersen MG, Jensen CS, Jensen J. 2015. Genetic and environmental variation in a commercial breeding program of perennial ryegrass. *Crop Science* 55: 631-640. <https://doi.org/10.2135/cropsci2014.06.0441>
- Field TRO, Ball R. 1978. Tactical use of fertilizer nitrogen. *Proceedings Agronomy Society of New Zealand* 8: 129-133.

- Field TRO, Forde MB. 1990. Effects of climate warming on the distribution of C4 grasses in New Zealand. *Proceedings of the New Zealand Grassland Association* 51: 47-50. <https://doi.org/10.33584/jnzc.1990.51.1914>
- Ford JL, Barrett BA. 2011. Improving red clover persistence under grazing. *Proceedings of the New Zealand Grassland Association* 73: 119-124. <https://doi.org/10.33584/jnzc.2011.73.2838>
- Forde BJ, Slack CR, Roughan PG, Whitehead HCM. 1976a. Growth of tropical and temperate grasses at Palmerston North: I. Warm-season yields with and without irrigation. *New Zealand Journal of Agricultural Research* 19: 135-142. <https://doi.org/10.1080/00288233.1976.10426759>
- Forde BJ, Slack CR, Roughan PG, Haslemore RM, McLeod MN. 1976b. Growth of tropical and temperate grasses at Palmerston North: II. Total nitrogen, soluble sugar starch and in vitro digestibility determinations. *New Zealand Journal of Agricultural Research* 19: 489-498. <https://doi.org/10.1080/00288233.1976.10420980>
- Foster CA. 1971. Interpopulation and intervarietal hybridization in *Lolium perenne* breeding: heterosis under non-competitive conditions. *Journal of Agricultural Science* 76: 107-130. <https://doi.org/10.1017/S0021859600015665>
- Frandsen KJ. 1986. Variability and inheritance of digestibility in perennial ryegrass (*Lolium perenne*), meadow fescue (*Festuca pratensis*) and cocksfoot (*Dactylis glomerata*). *Acta Agriculturae Scandinavica* 36: 241-263. <https://doi.org/10.1080/00015128609436528>
- Fraser TJ, Rowarth JS. 1996. Legumes, herbs or grass for lamb performance? *Proceedings of the New Zealand Grassland Association* 58: 49-52. <https://doi.org/10.33584/jnzc.1996.58.2213>
- Fritsche S, Poovalah C, MacRae E, Thorlgy G. 2018. A New Zealand perspective on the application and regulation of gene editing. *Frontiers in Plant Science* 9: 1323. <https://doi.org/10.3389/fpls.2018.01323>
- Geiger HH, Miedaner T. 1999. Hybrid rye and heterosis. In: Coors JG & Pandey S. Eds. *Genetics and exploitation of heterosis in crops*. Madison, Wisconsin, United States of America: ASA, CSSA, SSSA, pp. 439-450. <https://doi.org/10.2134/1999.geneticsandexploitation.c41>
- George RM, Barrett BA, Ghamkhar K. 2019. Evaluation of LiDAR scanning for measurement of yield in perennial ryegrass. *Journal of New Zealand Grasslands* 81: 55-60. <https://doi.org/10.33584/jnzc.2019.81.414>
- Ghamkhar K, Irie K, Hagedorn M, Hsiao J, Fourie J, Gebbie S, Hoyos-Villegas V, George R, Stewart A, Inch C, Werner A, Barrett B. 2019. Real-time, non-destructive and in-field foliage yield and growth rate measurement in perennial ryegrass (*Lolium perenne* L.). *Plant Methods* 15: 72. <https://doi.org/10.1186/s13007-019-0456-2>
- Gibbs JA. 2019. Estimating national greenhouse gas emissions from fertiliser and lime. In: Currie LD & Christensen CL. Eds. *Nutrient loss mitigations for compliance in agriculture. Occasional Report No. 32*. Palmerston North, New Zealand: Fertilizer and Lime Research Centre, Massey University. 5 p. <http://flrc.massey.ac.nz/publications.html>
- Goldson SL, Barker GM, Chapman HM, Popay AJ, Stewart AV, Caradus JR, Barratt BIP. 2020. Severe pest impacts on New Zealand pasture; The plight of an ecological outlier. *Journal of Insect Science* 20: 1-17. <https://doi.org/10.1093/jisesa/ieaa018>
- Guo BZ, Hendrix JW, An ZQ, Ferriss RS. 1992. Role of *Acremonium* endophyte of fescue on inhibition of colonization and reproduction of mycorrhizal fungi. *Mycologia* 84: 882-885. <https://doi.org/10.1080/00275514.1992.12026220>
- Gutzwiller A. 1993. The effect of a diet containing cyanogenetic glycosides on the selenium status and the thyroid function of sheep. *Animal Production* 57: 415-419. <https://doi.org/10.1017/S1357729800042740>
- Hageman IW, Lantinga EA, Schelplers H, Neuteboom JH. 1993. Herbage intake, digestibility characteristics and milk production of a diploid and two tetraploid cultivars of perennial ryegrass. *Proceedings of the XVII International Grasslands Congress*. Palmerston North, New Zealand. pp. 459-460.
