Opportunities and challenges for breeding perennial ryegrass cultivars with improved livestock production potential

T.J. Gilliland1†, T. Ball2, D. Hennessy3

1Institute of Global Food Security, School of Biological Sciences, Queen’s University Belfast, United Kingdom
2Deutsche Saatveredelung AG (DSV) United Kingdom Ltd, Top Dawkins Barn, Wardington, Banbury, OX17 1FE, England, UK
3Teagasc, Animal and Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland

Abstract

This review addresses key factors and impediments that govern the efficient transfer of nutrient energy from primary producing grassland to ruminant milk and meat. The review focuses on permanent improved grasslands, defined as “swards maintained at a high production potential by grass-to-grass renewal”, frequently of a 5- to 10-yr longevity. Breeding progress to date is examined as are the primary objectives for the next generation of cultivars. This involves aligning grass productivity to ruminant demand in three primary aspects, namely intake potential, nutritional value and productivity profile. The opportunity to selectively improve plant traits affecting sward structure, chemical composition, seasonality and ability to persist and perform under farm conditions is evaluated. The EU context involves appraising the impact of variables such as grass species and cultivar, regional abiotic stresses (water, temperature, nutrients, soil type, etc.), biotic stresses from disease and pests, regional diversity in sward management strategies, and the opportunity to minimise the environmental footprint of ruminant farming.

Keywords

Cultivar • livestock • perennial ryegrass • performance

Introduction

This paper is not intended to provide a comprehensive review of contemporary ryegrass genetics and agronomy knowledge, or to critique grass breeding strategies for improving productivity, climate tolerance or disease and pest resistance. Such bodies of work already exist (e.g. Humphreys, 1997; Conaghan & Casler, 2011; Kole, 2013a, 2013b). Rather, this paper focuses on current and future opportunities and challenges for improving the efficiency of nutritional energy transfer from primary producing perennial ryegrass (Lolium perenne L.) cultivars to ruminant milk and meat production. To identify the opportunities and understand the challenges require a holistic appreciation of the multifactorial nature of the grass seed industry, as argued by van Wijk & Reheul (1991). In addition to the process of breeding (genetics, genomics, epigenetics, logistics, response timelines and economics), there are official and regional evaluation thresholds designed to promote those cultivars that best furnish a diversity of on-farm end-user requirements (regional practices in grazing, “cut-n-carry” and conservation, tolerance of localised climatic, edaphic, disease and pest stresses). In addition to this is the substantial complicating factor that grass herbage is not an end product in itself but must be processed through ruminants into meat and milk, which adds key performance requirements associated with intake, ingestion and metabolic utilisation. This multifactorial requirement for cultivar improvement can be more simply defined in terms of three key factors of critical farm-level importance, as follows:

“A proficient and sustained delivery of highly utilisable, high-yielding herbage”.

“Proficiency” requires cultivars that make optimum use of soil nutrients and light capture with the capability to maintain high productivity under varying (or specific) sward management regimes (seasonal grazing patterns, ensilability, set-stocked/rotational/zero grazed, intensive, extensive, etc.) and regional growing stresses (disease, pest, temperature and moisture). “Sustained” reflects the need for cultivars with greater predictability and reliability across a growing season, over years and throughout as wide a climatic and edaphic range as possible.
“Utilisable” encompasses possibly the greatest challenge for cultivar improvement, namely addressing the poor conversion rates of herbage mass grown, and particularly its protein components, into ruminant product, while profiling productivity closer to livestock demand across a growing season. Breeding progress in these key factors will, by implication, also address important EU and global political and regulatory policies on environmental protection (Osterburg et al., 2010). Proficient use of input resources reduces nutrient leakage, sustaining a tolerance to stresses also contributes more resilience to climatic change, and better animal utilisation reduces the release of phosphate and nitrogenous compounds (ammonia, nitrous oxide) and methane by ruminants into air and ground waters (Jarvis et al., 1996). There are also substantial economic gains for farm business through a greater contribution from home-grown herbage (Dillon et al., 2005), which in turn benefits rural businesses and communities. These are all factors that are attracting increased political and societal scrutiny (Osterburg et al., 2010).

It has long been known and validated that grazing management to control the sward structure and nutritive value impacts substantially on grazing performance (Pérez-Prieto & Delagarde, 2012) to the extent that it can be modelled (Delagarde et al., 2011); however, this does not preclude the need for breeding progress in these characteristics as only breeding can raise the potential value of grassland above current ceilings. An evaluation of the opportunities and challenges to achieve this can be categorised into a number of key drivers, as described in the following section.

