

The impact of a forage plant breeder – the story of Herrick Sydney (Syd) Easton (1946 - 2023)

John R CARADUS^{1*}, R John M HAY², M Phil ROLSTON³, David E HUME⁴,
Marty J FAVILLE⁴, Derek R WOODFIELD⁵

¹Grasslanz Technology Ltd, Palmerston North, NZ

²Hay and Associates Ltd, Pukerua Bay, Wellington, NZ

³Seed Industry Research Centre, Christchurch, NZ

⁴AgResearch, Grasslands Research Centre, Palmerston North, NZ

⁵PGG Wrightson Seeds Ltd, Palmerston North, NZ

*Corresponding author: john.caradus@grasslanz.com

Abstract

Herrick Sydney (Syd) Easton was a forage plant breeder for 46 years. He bred at least 11 forage cultivars, in ryegrass, tall fescue and lucerne that were successfully licensed and commercialised, and he was a key part of the team that developed the successful *Epichloë* fungal endophyte products ‘Endosafe’, AR1, AR37, and ‘MaxP’ (‘MaxQ’ in USA). Syd’s development of measurement techniques and documentation of genetic variation for potentially valuable novel traits has been detailed in 130 refereed and significant publications, and he was an inventor or co-inventor of 13 patents and/or Plant Variety Rights. Syd made an important contribution in the understanding of endophyte-ryegrass interactions. Through his innovation and leadership, he led the multi-disciplinary AgResearch endophyte research programme, coordinating and writing the first successful funding application that consolidated the team. Coming from a farming family Syd connected with farmers and understood the value of highly supportive farmers and agricultural professionals who were able to critique, understand the value of, and use the technologies and knowledge delivered from the science research he was involved with. Like many others in the agricultural research profession, he gained immense satisfaction from seeing technologies resulting from his research being used on New Zealand farms.

Keywords: endophyte, *Epichloë*, lucerne, ryegrass, tall fescue

Background

Herrick Sydney (Syd) Easton, born into a dairy farming family in the Horowhenua, excelled at school and after graduating from Massey University, where he gained a Masters of Agricultural Science (1st Class Honours), joined the Grasslands Division of the Department of Scientific and Industrial Research (DSIR Grasslands)

in 1970. In 1972 he won a National Research Advisory Council (NRAC) Fellowship for PhD study overseas. He worked within an INRA research team in France and completed his PhD in plant quantitative genetics at the University of Paris XI. He had to submit his doctorate thesis and undertake his interview in French and managed both with aplomb. His Thesis Docteur ès Sciences Naturelles was entitled “Etude comparative d’effets génétiques chez des plantes diploïdes et tétraploïdes isogéniques de *Festuca pratensis* Huds.” - translated as - “A comparative study of genetic effects in isogenic diploid and tetraploid plants of *Festuca pratensis* Huds.”.

Syd returned to New Zealand in 1976 working for DSIR Grasslands as a research scientist plant breeder. In 1992, with the formation of AgResearch he moved into a leadership role as Programme Leader Endophyte Research and Ryegrass Improvement, a position he held until 2005 when he took over the role as Section Manager, Forage Improvement through until 2011. Syd moved into retirement but continued working in an Emeritus position until 2016.

Syd’s research has been detailed in more than 130 refereed and significant publications. It has included the development of measurement techniques, documentation of genetic variation for potentially valuable novel traits, and the interaction between *Epichloë* and the host grass. He was an inventor or co-inventor on 13 patents and/or Plant Variety Rights. Syd was also an invited plenary speaker at several international conferences including the International Symposium on *Neotyphodium* – Grass Interactions (1997), International Grassland Congress (Brazil, 2001), Australasian Plant Breeding Conference (2002, 2009), International Symposium on Fungal Endophytes of Grasses (2006), and the Australasian Dairy Science Symposium (2007). He participated frequently in New Zealand Grassland Association conferences with 33 publications. He held professional positions

on the Executive of the New Zealand Grassland Association, the Science Advisory Committee for the New Zealand Foundation for Research, Science and Technology, the Forage Technical Committee of NZ Plant Breeding Research Association, has been an AgResearch-appointed member on the Board of Grasslands Innovation Ltd, and a Trustee of New Zealand Germplasm Trust. His successful career was recognised by NZ Grassland Trust by awarding him the Ray Brougham Trophy at Tauranga in 2013, to acknowledge 40 years of leadership in forage breeding and endophyte technology. The respect with which Syd was held resulted in a tall fescue (*Festuca arundinacea*) cultivar bred by Grasslands Innovation being named 'Grasslands Easton' and commercially released in 2010. This was developed from 'Grasslands Advance', one of Syd's earlier cultivars, for the NZ market and contained the AR584 (MaxP®) endophyte increasing its resistance to several insect pests.

Approach

While we could celebrate Syd, the man and the colleague, the aim here is to overview the forage plant breeding research and science undertaken by Syd, highlighting the significant achievements and impacts that he has both individually, and as part of a wider team, contributed to. His significant involvement in understanding the important interaction between the *Epichloë* fungal endophyte and the host grass will also be outlined. The review will be built through reference to the journal and conference papers for which Syd during his working career was an author or co-author.