- Hancock K, Collette V, Chapman E, Hanson K, Temple S, Moraga R, Caradus J. 2014. Progress towards developing bloat-safe legumes for the farming industry. *Crop and Pasture Science* 65: 1107-1113. <https://doi.org/10.1071/CP13308>
- Hancock KR, Collette V, Fraser K, Greig M, Xue H, Richardson K, Jones C, Rasmussen S. 2012. Expression of the R2R3-MYB transcription factor TaMYB14 from *Trifolium arvense* activates proanthocyanidin biosynthesis in the legumes *Trifolium repens* and *Medicago sativa*. *Plant Physiology* 159: 1204-1220. <https://doi.org/10.1104/pp.112.195420>
- Hare MD, Rolston MP, Crush JR, Fraser TL. 1987. Puna chicory - a perennial herb for New Zealand pastures. *Proceedings of the Agronomy Society of New Zealand* 17: 45-49.
- Harmer M, Stewart AV, Woodfield DR. 2016. Genetic gain in perennial ryegrass forage yield in Australia and New Zealand. *Journal of New Zealand Grasslands* 78: 133-138. <https://doi.org/10.33584/jnzc.2016.78.514>
- Harris SL, Clark DA, Auldust MJ, Waugh CD, Laboyrie

- PG. 1997. Optimum white clover content for dairy pastures. *Proceedings of the New Zealand Grassland Association* 59: 29-33. <https://doi.org/10.33584/jnzc.1997.59.2261>
- Havey MJ. 2004. The use of cytoplasmic male sterility for hybrid seed production. In: Daniell H & Chase C. Eds. *Molecular biology and biotechnology of plant organelles*. Dordrecht, Netherlands: Springer, pp. 623-634. https://doi.org/10.1007/978-1-4020-3166-3_23
- Hayes BJ, Cogan NOI, Pembleton LW, Goddard ME, Wang J, Spangenberg GC, Forster JW. 2013. Prospects for genomic selection in forage plant species. *Plant Breeding* 132: 133-143. <https://doi.org/10.1111/pbr.12037>
- Herridge RP, Macknight RC, Brownfield LT. 2019. Prospects for F1 hybrid production in ryegrass. *New Zealand Journal of Agricultural Research* 63: 405-415. <https://doi.org/10.1080/00288233.2018.1559867>
- Hume DE, Stewart AV, Simpson WR, Johnson RD. 2020. *Epichloë* fungal endophytes play a fundamental role in New Zealand grasslands. *Journal of the Royal Society of New Zealand* 50: 279-298. <https://doi.org/10.1080/03036758.2020.1726415>
- Hyslop MG, Fraser TJ, Smith DR, TL Knight TL, Slay MWA, Moffat CA. 2000. Liveweight gain of young sheep grazing tall fescue or perennial ryegrass swards of different white clover content. *Proceedings of the New Zealand Society of Animal Production* 60: 51-54.