**Opportunities and challenges of improving key breeding drivers**

For the purposes of this overview, the key target traits for breeding improved livestock performance characteristics into perennial ryegrass cultivars are subdivided into “gross production”, “animal nutrition”, “animal intake”, “environmental impactors” and “performance consistency”.

**Gross production drivers**

There is documented evidence from Northwestern Europe that breeders have successfully and consistently achieved a productivity gain rate of around +0.4–0.6% per annum depending on the yield component and region (van Wijk & Reheul, 1991; Humphreys, 1999; Wilkins & Humphreys, 2003; Sampoux et al., 2011; McDonagh et al., 2016). Similar gains have also been reported in New Zealand (Easton et al., 2002). However, along with the traditionally other important breeding traits of persistence and disease resistance, the primary targets for improvement have differed little over 45 yr (Cooper & Breeze, 1971; Parsons et al., 2011). There are isolated examples of breeding for novel traits such as watersoluble carbohydrates (WSC) (Humphreys, 1989) or more recently digestible fibres (Parijs et al., 2017), but these are either isolated single-breed examples or of disputed value. Other novel approaches such as introgression of *Festuca* drought resistance genes into *Lolium* (Humphreys & Thomas, 1993) or exploratory studies into creating F1 hybrid ryegrasses using cytoplasmic male sterility (Deutsche Saatveredelung AG and Norddeutsche Pflanzenzucht Hans-Georg Lemke KG; personal communication) have not been financially or functionally suited to large-scale/routine breeding. So genetic gain has required progressive increases in total shoot production, making grass yield gains arguably at least as good a breeding achievement as in arable crops. Yield gain alone does not, however, achieve the requirements for greater proficiency, sustainability and utilisation of the herbage produced.

**Animal nutrition drivers**

A review of grassland productivity in Northern Ireland (AFBI, 2017) showed that the average utilised yield on farm was estimated at 5.0 t DM/ha per year (dairy 7.5 t DM/ha per year; beef and sheep 4.1 t DM/ha per year). In Ireland, the average grass utilised on dairy farms in 2015 was 7.8 t DM/ha (Hanrahan et al., 2018). These values fall within a wide variation of what is achievable across Europe, largely due to the broad range in grassland productivity potential and grass-fed livestock densities, impacted by differences in farming practices, for example, nitrogen (N) fertiliser use, mowing and grazing intensity and in supplementary diet levels (Chang et al., 2015). Hence, even within France, grass utilisation varies between 3 and 7 t DM/ha with a small number of farms greater than 7 t DM/ha in Brittany (L. Delaby, INRAE, personal communication). In contrast, the Northern Irish grass growth monitoring service (GrassCheck, www.agrisearch.org/grasscheck) has recorded on-farm yields of 14–16 t DM/ha per year with utilisation approaching 80% on the top 1% of best managed farms. However, as detailed elsewhere, the efficiency of use of ingested herbage energy and protein is disconcertingly low at around only 30% of the total intake. Underutilisation of grass grown has negative implications for nutrient use efficiency in grassland systems (Anon, 2016). It is also the key biological limit to livestock performance from grass, and so not a grass production ceiling but an animal intake and metabolisation shortfall. While this dynamic undoubtedly has evolutionary roots as ruminants evolved to only achieve maintenance plus one calving annually from natural grassland, commercial targets, as exemplified in advisory and press publications, typically set challenging targets of 5,000 L of milk from forage (Price, 2015; Mayne, 2018) and beef live weight gains in the region of 500 kg/yr (Irwin, 2019; Lively, 2019). To derive as much
as possible of this from grass requires breeding advances in the intake and nutritional traits to achieve 80% utilisation on farm. In this context, relatively modest genetic gains have been made in digestibility, at around 0.5–1.0 g/kg DM per annum (Wilkins & Humphreys, 2003; McDonagh et al., 2016). Furthermore, Wilkins & Humphreys (2003) concluded that the traits which impact on nutritive value include crude protein (CP) concentration, WSC, neutral detergent fibre (NDF) and organic matter digestibility (OMD). Selection for high WSC has been shown to improve CP metabolism of grazed grass (Miller et al., 2001) and silage (Merry et al., 2006), and to reduce N excreted in the urine. Therefore, this is an area where greater breeding emphasis is now required to satisfy leading grassland farmers’ requirements.