The research of Dr Syd Easton

Syd was involved in the full spectrum of activities associated with plant breeding, from germplasm collection, measurement and identification of genetic variation, selection of valuable traits, and creation of commercially available cultivars. He understood the complexity of genotype x environment interactions and its impact on selection criteria. Later in his career he interacted with molecular biologists to better understand the value of, and opportunities provided by, the use of marker-assisted selection (MAS) and genomic selection. However, in addition to being a competent and productive plant breeder Syd was heavily involved in the integration of novel *Epichloë* fungal endophyte strains into ryegrass and tall fescue germplasm.

Germplasm collection and quantification of genetic variation

All pasture and forage species used in New Zealand's pastoral agricultural systems (except the high country tussock lands) are non-native imported species. The benefit of offshore ecotype collections of the species

used in New Zealand's pastures had been previously demonstrated by hybridising them with material adapted to New Zealand (Corkill et al. 1981). Syd participated in two significant germplasm collections outside of New Zealand.

The first, undertaken in 1986 with Dr Margot Forde was to south and northwest Spain, Portugal, and in central and northern Italy (Forde and Easton 1986). This collection was of particular interest because it was made at a similar latitude to New Zealand although in the Northern Hemisphere, but more importantly it was also close to the geographic origin of many of the pasture species of importance to New Zealand. It is in these regions that one might expect to find maximum genetic diversity, which to a breeder is of great significance when selecting for traits of value. The aim was to sample populations in old grassland areas in maritime and transition zones of southern Europe (between Mediterranean and Atlantic environments) and was predominantly undertaken in collaboration with the French INRA based at Clermont-Ferrand. A total of 466 grass and 778 legume seed samples were collected over an 11-week period.

Perennial ryegrass (*Lolium perenne*) populations from southwest Europe were characterised by Syd and other breeders across three sites in each of New Zealand and France, and one site in Spain (Easton et al. 1989). This collection provided key perennial ryegrass germplasm for NZ forage breeding programmes, and in particular those with combined late winter-early spring growth and late flowering. These tended to come from north Portugal, Galicia, and Asturias regions of the Iberian Peninsula.

A total of 128 white clover (*Trifolium repens*) populations collected from southwest Europe were characterised to show that they could be grouped into five meaningful clusters based on important morphological, flowering and growth data (Caradus et al. 1990). This clustering was like that of a world collection of 109 cultivars (Caradus et al. 1989) except for one group of very small-leaved, prostrate, non-productive group composed mainly of wild populations. As with all ecotype collections most lines perform poorly compared with control cultivars but there is always some that show improved traits. Selections from the southwest Europe white clover collection resulted in improved annual and seasonal growth at some sites and could be used in hybridisation with existing cultivars (Caradus et al. 2002).

A second collection trip to Chile (1992) was undertaken with Chilean and Japanese colleagues (Sakamoto 1992). The predominant genus collected was *Bromus*.

Table 1 Trait selections explored in perennial ryegrass and their importance.

Trait	Outcome	Reference
Reduced leaf shear strength	Heritable trait; may increase rates of voluntary intake by ruminants	MacKinnon et al. 1988; Easton 1989
Crown rust (<i>Puccinia coronata</i>)	Significant variation between cultivars and further improvement for rust resistance could be achieved	Easton et al. 1989
Root distribution	While root growth and root/shoot ratio had heritability of 0.35 and 0.29, respectively; root distribution down profile had heritability of only 0.1; no relationship between nitrate interception and patterns of distribution of DM weight of roots	Crush et al. 2006, 2007, 2009; Crush and Easton 2009
Soluble carbohydrate levels	Cultivars selected for elevated fructan showed consistently higher concentrations of soluble carbohydrate, and lower concentrations of crude protein	Easton et al. 2009a
Resilience	The persistence of modern pasture cultivars is not poorer than their predecessors	Easton et al. 2011
Plant-mediated proteolysis (PMP)	It is possible to further reduce PMP by selection within ryegrass populations and therefore reduce N loss from fresh forage entering the rumen	Barrett et al. 2007
Ryegrass host control of endophyte traits	Host plant selection may enable development of pastures with controlled levels of endophyte metabolites, with heritabilities for alkaloids up to 0.72	Easton et al. 2002a
Seed yield	Identification of QTL traits associated with seed yield	Sartie et al. 2006

As a plant breeder Syd was driven to understand the levels of genetic variation and understand their control and heritability and therefore application to plant breeding. Several traits applicable to perennial ryegrass were quantified (Table 1). Some of these traits still have the potential to make an impact. For example, root distribution may have an impact with more sporadic rainfall events from climate change, developing elevated fructan levels may influence methane production, and reducing plant-mediated proteolysis may well help redistribute N excretion pathways toward faecal outputs rather than urinary outputs, with a potential to reduce nitrate leaching and nitrous oxide emissions.