- Islam MS, Studer B, Møller IM, Asp T. 2014. Genetics and biology of cytoplasmic male sterility and its applications in forage and turf grass breeding. *Plant Breeding* 133: 299-312. <https://doi.org/10.1111/pbr.12155>
- Jighly A, Lin Z, Pembleton LW, Cogan NOI, Spangenberg GC, Hayes BJ, Daetwyler HD. 2019. Boosting Genetic gain in allogamous crops via speed breeding and genomic selection. *Frontiers in Plant Science* 10: 1364. <https://doi.org/10.3389/fpls.2019.01364>
- Johnson LJ, de Bonth ACM, Briggs LR, Caradus JR, Finch SC, Fleetwood DJ, Fletcher LR, Hume DE, Johnson RD, Popay AJ, Tapper BA, Simpson WR, Voisey CR, Card SD. 2013. The exploitation of epichloae endophytes for agricultural benefit. *Fungal Diversity* 60: 171-188. <https://doi.org/10.1007/s13225-013-0239-4>
- Johnson LJ, Voisey CR, Faville MJ, Moon CD, Simpson WR, Johnson RD, Stewart AV, Caradus JR, Hume DE. 2019. Advances and perspectives in breeding for improved grass-endophyte associations. In: Huguenin-Elie O, Studer B, Kolliker R, Reheul D, Probo M, Barre P, Feuerstein U, Roldan-Ruiz I, Mariotte P & Hopkins A. Eds. *Improving sown grasslands through breeding and management*, Joint Symposium EFG/Eucarpia, Zurich, Switzerland, 24 to 27 June 2019. Eucarpia. *Grassland Science in Europe* 24: 351-363.
- Judson HG, Fraser PM, Peterson ME, Edwards GR. 2018. Specific genotypes of plantain (*Plantago lanceolata*) vary in their impact on sheep urine volume and nitrification in the urine patch. *Journal of New Zealand Grasslands* 80:125-128. <https://doi.org/10.33584/jnzc.2018.80.335>
- Judson HG, McAnulty R, Sedcole R. 2009. Evaluation of 'Ceres Tonic' plantain (*Plantago lanceolata*) as a lactation feed for twin-bearing ewes. *Proceedings of the New Zealand Grassland Association* 71: 201-205. <https://doi.org/10.33584/jnzc.2009.71.2749>
- Kerr GA. 1987. Evaluation of perennial ryegrass cultivars in New Zealand. *Proceedings of the New Zealand Grassland Association* 48: 137-141. <https://doi.org/10.33584/jnzc.1987.48.1797>
- Kiang A, Connolly V, McDonnell D, Kavanagh T. 1993. Cytoplasmic male sterility (CMS) in *Lolium perenne* L. 1. Development of a diagnostic probe for the male-sterile cytoplasm. *Theoretical and Applied Genetics* 86: 781-787. <https://doi.org/10.1007/BF00222670>
- Kiang AS, Kavanagh TA. 1996. Cytoplasmic male sterility (CMS) in *Lolium perenne* L. 2. The mitochondrial genome of a CMS line is rearranged and contains a chimaeric atp 9 gene. *Theoretical and Applied Genetics* 92: 308-315. <https://doi.org/10.1007/s001220050129>
- Kucey RMN, Paul EA 1982. Biomass of mycorrhizal fungi associated with bean roots. *Soil Biology and Biochemistry* 14: 413-414. [https://doi.org/10.1016/0038-0717\(82\)90014-1](https://doi.org/10.1016/0038-0717(82)90014-1)
- Kumar R, Bohra A, Pandey AK, Pandey MK, Kumar A. 2017. Metabolomics for plant improvement: status and prospects. *Frontiers in Plant Science* 8: issue 1302. <https://doi.org/10.3389/fpls.2017.01302>
- Lee JM, Matthew C, Thom ER, Chapman DF. 2012. Perennial ryegrass breeding in New Zealand: a dairy industry perspective. *Crop and Pasture Science* 63: 107-127. <https://doi.org/10.1071/CP11282>
- Levy EB. 1932. Strain developments in herbage plants. *Proceedings of the New Zealand Grassland Association* 1: 1-5. <https://doi.org/10.33584/jnzc.1932.1.757>
- Li GD, Kemp PD. 2005. Forage chicory (*Cichorium intybus* L.): A review of its agronomy and animal production. *Advances in Agronomy* 88: 187-222. [https://doi.org/10.1016/S0065-2113\(05\)88005-8](https://doi.org/10.1016/S0065-2113(05)88005-8)
- Li X, Wei Y, Acharya A, Hansen JL, Crawford JL, Viands DR, Michaud R, Claessens A, Brummer EC. 2015. Genomic prediction of biomass yield in two selection cycles of a tetraploid alfalfa breeding population. *The Plant Genome* 8: 1-10. <https://doi.org/10.3835/plantgenome2014.12.0090>

- Lightbourne M. 2009. The FAO multilateral system for plant genetic resources for food and agriculture: Better than bilateralism? *Washington University Journal of Law and Policy* 30: 465-507.