**Animal intake drivers**

The other pillar of utilisation is physical intake by grazing animals. Smit et al. (2005a) showed significant differences between six perennial ryegrass (*Lolium perenne* L.) cultivars for sward surface height (SSH), bulk density (BD), proportion of green leaf (PGF), tiller density (TD), tiller weight (TW) and length of sheath (LS), but not extended tiller height (ETH) or length of leaf blade (LLB). They further reported that herbage intake was significantly associated with SSH and PGF (Smit et al., 2005b). As this was only observed in one of two experimental years, inconsistency might limit the on-farm benefits from breeding advances in these intake characters. In contrast, a number of experiments have shown that the greater the free leaf lamina (FLL) (Wims et al., 2013; Cashman, 2014) and/or sward leaf content (Gowen et al., 2003; Flores-Lesama et al., 2006; Beecher et al., 2015), the greater the animal performance. For example, Cashman (2014) and Wims et al. (2013) found an average difference of 1.6 kg milk/cow per day between grazed perennial ryegrass cultivars with the highest and lowest FLL content. Furthermore, McDonagh (2017) and Byrne et al. (2018) showed that FLL length is a good indicator of grass utilisation because as it increases, the pseudostem and true stem contents decline, sward digestibility rises, and post-grazing sward height reduces. McDonagh (2017) also found a strong relationship between pre-grazing FLL length measured through the growing season in grazed swards and flag-leaf length in spaced plants. In addition, Sampoux et al. (2011), when comparing seven natural perennial ryegrass populations and 21 cultivars from the last 40 yr, found a clear association of leaf and lamina lengths with spring and summer DM yields. Their data showed a possible negative impact of long leaves on sward persistency, but concluded that breeding for longer leaves and a high leaf elongation rate would improve the interception efficiency of incident radiation during re-growth, which they expect would most significantly increase spring yields.

Tubritt et al. (2018) found significant differences in post-grazing sward heights (3.7–4.8 cm) between 30 perennial ryegrass cultivars when cattle grazed. Disappointingly, there was also a significant negative relationship between grazed yield and post-grazing sward height as the lowest yielding cultivars had the lowest post-grazing sward heights and vice versa. There was, however, clear evidence that this relationship was not obligated ($R^2 = 0.41$) as, for example, some cultivars with similarly good post-grazing sward height values differed significantly by around 3 t DM/ha in grazed grass yield. While consistency over and within years still needs to be established, this evidence of cultivar diversity indicates a potential breeding trait to improve animal utilisation. Furthermore, if ongoing investigation confirms that secondary head development is reduced following lower post-grazing sward heights, this trait would also indicate enhanced herbage grazing quality on farm, which is known to further enhance utilisation (O’Donovan & Delaby, 2005).

Furthermore, McDonagh (2017) showed that differences in FLL, measured in swards, were a good indicator of intake by grazing cattle and that these differences correlated closely to spaced plant-measured leaf length differences (spLL), both when swards were in the reproductive ($R^2 = 0.88$) and vegetative ($R^2 = 0.99$) phases. Given that the sward and spaced plant measurements came from distantly separated locations and different years, FLL/spLL appears to be a trait that both impacts on animal intake/utilisation and is amenable to selection in breeders’ plant nurseries. The magnitude of the benefit to grassland farming of improved grass quality and intake has recently been estimated from AFBI studies in Northern Ireland. Improving grass utilisation by 1 t DM/ha, combined with improved grass quality, can potentially increase the margin over feed costs by £204–334/ha per year on dairy farms or £160–218/ha on beef farms (Anon, 2016). This dairy benefit was largely driven by reduced concentrate feed costs while the improved beef performance was due to a 21% per ha reduction in concentrates, an increase of 19% per ha in stocking rate and an improved live weight gain of 35% per ha from grass. Similarly, Teagasc figures show that a 1 t DM/ha increase in grass utilisation on dairy farms in Ireland is worth an additional €173 net profit/ha (Hanrahan et al., 2018).