Plant breeding achievements

Syd was active in promoting the benefits of pasture plant breeding to improving animal productivity and health (Woodfield and Easton 2004). That seminal review concluded that “plant breeding in New Zealand has delivered improvements in annual and seasonal yield and forage quality, provided alternative species with desirable properties, and provided genetic solutions that alleviate detrimental effects of phytoestrogens and fungal endophytes on livestock”. Understanding the determinants of product quantity and quality which include productivity, seasonal growth, protein/energy balance, by-pass protein level, leaf properties affecting

intake, resistance to foliar diseases, and compounds that affect animal health and welfare, reproductive fertility, and product flavour and texture are significant drivers (Caradus et al. 2000) for improving the grazing values of pasture. Gains made through plant breeding have been summarised but with the realisation that genetic changes in single factors often do not impact on field performance; to achieve that “research into the interactions between these factors and their genetic control will be needed to extend the ability of pastures to feed high producing livestock” (Easton et al. 2002b).

Syd's plant breeding achievements have been marked by a progression of successful cultivars, some of them breaking new ground. He bred the first New Zealand lucerne (*Medicago sativa*) cultivar, Grasslands Oranga, combining resistance to bacterial wilt (*Corynebacterium michiganense* pv. *insidiosum*) and resistance to blue green aphid (*Acyrtosiphon kondoi*) (Easton and Cornege 1984). A 23 parent synthetic Grasslands Oranga was a leafy cultivar developed by mass selection from cultivar WL311 where plants were first subjected to aphid attack and then surviving genotypes soaked in bacterial wilt inoculum. Field trials determined that Grasslands Oranga persisted well under both cutting and grazing and was suitable for all lucerne growing regions of New Zealand.

A major focus for Syd was the breeding of improved ryegrass cultivars (Easton 1983). Many of these incorporated genetic variation from within New Zealand ecotype populations (e.g. Mangere ecotypes) and high performing overseas material (Burgess and Easton 1986). He bred the first late-flowering New Zealand-adapted perennial ryegrass cultivar, Grasslands Impact, combining good early spring growth with significantly later reproductive development than the earlier norms, thus enabling better forage quality in late spring. Grasslands Impact, released in the 1990s, was bred from perennial ryegrass germplasm collected from northwest Spain (obtained during the 1986 Europe collecting expedition) along with selections from Grasslands Nui (Stewart 2006; Sartie et al. 2009). It was noted to have a low level of annual ryegrass gene content (Crush et al. 2007). Grasslands Impact was noted as having far greater stoloniferous growth compared with the cultivar Yatsyn 1, noted as providing a distinct advantage over other genotypes in survival and maintenance of plant and tiller density in pasture (Donaghy 1999). Most late-flowering perennial and hybrid ryegrass cultivars on the NZ market, including Tolosa, Arrow and the tetraploid Banquet, have Grasslands Impact as a parent.

Syd developed several other successful ryegrass cultivars including Grasslands Samson which is still being sold 30 years later. Developed as a general purpose ryegrass from old Grasslands Nui pastures in dry regions of both North and South Islands but

including some Hawkes Bay ecotype germplasm (Stewart 1986), it was selected for low levels of rust infection and for persistence in difficult environments (Grasslanz 2007). Grasslands Samson is based on eight parent genotypes and tends to be erect and to have larger tillers, broader leaves, shorter leaf sheaths, and fewer tillers per plant on average than Grasslands Impact which is more prostrate with a later flowering date (Donaghy 1999; Sartie et al. 2009). Syd had close association with the breeding of the ryegrass hybrids Grasslands Supreme and the tetraploid Grasslands Ohau. Grasslands Supreme was selected from persistent germplasm from southern South Island for superior all-year round growth and excellent disease resistance (Grasslanz 2007). Grasslands Ohau was selected for exceptional winter growth and, as a tetraploid, had high forage quality.

He also developed tall fescue cultivars, including Grasslands Advance, with radically improved palatability characteristics combined with improved seedling vigour (Easton and Pennell 1993; Hay et al. 1997), which is particularly suitable for difficult environments with grass grub (*Costelytra zealandica*), and Argentine stem weevil (*Listronotus bonariensis*) infestations, and a range of soils, including wet and dry and those with peat or saline conditions (Easton et al. 1994; Grasslanz 2007). Selection for seed yield improvement was shown to be possible (Rolston et al. 2006). Grasslands Easton tall fescue was bred for increased spring and summer production from Grasslands Advance and carried MaxP endophyte for increased insect tolerance and persistence.

Syd studied genetic variation in a range of other forage species, including cocksfoot (*Dactylis glomerata*) (Easton and Barclay 1973), Yorkshire fog (*Holcus lanatus*) (Clements and Easton 1974), and meadow fescue (*Festuca pratensis*) (Easton 1975). As a co-author he also provided the history of ryegrass use and development from the early days of bush burn mixtures to the late 1980s (Hunt and Easton 1989). He was also able to manage large data sets to provide cultivar performance across New Zealand for perennial ryegrass (Easton et al. 2001) and for annual and hybrid ryegrasses (Easton et al. 1997).