- Lin Z, Cogan NOI, Pembleton LW, Spangenberg GC, Forster J, Hayes B, Daetwyler HD. 2016. Genetic gain and inbreeding from genomic selection in a simulated breeding program for perennial ryegrass. *The Plant Genome* 9. 12 p. <https://doi.org/10.3835/plantgenome2015.06.0046>
- Lindsay CL, Kemp PD, Kenyon PR, Morris ST. 2007. Summer lamb finishing on forage crops. *Proceedings of the New Zealand Society of Animal Production* 67: 121-125.
- Liu S. 2015. *Application of molecular markers in selected breeding material and plant genetic resources of Lolium perenne L.* Ph.D. thesis, Faculty of Agricultural Sciences, Georg-August-University Göttingen, Germany. 139 p.
- Lolicato S, Rumball W. 1994. Past and present improvement of cocksfoot (*Dactylis glomerata* L.) in Australia and New Zealand. *New Zealand Journal of Agricultural Research* 37: 379-390. <https://doi.org/10.1080/00288233.1994.9513075>
- Ludemann CI, Wims CM, Chapman DF. 2017. Validation of perennial ryegrass cultivar Forage Value Index rankings using independent trial data. *Journal of New Zealand Grasslands* 79: 89-96. <https://doi.org/10.33584/jnzc.2017.79.562>
- Lugtenberg BJJ, Malfanova N, Kamiloa F, Berg G. 2013. Plant growth promotion by microbes. In: de Bruijn FJ. Ed. *Molecular microbial ecology of the rhizosphere, Volume 2*. Hoboken, New Jersey, United States of America: John Wiley & Sons Inc., pp. 561-573. <https://doi.org/10.1002/9781118297674.ch53>
- Mack KML, Rudgers JA. 2008. Balancing multiple mutualists: Asymmetric interactions among plants, arbuscular mycorrhizal fungi, and fungal endophytes. *Oikos* 117: 310-320. <https://doi.org/10.1111/j.2007.0030-1299.15973.x>
- Macleod CJA, Humphreys MW, Whalley WR, Turner L, Binley A, Watts CW, Skøt L, Joynes A, Hawkins S, King IP, O'Donovan S, Haygarth PM. 2013. A novel grass hybrid to reduce flood generation in temperate regions. *Scientific Reports* 3: 1-7. <https://doi.org/10.1038/srep01683>
- McClearn B, Gilliland T, Guy C, Dineen M, Coughlan F, McCarthy B. 2020. The effect of perennial ryegrass ploidy and white clover inclusion on milk production of dairy cows. *Animal Production Science* 60: 143-147. <https://doi.org/10.1071/AN18539>
- McCouch S. 2004. Diversifying selection in plant breeding. *PLOS Biology* 2: e347. <https://doi.org/10.1371/journal.pbio.0020347>
- McDermott P. 2008. The mitochondrial genome of a cytoplasmic male sterile line of perennial ryegrass (*Lolium perenne* L.) contains an integrated linear plasmid-like element. *Theoretical and Applied Genetics* 117: 459-470. <https://doi.org/10.1007/s00122-008-0790-7>
- Ministry for the Environment. 2010. *Land use – environmental snapshot*. Retrieved 11 September 2021 from: https://environment.govt.nz/assets/Publications/Files/land-use_0_0.pdf
- Minneé EMK, Knight TL, Sutherland BL, Vlaming JB, Fletcher LR, Clark DA. 2010. Herbage production from perennial ryegrass and tall fescue pastures under irrigation in the Canterbury and Waikato regions of New Zealand. *Proceedings of the New Zealand Grassland Association* 72: 185-190. <https://doi.org/10.33584/jnzc.2010.72.2790>
- Monk S, Moot DJ, Belgrave B, Rolston MP, Caradus JR. 2016. Availability of seed for hill country adapted forage legumes. In: Thom ER. Ed. *Hill Country Symposium. Grassland Research and Practice Series 16*. Dunedin, New Zealand: New Zealand Grassland Association, pp. 257-268. <https://doi.org/10.33584/rps.16.2016.3237>
- Moorhead AJE, Judson HG, Stewart AV. 2002. Liveweight gain of lambs grazing 'Ceres Tonic' plantain (*Plantago lanceolata*) or perennial ryegrass (*Lolium perenne*). *Proceedings of the New Zealand Society of Animal Production* 62: 171-173.