**Environmental impact drivers**

There is increasing regulatory pressure on grassland farming to mitigate emissions of greenhouse gases (GHGs), to reduce nutrient losses to ground waters and to sequester carbon into soil sinks (ACRE, 2007). In the UK, 59% of total agricultural ammonia emissions come from ruminant farming (24% beef, 31% dairy, 4% sheep; Misselbrook et al., 2016) with agricultural livestock producing upwards of 9% of total anthropogenic GHG emissions as methane and nitrous oxide (Gill et al., 2010). In a less urbanised/industrialised region such
as Northern Ireland, ruminant emissions rise to over 70% of total emissions. In dairy cattle offered 35% concentrates and 65% fresh grass, livestock metabolism studies have shown the following:

- Of the gross energy intake, 30% was lost in excretions, 6% as methane, 36% lost as heat, 23% retained in milk with 5% retained in the body (Hynes et al., 2016a).
- Of the total protein fraction, tracked as total N, only 27% and 2% was retained in milk and body, respectively, with 34% lost in faeces and 37% in urine (Hynes et al., 2016b).
- Of the phosphate ingested, only 33% was transferred to milk with 3.5% retained and the remaining 63.5% excreted, almost entirely within faeces (Ferris et al., 2010).

A critical grass-breeding challenge is, therefore, to decrease these losses by better transfer of the ingested herbage into animal product. The nutritive composition of the grass has a major role to play here, with increased metabolisable energy content of herbage shown to improve conversion into animal product which, for example, can lower nitrous oxide ($N_2O$) emissions by reducing N excretion in the urine (Miller et al., 2001). Increasing herbage WSC content has also been implicated in reducing enteric methane eructation from ruminants (Martin et al., 2010; Shibata & Terada, 2010). Here again there is opportunity for breeding intervention as there are many studies reporting cultivar differences in, for example, WSC, CP, fatty acids, fibre digestibility and DM digestibility (DMD) (Wilkins et al., 2000; Miller et al., 2001; Gilliland et al., 2002; Tas et al., 2005; Merry et al., 2006; Downing & French, 2009) with varying evidence of improved intake and animal outputs.

**Performance consistency drivers**

If farmers are to place greater reliance on grass for their livestock nutrient supply, then greater predictability and reliability across varying growing conditions are required. Talbot (1984), in assessing the sources of variation in grass cultivar trials located across the UK, concluded that years and locations imposed the biggest variances and were interchangeable. Therefore, cultivar-testing protocols that involve multiple years, locations and retesting cycles identify those cultivars that not only achieve higher overall performances but also have a greater resilience than those not approved.

On a macro “EU-wide” scale, Table 1 shows the number of perennial ryegrass cultivars registered on the EU Common Catalogue of Varieties (https://ec.europa.eu/food/plant/plant_propagation_material/plant_variety_catalogues_databases_en, 2017) compared to several major forage grass species and arable crops. Widely adapted cultivars are preferable from an agribusiness aspect as production costs are lower if fewer cultivars are produced in larger quantities. There are, however, complicating agri-economic factors underlying decisions on which country or how many countries a breeder will submit a new cultivar for registration and subsequent commercialisation, including testing costs, market volume, market structure of competing companies as well as the inability to penetrate that market without a local independent recommendation. Furthermore, after making multiple national submissions to gain regionally approved performance data, breeders can reduce ongoing maintenance costs by only retaining one member state registration for EU market rights. Region-specific requirements for high disease resistance (e.g. rust resistance in France, *Puccinia* spp.) or high winter hardiness (e.g. in Germany and Nordic regions) impose large differentials in the regional adaptation of grass cultivars, but no greater than among arable crops. So, while the data need to be interpreted with considerable caution and given that arable crops mostly have higher value and higher volume markets than perennial ryegrass and must be resown annually, there is no evidence from the numbers of registered cultivars that perennial ryegrass is more widely adapted across Europe than arable cultivars, despite its allogamy.

At a national level, Long et al. (2010) reported that of the 120 perennial ryegrass cultivars recommended in the UK and Ireland, only 10% were on all four recommended lists (England and Wales, Ireland, Northern Ireland, and Scotland) and 43% of the cultivars were only approved in one region (Table 2). This confirms observations from studies on cultivar ranking consistency. Wilkins (1989) and Wims et al. (2009) reported re-ranking under different growing conditions and concluded that this justified the need for regional recommended lists and explained regional variations in breeding gains reported.