Incorporating new molecular selection techniques into plant breeding

During the 1990s the use of DNA markers, linked to genes, was researched as means of improving the efficiency of selection in applied plant breeding. By the 2000s Syd, along with other forage plant breeders, was keen to explore the application of marker assisted selection (MAS) (Barrett et al. 2001; Faville et al. 2003; Barrett et al. 2006) and was involved in work to discover markers linked to herbage production

related traits (Sartie et al. 2011; Faville et al. 2012), root distribution (Faville et al. 2006; Crush et al. 2006; Crush et al. 2007) and seed production (Sartie et al. 2006, 2018). Future objectives, direction and requirements for forage plant breeding to continue to support pastoral farming was thoroughly reviewed and concluded that “future grass breeding, aided by MAS and genetic modification of both plants and endophytes, will place strong emphasis on feeding value for optimal animal performances, especially in intensive systems” (Williams et al. 2007). They also pointed out that “the current Hazardous Substances and New Organisms regulatory environment is not conducive to timely research and innovation on new species for agriculture and needs reconsideration by law makers”.

As evidence emerged that MAS may be less effective for genetically complex traits like herbage yield, Syd was instrumental in supporting research that shifted focus to the development of genomic selection as an effective molecular breeding approach for perennial ryegrass (Easton et al. 2015; Faville et al. 2018).

***Epichloë* research, results and impact**

Syd made an important contribution to understanding the genetics of the interaction between the host plant and the endophyte, and the importance of *Epichloë* endophyte for ryegrass survival when predated by a number of introduced insect pests (Easton 1999). The host plant genotype is now understood to regulate the extent of alkaloid expression (Fletcher and Easton 1997; Easton et al. 2002a; Easton 2007a and b; Fletcher et al. 2006; Popay and Easton 2006) as well as the ease of seed transmission (Gagic et al. 2018). Syd was involved with the research team attempting to understand the impact of *Epichloë* endophytes on ryegrass tolerance to high temperature and water stress (Eerens et al. 1998a), pasture production (Eerens et al. 1998b), sheep production (Eerens et al. 1998c), white clover content (Eerens et al. 1998d), and plant parasitic nematodes (Eerens et al. 1998e). He was also involved in demonstrating the value of an animal safe endophyte in tall fescue for protection against insect pests resulting in a yield difference of over 50% over 3 years (Cooper et al. 2002).

As a plant breeder Syd was intimately involved in the commercialisation of endophyte strains Endosafe[®], AR1 and AR37 in ryegrass, and AR542 (MaxP[®] in Australasia or MaxQ[®] in USA) and AR584 (MaxP[®] in Australasia or MaxQ II[®] in USA) in tall fescue (Easton et al. 2001; Fribourg et al. 2002; Easton and Fletcher 2006). In New Zealand, Syd demonstrated the benefit of having an animal safe endophyte in tall fescue in regions with heavy pest burdens (Easton and Cooper 1997).

Syd was involved in the development of Endosafe[®] endophyte containing ryegrasses that were animal safety tested in the early 1990s. Endosafe[®] had been identified as a strain that produced peramine to control Argentine stem weevil (Fletcher et al. 2006) but did not produce lolitrem B and so was presumed safe for use with animals because it would not cause ryegrass staggers (Easton et al. 2001). However, another alkaloid was associated with the Endosafe[®] strain, ergovaline and which when expressed at high levels can cause heat stress in animals (Easton et al. 1993 and 1996; Easton and Couchman 1999). This led to it Endosafe[®] being withdrawn from the market except in the hybrid ryegrass Grasslands Greenstone where the level of ergovaline was relatively low, and no livestock health problems had been encountered (Easton et al. 2001). While concerning at the time this development led to the understanding that it is the plant host genotype which determines the level of expression of alkaloid production, with different plant genotypes creating different outcomes.

The desire to produce loline alkaloids in ryegrass was a long-term goal that interested Syd (Easton et al. 2009b). Loline alkaloids are non-toxic to livestock and yet protect the host plant against a wide range of insect pests. However, loline producing endophytes are only found in fescues not ryegrass and so the challenge continues to be moving *Epichloë* species across taxa and maintaining satisfactory transmission rates.

Syd was also involved early in the *Epichloë* endophyte cereal programme (Caradus et al. 2006) and was heavily involved in writing the first successful application to MBIE for government support. This programme has the potential to revolutionise pest and disease control in cereals such as wheat (Simpson et al. 2014).

A study was undertaken on Maud and Tiritiri Matangi Islands to determine if toxic fungal endophytes of tall fescue were responsible for the low reproductive rate of takahe (*Porphyrio hochstetteri*) on New Zealand offshore islands (Jamieson and Easton 2002). Endophyte infected tall fescue was found to not be the cause of the low reproductive rate because despite extensive surveys, tall fescue was not observed on either island.

Conclusions

Syd Easton's contribution over 46 years made a significant and lasting impact through excellent science and research endeavour in both forage plant breeding and *Epichloë* endophyte technologies. Syd was pragmatic and his ‘down-to-earth’ style enabled him to communicate directly and effectively to farmers, farm advisors and commercial companies about extracting the best performance from his new cultivars. His

working career provides an example of the impact that research based on good science and perseverance can make, and can continue to make, on the delivery of products and technologies to pastoral farmers in New Zealand. This should be an inspiration to younger researchers.