- Moorhead AJE, Piggot GJ. 2009. The performance of pasture mixes containing 'Ceres Tonic' plantain (*Plantago lanceolata*) in Northland. *Proceedings of the New Zealand Grassland Association* 71: 195-199. <https://doi.org/10.33584/jnzc.2009.71.2757>
- Müller J. 2003. Artificial infection by endophytes affect growth and mycorrhizal colonization of *Lolium perenne*. *Functional Plant Biology* 30: 419-424. <https://doi.org/10.1071/FP02189>
- Newman M, Savage J. 2009. Benchmarking – Key drivers for successful dairy business. *Proceedings of the South Island Dairy Event (SIDE)* pp. 184-195. <https://www.side.org.nz/proceedings/>
- Nixon C. 2016. *How valuable is that plant species? Application of a method for enumerating the contribution of selected plant species to New Zealand's GDP* [MPI Technical Paper No: 2016/62]. Ministry for Primary Industries, Wellington, New Zealand. 227 p.
- Novas MV, Cabral D, Godeas AM. 2005. Interaction between grass endophytes and mycorrhizas in *Bromus setifolius* from Patagonia, Argentina. *Symbiosis* 40: 23-30.
- O'Connor JR, Lyons TB, Jahufer MZZ, Faville M, Barrett BA. 2015. Identifying potential heterosis in perennial ryegrass. *Journal of New Zealand Grasslands* 77: 227-232. <https://doi.org/10.33584/>

- jnzg.2015.77.456
- Ong CK, Marshall C, Saoar GR. 1978. The physiology of tiller death in grasses. 2. Causes of tiller death in a grass sward. *Grass and Forage Science* 33: 205-211. <https://doi.org/10.1111/j.1365-2494.1978.tb00821.x>
- Parsons AJ, Edwards GR, Newton PCD, Chapman DF, Caradus JR, Rasmussen S, Rowarth JS. 2011. Past lessons and future prospects: plant breeding in cool temperate pastures. *Grass and Forage Science* 66: 153-172. <https://doi.org/10.1111/j.1365-2494.2011.00785.x>
- Pastoral Industry Forage Discussion Document. 2017. *Pastoral Industry Forage Discussion Document 2016-2036*. James Morrison Consulting Ltd. <https://beeflambnz.com/sites/default/files/levies/files/Forage%20Discussion%20Document%20November%202017.pdf>
- Pazos-Navarro M, Castello M, Bennett RG, Nichols P, Croser J. 2017. *In vitro*-assisted single-seed descent for breeding-cycle compression in subterranean clover (*Trifolium subterraneum* L.). *Crop & Pasture Science* 68: 958-966. <https://doi.org/10.1071/CP17067>
- Pedreira CGS, Silva VJ, Maria DC, Ferragine MDC, Bouton JH, Tonato F, Otani L, Basto DC. 2020. Validating the NAAIC alfalfa grazing tolerance standard test and assessing physiological responses to grazing in a tropical environment. *Crop Science* 60: 1702-1710. <https://doi.org/10.1002/csc2.20145>
- Pembleton LW, Shinozuka H, Wang J, Spangenberg GC, Forster JW, Cogan NO. 2015. Design of an F1 hybrid breeding strategy for ryegrasses based on selection of self-incompatibility locus-specific alleles. *Frontiers in Plant Science* 6: 764. <https://doi.org/10.3389/fpls.2015.00764>
- Penno JW, Bryant AM, MacDonald HA, Carter WA. 1996. Enhancing pasture-based dairying with supplementary feeds. *Proceedings of the New Zealand Grassland Association* 58: 113-118. <https://doi.org/10.33584/jnzg.1996.58.2234>
- Popay AJ, Jensen JG. 2005. Soil biota associated with endophyte-infected tall fescue in the field. *New Zealand Plant Protection* 58: 117-121. <https://doi.org/10.30843/nzpp.2005.58.4282>
- Popay AJ, Tapper BA, Podmore C. 2009. Endophyte-infected meadow fescue and loline alkaloids affect Argentine stem weevil larvae. *New Zealand Plant Protection* 62: 19-27. <https://doi.org/10.30843/nzpp.2009.62.4801>
- Porter SS, Sachs JL. 2020. Agriculture and the disruption of plant-microbial symbiosis. *Trends in Ecology and Evolution* 35: 426-439. <https://doi.org/10.1016/j.tree.2020.01.006>
- Powell C. 1976. Mycorrhizal fungi stimulate clover growth in New Zealand hill country soils. *Nature* 264: 436-438. <https://doi.org/10.1038/264436a0>
- Resende, RMS, Casler MD, de Resende MDV. 2014. Genomic selection in forage breeding: accuracy and methods. *Crop Science* 54: 143-156. <https://doi.org/10.2135/cropsci2013.05.0353>
- Rhodes I. 1973 the relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.). *Journal of Agricultural Science (Cambridge)* 80: 171-176. <https://doi.org/10.1017/S002185960005718X>
- Rhodes I, Harris W. 1979. The nature and basis of differences in sward composition and yield in ryegrass-white clover mixtures. *British Grasslands Society Occasional Symposium no. 10*: 55-60.
- Riday H, Brummer EC. 2014. Vigor and persistence of birdsfoot trefoil populations selected with or without an orchardgrass companion evaluated in grass sod. *Crop Science* 54: 2070-2076. <https://doi.org/10.2135/cropsci2014.02.0147>
- Rijswijk K, Brazendale R. 2016. Pasture renewal practices, experience and attitudes: a comparison over time. *Journal of New Zealand Grasslands* 78: 51-56. <https://doi.org/10.33584/jnzg.2016.78.520>
- Rogers NI, Putt HB. 1997. Economic nitrogen responses on wet Northland soils. *Proceedings of the New Zealand Grassland Association* 59: 129-130. <https://doi.org/10.33584/jnzg.1997.59.2275>
- Rolleston WBR. 2016. Conditions for co-existence of genetic modification in a pasture based system – a farmer perspective. *Journal of New Zealand Grasslands* 78: 83-88. <https://doi.org/10.33584/jnzg.2016.78.509>
- Rowe DE, Brink GE. 1993. Heritabilities and genetic correlations of white clover clones grown in three environments. *Crop Science* 33: 1149-1152. <https://doi.org/10.2135/cropsci1993.0011183X003300060008x>
- Rumball W. 1982. 'Grasslands Kara' cocksfoot (*Dactylis glomerata* L.). *New Zealand Journal of Experimental Agriculture* 10: 49-50. <https://doi.org/10.1080/03015521.1982.10427841>
- Rumball W. 1986. 'Grasslands Puna' chicory (*Cichorium intybus* L.). *New Zealand Journal of Agricultural Research* 14: 105-107. <https://doi.org/10.1080/03015521.1986.10426133>
- Russell WA. 1991. Genetic improvement of maize yields. *Advances in Agronomy* 46: 245-298. [https://doi.org/10.1016/S0065-2113\(08\)60582-9](https://doi.org/10.1016/S0065-2113(08)60582-9)
- Rys GJ, Ritchie IM, Smith RG, Thomson NA, Crouchley G, Stiefel W. 1977. The performance of 'Grasslands Matua' prairie grass in the southern North Island. *Proceedings of the New Zealand Grassland Association* 39: 148-155. <https://doi.org/10.33584/jnzg.1977.39.1491>
- Shea K. 2014. *Monsanto Company and Forage Genetics International; Determination of Nonregulatory*

- Status of Genetically Engineered Alfalfa. *Federal Register* 79: No. 217. pp. 66686-66687.
- Shi S, Wakelin S, Ballard R, Caradus J, O'Callaghan M. 2019. Increasing biological nitrogen fixation by white clover-rhizobia symbiosis. *Journal of New Zealand Grasslands* 81: 231-234. <https://doi.org/10.33584/jnzc.2019.81.380>
- Sprague GF. 1983. Heterosis in maize: Theory and practice. In: Frankel R. Ed. *Monographs on theoretical and applied genetics; Heterosis: Reappraisal of theory and practice. Chapter 2*. Berlin, Heidelberg, Germany: Springer-Verlag, pp. 47-70. https://doi.org/10.1007/978-3-642-81977-3_2
- Stewart AV. 1992. 'Grasslands Gala' grazing brome - (*Bromus stamineus* Desv.) - a new dryland pasture grass. *New Zealand Journal of Agricultural Research* 35: 349-353. <https://doi.org/10.1080/00288233.1992.10427513>
- Stewart AV. 1996. Plantain (*Plantago lanceolata*) – a potential pasture species. *Proceedings of the New Zealand Grassland Association* 58: 77-86. <https://doi.org/10.33584/jnzc.1996.58.2221>
- Stewart AV. 2006. Genetic origins of New Zealand perennial ryegrass (*Lolium perenne*) cultivars. In: Mercer CF. Ed. *Advances in Plant Breeding. Grassland Research and Practice Series 12*. Dunedin, New Zealand: New Zealand Grassland Association, pp. 55-62. <https://doi.org/10.33584/rps.12.2006.3042>
- Stewart AV, Hayes R. 2011. Ryegrass breeding – balancing trait priorities. *Irish Journal of Agricultural and Food Research* 50: 31-46.