REFERENCES

- Barrett B, Faville M, Sartie A, Hume D, Jahufer Z, Hickey M, Baird I, Pennell C, Ryan D, Cooper B, Woodfield D, Easton S. 2006. Forage improvement via marker-assisted selection. In: Mercer CF. Ed. *Breeding for Success: Diversity in Action*. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 596-603. *Advances in Pasture Plant Breeding. NZ Grassland Association Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3030>
- Barrett B, Griffiths A, Mercer C, Ellison N, Faville M, Easton HS, Woodfield DR. 2001. Marker-assisted selection to accelerate forage improvement. *Proceedings of the New Zealand Grassland Association 63*: 241-245. <https://doi.org/10.33584/jnzg.2001.63.2411>
- Barrett BA, Pacheco D, McNabb WC, Easton HS. 2007. Opportunities to improve nitrogen utilisation in the rumen by reduction in plant-mediated proteolysis. *Proceedings of the New Zealand Grassland Association 69*: 187-192. <https://doi.org/10.33584/jnzg.2007.69.2660>
- Burgess RE, Easton HS. 1986. Old pasture populations of ryegrass in New Zealand and their use in plant breeding. In: Williams TA, Wratt GS. Eds. *Plant Breeding Symposium*. New Zealand Agronomy Society Special Publication No. 5: 295-301.
- Caradus JR, Eerens H, Cooper B, Forde M. 2002. White clover breeding lines derived from southwest Europe ecotypes. In: McComb JA. Ed. *Plant Breeding for the 11th Millennium. Proceedings of the 12th Australasian Plant Breeding Conference*, 15 to 20 September 2002, Perth, Australia. Pp 724-727.
- Caradus JR, Forde MB, Wewala S, Mackay AC. 1990. Description and classification of a white clover (*Trifolium repens* L.) germplasm collection from Southwest Europe. *New Zealand Journal of Agricultural Research 33*: 367-375. <https://doi.org/10.1080/00288233.1990.10428433>
- Caradus JR, Hume DE, Easton HS. 2006. Application of fungal endophytes to cereals. In: Bender G, Meibusch P, Blumenthal M. (Organisers). *The contribution of soil biology to healthy soils*. Identification of priorities for future research. GRDC workshop, 12-13 December 2006, Australian National University, Canberra, Australia. Pp. 7
- Caradus JR, Mackay AC, Woodfield DR, van den Bosch J, Wewala S. 1989. Classification of a world collection of white clover cultivars. *Euphytica 42*: 183-196. <https://doi.org/10.1007/BF00042631>
- Caradus JR, Woodfield DR, Easton HS. 2000. Improved grazing value of pasture cultivars for temperate environments. In: Stone GM. Ed. *Animal production for a consuming world*. Vol. B. Proceedings of the 9th Congress of the Asian-Australasian Association of Animal Production Societies and 23rd Biennial Conference of the Australian Society of Animal Production. 3-7 July 2000, Sydney, Australia. *Asian-Australasian Journal of Animal Sciences 13*: Supplement vol B: 5-8.
- Clements RJ, Easton, HS. 1974. Genetic shifts in a Yorkshire fog population grazed by sheep. I Population changes induced by hard continuous grazing. *Proceedings of the New Zealand Grassland Association 35*: 268-277. <https://doi.org/10.33584/jnzg.1973.35.1367>
- Cooper BM, Easton HS, Hume DE, Popay AJ, Baird DB. 2002. Improved performance in Northland New Zealand of tall fescue with a selected endophyte. In: McComb JA. Ed. *Plant Breeding for the 11th Millennium. Proceedings of the 12th Australasian Plant Breeding Conference*, 15 to 20 September 2002, Perth, Australia. Pp 379-381.
- 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/jnzg.1981.42.1568>
- Crush JR, Easton HS. 2009. Breeding for root system shape in perennial ryegrass (*Lolium perenne* L.). *Proceedings International Society of Root research and Applications (RootRAP)*, 2-4 September 2009, Boku, Vienna, Austria. #199-2. [Accessed 18 March 2023]. https://www.researchgate.net/profile/J-Crush/publication/268365235_Breeding_for_root_system_shape_in_perennial_ryegrass_Lolium_perenne_L/links/54dbdab40cf2a7769d941c99/Breeding-for-root-system-shape-in-perennial-ryegrass-Lolium-perenne-L.pdf
- Crush JR, Easton, HS, Waller, JE. 2006. Genetic variation in perennial ryegrass for root profile characteristics. In: Mercer CF. Ed. *Breeding for Success: Diversity in Action*. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. pp. 1073-1077. *Advances in Pasture Plant Breeding. NZ Grassland Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3040>
- Crush JR, Easton HS, Waller JE, Hume E, Faville MJ. 2007. Genotypic variation in patterns of root distribution, nitrate interception and response to moisture stress of a perennial ryegrass (*Lolium*

- perenne L.) mapping population. *Grass and Forage Science* 62: 265-273. <https://doi.org/10.1111/j.1365-2494.2007.00583.x>
- Crush JR, Nichols SN, Easton HS, Ouyang L, Hume DE. 2009. Comparisons between wild populations and bred perennial ryegrasses for root growth and root/shoot partitioning. *New Zealand Journal of Agricultural Research* 52: 161–169. <https://doi.org/10.1080/00288230909510500>
- Donaghy DJ. 1999. The role of stolon formation in survival of ‘Impact’ perennial ryegrass plants over summer in Tasmanian Institute of Agricultural Research Industry Report. 15 p. [Accessed 1 March 2022]. <http://www.regional.org.au/au/asa/2001/3/d/donaghy.htm>
- Easton HS. 1975. Comparison of artificial tetraploids with isogenic diploids in meadow fescue. *Proceedings of the Eucarpia Fodder Crops Section Meeting*, Zurich. Pp 39-42.
- Easton HS. 1983. Ryegrasses. In: Williams TA, Wratt GS. Eds. Plant Breeding Symposium. *New Zealand Agronomy Society Special Publication No. 5*: 226-239.
- Easton HS. 1989. Variability of leaf shear strength in perennial ryegrass. *New Zealand Journal of Agricultural Research* 32: 1-6. <https://doi.org/10.1080/00288233.1989.10423470>
- Easton HS. 1999. Endophyte in New Zealand ryegrass pastures, an overview. In: Woodfield DR, Matthew C. (Eds.) Ryegrass Endophyte: An Essential NZ Symbiosis. *NZ Grassland Association Research and Practice Series 7*: 1-9. <https://doi.org/10.33584/rps.7.1999.3384>
- Easton HS. 2007a. Grasses and *Neotyphodium* endophytes: co-adaptation and adaptive breeding. *Euphytica* 154: 295-306. <https://doi.org/10.1007/s10681-006-9187-3>
- Easton HS. 2007b. Grass breeding and *Neotyphodium* endophytes. In: Rosellini D, Veronesi F. Eds. *Breeding and seed production for conventional and organic agriculture*. XXVI Meeting of the Eucarpia Fodder Crops and Amenity Grasses Section. Università degli Studi di Perugia - Facoltà di Agraria, Perugia, September 2006. pp. 290-294.
- Easton HS, Amyes JM, Cameron NE, Green RB, Kerr GA, Norriss MG, Stewart AV. 2002b. 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/jnzc.2002.64.2455>
- Easton HS, Barclay PC. 1973. Evaluation of cocksfoot (*Dactylis glomerata* L.). *New Zealand Journal of Agricultural Research* 16: 25-30. <https://doi.org/10.1080/00288233.1973.10421154>
- Easton S, Baird DA, Baxter GO, Cameron NI, Hainsworth RO, Johnston CH, Kerr GR, Lyons T, McCabe RO, Nichol WA, Norriss MI. 1997. Annual and hybrid ryegrass cultivars in New Zealand. *Proceedings of the New Zealand Grassland Association* 59: 239-244. <https://doi.org/10.33584/jnzc.1997.59.2248>
- Easton HS, Baird DB, Cameron NE, Kerr GA, Norriss M, Stewart AV. 2001. Perennial ryegrass cultivars: herbage dry matter yield in multi-site plot trials. *Proceedings of the New Zealand Grassland Association* 63: 183-188. <https://doi.org/10.33584/jnzc.2001.63.2408>
- Easton HS, Charmet G, Forde B, Oliveira JA, Widdup KH, Cooper BM, Bion A, Balfourier F. 1989. Perennial ryegrass from temperate south Europe. *Proceedings XVI International Grassland Congress* 287-288.
- Easton HS, Christensen MJ, Eerens JP, Fletcher LR, Hume DE, Keogh RG, Lane GA, Latch GC, Pennell CG, Popay AJ, Rolston MP, Sutherland BL, Tapper BA. 2001. Ryegrass endophyte: a New Zealand grassland success story. *Proceedings of the New Zealand Grassland Association* 63: 37-46. <https://doi.org/10.33584/jnzc.2001.63.2429>
- Easton HS, Cooper BM. 1997. Field performance of tall fescue with low infection with *Neotyphodium* endophyte. Proceedings of the 3rd international symposium on *Neotyphodium*/grass interactions, 28-31 May 1997. In: Bacon CW, Hill HS. Eds. *Neotyphodium/Grass Interactions*, Springer, Boston, MA. Pp. 251-253. https://doi.org/10.1007/978-1-4899-0271-9_44
- Easton HS, Cooper BM, Fraser TJ, Widdup KH. 1989. Crown rust on perennial ryegrass in field trials. *Proceedings New Zealand Grassland Association* 50: 253-254. <https://doi.org/10.33584/jnzc.1989.50.1867>
- Easton HS, Cornege E. 1984. ‘Grasslands Oranga’ lucerne (*Medicago sativa*). *New Zealand Journal of Experimental Agriculture* 12: 283-286
- Easton HS, Couchman JN. 1999. Ryegrass endophyte and cattle growth in Northland. In: Woodfield DR, Matthew C. Eds. Ryegrass Endophyte: An Essential NZ Symbiosis. *NZ Grassland Association Research and Practice Series 7*: 57-62. <https://doi.org/10.33584/rps.7.1999.3397>
- Easton HS, Fletcher LR. 2006. The importance of endophyte in agricultural systems-changing plant and animal productivity. In: Popay AJ, Thom ER. Eds. Proceedings of the 6th International Symposium on Fungal Endophytes of Grasses. *NZ Grassland Association Research and Practice Series. 13*: 11-18. <https://doi.org/10.33584/rps.13.2006.3080>