- Stubber CW. 1994 Heterosis in plant breeding. In: Janick J. Ed. *Plant breeding reviews 12*. Hoboken, New Jersey, United States of America: John Wiley & Sons, Inc, pp. 227-251. <https://doi.org/10.1002/9780470650493.ch8>
- Subbaraj AK, Huege J, Fraser K, Cao M, Rasmussen S, Faville M, Harrison SJ, Jones C. 2019. A large-scale metabolomics study to harness chemical diversity and explore biochemical mechanisms in ryegrass. *Communications Biology* 2: Article no: 87. 17 p. <https://doi.org/10.1038/s42003-019-0289-6>
- Sun X, Luo N, Longhurst B, Luo J. 2008. Fertiliser nitrogen and factors affecting pasture responses. *The Open Agriculture Journal* 2: 35-42. [doi.10.2174/1874331500802010035](https://doi.org/10.2174/1874331500802010035)
- Sykes VR, Allen FL, DeSantis AC, Saxton AM, Bhandari HS, West DR, Hughes EW, Bobbitt ME, Benelli VG. 2017. Efficiency of spaced-plant selection in improving sward biomass and ethanol yield in switchgrass. *Crop Science* 57: 253-263. <https://doi.org/10.2135/cropsci2016.07.0596>
- Tanksley SD, McCouch SR. 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* 277: 1063-1066. <https://doi.org/10.1126/science.277.5329.1063>
- The New Zealand Government. 2016. *GMO Regulations Clarified, 5 April 2016*. Retrieved 11 September 2021 from: <https://www.beehive.govt.nz/release/gmo-regulations-clarified>
- Thomas S, Wallace D, Beare M. 2014. *Pasture Renewal Activity Data and Factors for New Zealand* [Plant & Food Research Client Report No. 10389, 10670. Plant & Food Research Contract No. 16806]. The New Zealand Institute for Plant & Food Research Ltd, Auckland, New Zealand. 65p. <https://www.mpi.govt.nz/dmsdocument/10640/direct>
- Tozer KN, Cameron CA, Thom ER. 2011. Pasture persistence: farmer observations and field measurements. In: Mercer CF. Ed. *Pasture Persistence Symposium. Grassland Research and Practice Series 15*. Dunedin, New Zealand: New Zealand Grassland Association, pp. 25-30. <https://doi.org/10.33584/rps.15.2011.3216>
- van den Bosch J, Mercer CF. 1996. Variation in white clover for root-knot nematode resistance. *New Zealand Journal of Agricultural Research* 39: 137-48. <https://doi.org/10.1080/00288233.1996.9513172>
- van den Bosch J, Mercer CF, Grant JL. 1997. Variation in white clover for resistance to clover cyst nematode. *New Zealand Journal of Agricultural Research* 40: 223-9. <https://doi.org/10.1080/00288233.1997.9513241>
- Vipond JE, Swift G, McClelland TH, Fitzsimons J, Milne JA, Hunter EA. 1993. A comparison of diploid and tetraploid ryegrass and tetraploid white clover swards under continuous sheep stocking at controlled sward heights. 2. Animal production. *Grass and Forage Science* 48: 290-300. <https://doi.org/10.1111/j.1365-2494.1993.tb01862.x>
- Waghorn GC, Clark DA. 2004. Feeding value of pastures for ruminants. *New Zealand Veterinary Journal* 52: 320-331. <https://doi.org/10.1080/00480169.2004.36448>
- Waldron BL, Robins JG, Peel MD, Jensen KB. 2008. Predicted efficiency of spaced-plant selection to indirectly improve tall fescue sward yield and quality. *Crop Science* 48: 443-449. <https://doi.org/10.2135/cropsci2007.06.0354>
- Wang Z-Y, Brummer EC. 2012. Is genetic engineering ever going to take off in forage, turf and bioenergy crop breeding? *Annals of Botany* 110: 1317-25. <https://doi.org/10.1093/aob/mcs027>
- Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey M-D, Hatta, Asyraf MAMd, Hinchliffe A, Steed A, Reynolds D, et al. 2018. Speed breeding is a powerful tool to accelerate crop research and breeding. *Nature Plants* 4: 23-29. [doi.10.1038/s41477-017-0083-8](https://doi.org/10.1038/s41477-017-0083-8)