- 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* 177: 233-237. <https://doi.org/10.33584/jnzg.2015.77.455>
- Easton HS, Lane GA, Tapper BA. 1993. Ergovaline in endophyte-infected ryegrass pastures. Proceedings of a Symposium on Mycotoxicosis of Grassland Farming. *New Zealand Veterinary Journal* 41: 214.
- Easton HS, Lane GA, Tapper BA, Keogh RG, Cooper BM, Blackwell M, Anderson M, Fletcher LR. 1996. Ryegrass endophyte-related heat stress in cattle. *Proceedings New Zealand Grassland Association* 57: 37-41. <https://doi.org/10.33584/jnzg.1995.57.2181>
- Easton HS, Latch GCM, Tapper BA, Ball OJ-P. 2002a. Ryegrass host genetic control of concentrations of endophyte-derived alkaloids. *Crop Science* 42: 51-57. <https://doi.org/10.2135/cropsci2002.5100>
- 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. 2009b. Loline alkaloids for better protection of pastures from insects. *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 HS, Stewart AV, Kerr GA. 2011. Ryegrass in pastures-breeding for resilience. In: Mercer CF. (Ed.) Pasture Persistence Symposium. *NZ Grassland Association Research and Practice Series* 15: 139-147. <https://doi.org/10.33584/rps.15.2011.3208>
- Easton HS, Stewart AV, Lyons TB, Parris M, Charrier S. 2009b. Improving soluble carbohydrate content of perennial ryegrass herbage. *Proceedings of the New Zealand Grassland Association* 71: 161-166. <https://doi.org/10.33584/jnzg.2009.71.2745>
- Eerens JPJ, Lucas RJ, Easton HS, White JGH. 1998a. Influence of the endophyte (*Neotyphodium lolii*) on morphology, physiology, and alkaloid synthesis of perennial ryegrass during high temperature and water stress. *New Zealand Journal Agricultural Research* 41: 219-226. <https://doi.org/10.1080/00288233.1998.9513305>
- Eerens JPJ, Lucas RJ, Easton HS, White JGH, Miller KB. 1998b. Influence of the ryegrass endophyte (*Neotyphodium lolii*) in a cool-moist environment. I. Pasture production. *New Zealand Journal Agricultural Research* 41: 39-48. <https://doi.org/10.1080/00288233.1998.9513286>
- Eerens JPJ, Lucas RJ, Easton HS, White JGH, Miller KB. 1998c. Influence of the ryegrass endophyte (*Neotyphodium lolii*) in a cool-moist environment. II. Sheep production. *New Zealand Journal Agricultural Research* 41: 191-199. <https://doi.org/10.1080/00288233.1998.9513302>
- Eerens JPJ, Lucas RJ, Easton HS, White JGH, Miller KB. 1998d. Influence of the ryegrass endophyte (*Neotyphodium lolii*) in a cool-moist environment. III. Interaction with white clover. *New Zealand Journal Agricultural Research* 41: 201-207. <https://doi.org/10.1080/00288233.1998.9513303>
- Eerens JPJ, Viske, MHPW, Lucas RJ, Easton HS, White JGH. 1998e. Influence of the ryegrass endophyte (*Neotyphodium lolii*) in a cool-moist environment. IV. Plant parasitic nematodes. *New Zealand Journal of Agricultural Research* 41: 209-217. <https://doi.org/10.1080/00288233.1998.9513304>
- Faville M, Barrett B, Griffiths A, Schreiber M, Mercer C, Baird I, Ellison N, Bryan G, Woodfield D, Forster J, Ong B, Sawbridge T, Spangenberg G, Easton HS. 2003. Implementing molecular marker technology in forage improvement. *Proceedings of the New Zealand Grassland Association* 65: 229-238. <https://doi.org/10.33584/jnzg.2003.65.2498>
- Faville, M.J., Crush, J.R., Easton, H.S. 2006. At the root of it all: a QTL analysis of root distribution in perennial ryegrass. In: Mercer CF. Ed. Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 1085-1090. Advances in Pasture Plant Breeding. *NZ Grassland Association Research and Practice Series* 12. <https://doi.org/10.33584/rps.12.2006.3047>
- 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, Jahufer MZZ, Hume DE, Cooper BM, Pennell CGL, Ryan DL and H. Sydney Easton 2012. A quantitative trait locus analysis of herbage biomass production in perennial ryegrass. *New Zealand Journal of Agricultural Research* 55: 263-281. <https://doi.org/10.1080/00288233.2012.691205>
- Fletcher LR, Easton HS. 1997. The evaluation and use of endophytes for pasture improvement. Plenary paper, Proceedings of the 3rd International Symposium on *Neotyphodium/Grass Interactions*, 28-31 May 1997. In: Bacon CW, Hill HS. Eds. *Neotyphodium/Grass Interactions*. Springer, Boston, MA. Pp. 209-227. https://doi.org/10.1007/978-1-4899-0271-9_39
- Fletcher L, Easton S, Popay A, Tapper B, Hume D. 2006. Plant and endophyte genotype affects peramine

- concentrations in ryegrass/endophyte associations. In: Mercer CF. Ed. Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 520-525. Advances in Pasture Plant Breeding. *NZ Grassland Association Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3019>
- Forde MB, Easton HS. 1986. Report of the New Zealand-France-IBPGR forage germplasm collecting expedition to southwest Europe 1986. AgResearch, Palmerston North. Pp. 29. Available from the corresponding author.
- Fribourg HA, Waller JC, Latch GCM, Fletcher LR, Easton HS, Stratton A.E. 2002. Evaluation under grazing of *Festuca arundinacea* cultivars infected with nontoxic endophytes. In: *Proceedings of the 19th Congress of the European Grassland Federation*. La Rochelle, France. Grassland Science in Europe 7:530-531.
- Gagic M, Faville MJ, Zhang W, Forester NT, Rolston MP, Johnson RD, Ganesh S, Koolaard JP, Easton HS, Hudson D, Johnson LJ. 2018. Seed transmission of *Epichloë* endophytes in *Lolium perenne* is heavily influenced by host genetics. *Frontiers in Plant Science* 9: Article 1580. <https://doi.org/10.3389/fpls.2018.01580>
- Grasslanz 2007. *Forage product Handbook*. Grasslanz Technology Ltd. Palmerston North. Pp. 52. ISBN 978-0-473-12783-1.
- Hay RJM, Lyons TB, Easton HS. 1997. Evaluation of Grasslands Advance tall fescue under grazing. *Proceedings of the XVIII International Grasslands Congress*, 8 -91 June 1997, Winnipeg, Manitoba, Saskatoon, and Saskatchewan Canada. ID No. 828. Session 22, Pp. 87-88.
- Hunt WF, Easton HS. 1989. Fifty years of ryegrass research in New Zealand. *Proceedings New Zealand Grassland Association* 50: 11-23. <https://doi.org/10.33584/jnzc.1989.50.1876>
- Jamieson IG, Easton HS. 2002. Does a toxic fungal endophyte of tall fescue affect reproduction of takahe on offshore islands? Wellington: Department of Conservation; Pp. 8. [Accessed 17 March 2023]. <https://www.doc.govt.nz/Documents/science-and-technical/DSIS89.pdf>
- MacKinnon BW, Easton HS, Barry TN, Sedcole JR. 1988. The effect of reduced leaf shear strength on the nutritive value of perennial ryegrass. *Journal of Agricultural Science, Cambridge* 111: 469-474. <https://doi.org/10.1017/S0021859600083659>
- Popay AJ, Easton HS. 2006. Interactions between host plant genotype and *Neotyphodium* fungal endophytes affects insects. In: Mercer CF. Ed. Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 561-567. Advances in Pasture Plant Breeding. *NZ Grassland Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3020>
- Rolston MP, Easton HS, Widdup KH, Amadeo J, Archie W, Lyons T B. 2006. Improvement of seed yield potential in tall fescue. In: Mercer CF. Ed. Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 371-376. Advances in Pasture Plant Breeding. *NZ Grassland Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3038>
- Sakamoto S. 1992. A preliminary report of plant genetic resources collection expedition of the VIII to X Regions of Chile (January 17 to 28th, 1992). Pp. 3. Available from the corresponding author.
- Sartie AM, Easton HS, Faville MJ, Matthew C. 2006. Quantitative trait loci for seed production traits in perennial ryegrass (*Lolium perenne* L.). In: Mercer CF. (Ed.) Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 377-382. Advances in Pasture Plant Breeding. *NZ Grassland Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3039>
- Sartie AM, H. S. Easton HS, Matthew C. 2009. Plant morphology differences in two perennial ryegrass cultivars. *New Zealand Journal of Agricultural Research* 52: 391-398. <https://doi.org/10.1080/00288230909510521>
- Sartie AM, Easton HS, Matthew C, Rolston MP, Faville MJ. 2018. Seed yield in perennial ryegrass (*Lolium perenne* L.): comparative importance of component traits and detection of seed-yield-related QTL. *Euphytica* 214: Article 226. <https://doi.org/10.1007/s10681-018-2307-z>
- Sartie AM, Matthew C, Easton HS, Faville MJ. 2011. Phenotypic and QTL analyses of herbage production-related traits in perennial ryegrass (*Lolium perenne* L.) *Euphytica* 182: 295-315. <https://doi.org/10.1007/s10681-011-0400-7>
- Simpson WR, Faville MJ, Moraga RA, Williams WM, McManus MT, Johnson RD. 2014. *Epichloë* fungal endophytes and the formation of synthetic symbioses in Hordeae (=Triticeae) grasses. *Journal of Systematics and Evolution* 52: 794-806. <https://doi.org/10.1111/jse.12107>
- Stewart AV. 2006. Genetic origins of perennial ryegrass (*Lolium perenne*) for New Zealand pastures. In: Mercer CF. Ed. Breeding for Success: Diversity in Action. Proceedings of the 13th Australasian Plant Breeding Conference, Christchurch, New Zealand 18-21 April 2006. Pp. 11-20. Advances in Pasture

- Plant Breeding. *NZ Grassland Association Research and Practice Series 12*. <https://doi.org/10.33584/rps.12.2006.3042>
- Williams WM, Easton HS, Jones CS. 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>
- 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>