- Wheeler DM, Edmeades DC, Smith DR, Wedderburn ME. 1992. Screening perennial rye-grass from New Zealand for aluminium tolerance. *Plant and Soil* 146: 9-19. <https://doi.org/10.1007/BF00011990>
- White DWR. 1988. Use of cell and molecular genetic manipulation to improve pasture plants. *Proceedings of the New Zealand Grassland Association* 49: 67-72. <https://doi.org/10.33584/jnzc.1988.49.1828>
- Widdup KH, Ford JL, Cousins GR, Woodfield DR, Caradus JR, Barrett BA. 2015. A comparison of New Zealand and overseas white clover cultivars under grazing in New Zealand. *Journal of New Zealand Grasslands* 77: 51-56. <https://doi.org/10.33584/jnzc.2015.77.483>
- Williams W, Easton H, Jones C. 2007. Future options and targets for pasture plant breeding in New Zealand. *New Zealand Journal of Agricultural Research* 50: 223-248. <https://doi.org/10.1080/00288230709510292>
- Willocks MJ. 1999. Commercialisation of genetically modified crops in New Zealand. *Proceedings of the New Zealand Grassland Association* 61: 117-119. <https://doi.org/10.33584/jnzc.1999.61.2346>
- Wims CM, Ludemann CI, Phillips H, Chapman DF. 2017. The economic value to dairy systems of genetic gains in the nutritive value of perennial ryegrass in grass-clover pastures. *Animal Production Science* 57: 1357-1365. <https://doi.org/10.1071/ANI6487>
- Winichayakul S, Cookson R, Scott R, Zhou J, Zou X, Roldan M, Richardson K, Roberts N. 2008. Delivery of grasses with high levels of unsaturated, protected fatty acids. *Proceedings of the New Zealand Grassland Association* 70: 211-216. <https://doi.org/10.33584/jnzc.2008.70.2721>
- Wit F. 1974. Cytoplasmic male sterility in ryegrasses (*Lolium* spp.) detected after intergeneric hybridization. *Euphytica* 23: 31-38. <https://doi.org/10.1007/BF00032737>
- Woodfield DR. 1999. Genetic improvements in New Zealand forage cultivars. *Proceedings of the New Zealand Grassland Association* 61: 3-7. <https://doi.org/10.33584/jnzc.1999.61.2355>
- Woodfield DR, Caradus JR. 1990. Estimates of heritability for, and relationships between, root and shoot characters of white clover. II. Regression of progeny on mid-parent. *Euphytica* 46: 211-215. <https://doi.org/10.1007/BF00027220>
- Woodfield DR, Caradus JR. 1996. Factors affecting white clover persistence in New Zealand pastures. *Proceedings of the New Zealand Grassland Association* 58: 229-235. <https://doi.org/10.1007/BF00027220>
- Woodfield DR, Easton HS. 2004. Advances in pasture plant breeding for animal productivity and health. *New Zealand Veterinary Journal* 52: 300-310. <https://doi.org/10.1080/00480169.2004.36446>
- Woodfield DR, Judson H. 2018. Balancing pasture productivity with environmental and animal health requirements. In: Marshall A & Collins R. Eds. *Improving grassland and pasture management in temperate agriculture*. Cambridge, United Kingdom: Burleigh Dodds Science Publishing, pp. 257-272. <https://doi.org/10.1201/9781351114561-12>
- Woodfield DR, Roldan MB, Voisey CR, Cousins GR, Caradus JR. 2019. Improving environmental benefits of white clover through condensed tannin expression. *Journal of New Zealand Grasslands* 81: 195-202. <https://doi.org/10.33584/jnzc.2019.81.382>
- Wratt GS, Smith HC. 1983. *Plant breeding in New Zealand*. Butterworths, DSIR, Wellington, New Zealand. 309 p.
- Wynn-Williams RB. 1987. Plant breeders' rights legislation with special reference to native plants. *Tuatara, Journal of the Biological Society* 29: 8-12.