### Table 1: Number of cultivars registered on the EU Common Catalogue 2017

| Forage grasses          | Perennial ryegrass 6701 | Italian ryegrass 248 | Hybrid ryegrass 107 |
|-------------------------|-------------------------|----------------------|---------------------|
| Meadow Fescue 103       | Tall Fescue 324         | Cocksfoot 160        | Festulolium 44      |
| Arable Crops            | Barley 2-row 985        | Barley 6-row 393     | Wheat 2417          |
|                         | Oats 358 (+39 naked)    | Potato 1632          | Sugar beet 1645     |

*Estimated from a total listing of 1093 amenity and forage cultivars*
by Wilkins & Humphreys (2003). This is understandable as a cultivar that is dormant enough to survive a northern Britain winter would be expected to have low spring yields in the south-west of Ireland, where the winter period is much shorter and prolonged frost is uncommon. Conversely, cultivars that perform well in the south-west of Ireland by not being winter dormant tend to suffer winter damage at northern sites. However, even in a relatively confined and benign maritime region such as Northern Ireland, substantial production variations can occur over relatively short distances. Table 3a shows the variation in yields and weather variances recorded across 30 dairy and beef farms in the six counties of Northern Ireland during May 2017. All these farms were operating to an optimum management level in what were not extreme weather conditions. In this year, growth in Armagh and Down was 0.95 t DM/ha lower than the average of the other counties and 1.25 t DM/ha less than Antrim. By contrast in 2018, when there was severe moisture stress during much of the main growing season of late June, July and August in some of the regions, daily growth rates were down by 6.4 kg DM/ha overall, with the Antrim and Armagh regions down by 20% in daily growth and by similar reduction in total yield (Table 3b). Such extreme weather responses are not uncommon at a micro level. For example, the long-term perennial ryegrass cultivar performance trials at AFBI Crossnacreevy, Northern Ireland, show 10-yr average yields for perennial ryegrass of 12.3 t DM/ha yr under a simulated grazing management and 16.4 t DM/ha yr under a conservation management, with an annual variation of +/−5.5 t DM and +/−7.2 t DM/ha per year, respectively (Meehan, 2016). Despite this baseline production variation due to seasonal conditions, commercially successful cultivars must not significantly re-rank in their key characteristics. Otherwise, it would be impossible to provide a reliable measure of their relative potential on different farms and in different years. There is both longstanding and recent evidence to show this is not a weakness within the scope of normal management practices. McDonagh (2017) found that eight perennial ryegrass cultivars did not re-rank to any great extent in production, quality or persistence, despite different N application rates and defoliation frequencies. Similarly, Aldrich & Elliott (1974) found no re-ranking between cutting and grazing systems. So, breeding programmes have delivered an acceptable level of resilience in terms of relative cultivar performance, albeit not an immunity to more

| Region (county) | Total rainfall (mm) | Average daily temperature (°C) | Daily growth rate (kg DM/ha) | Total yield (t DM/ha) |
|----------------|---------------------|-------------------------------|-----------------------------|----------------------|
| Antrim         | 49.9                | 12.0                          | 101.9                       | 3.16                 |
| Armagh         | 42.4                | 12.4                          | 63.4                        | 1.97                 |
| Down           | 35.3                | 11.9                          | 60.3                        | 1.87                 |
| Fermanagh      | 46.8                | 12.3                          | 87.8                        | 2.72                 |
| Londonderry    | 35.7                | 12.2                          | 89.0                        | 2.76                 |
| Tyrone         | 53.2                | 12.3                          | 92.2                        | 2.86                 |
| Average        | 43.9                | 12.2                          | 82.4                        | 2.56                 |

Table 3a: May 2017

| Region (county) | Total rainfall (mm) | Average daily temperature (°C) | Daily growth rate (kg DM/ha) | Total yield (t DM/ha) |
|----------------|---------------------|-------------------------------|-----------------------------|----------------------|
| Antrim         | 297                 | 13.1                          | 53.4                        | 9.0                  |
| Armagh         | 295                 | 13.7                          | 46.8                        | 7.9                  |
| Down           | 233                 | 13.2                          | 49.5                        | 8.4                  |
| Fermanagh      | 330                 | 12.4                          | 64.0                        | 10.8                 |
| Londonderry    | 302                 | 12.4                          | 59.8                        | 10.1                 |
| Tyrone         | 351                 | 13.0                          | 68.1                        | 11.5                 |
| Average        | 301                 | 13.0                          | 56.9                        | 9.5                  |

Table 3b: Growing season to end of August 2018
acute weather events such as severe droughts, excessive rainfall or temperature extremes that cause sward production collapses. Challenges of this magnitude, although predicted to be more frequent given climate change modelling (EASAC, 2018), are currently beyond the capability of grass breeding to address either locally or EU-wide. The only partial remedial measures come not from breeding but through local advisory monitoring services such as GrassCheck (www.agrisearch.org/grasscheck). This uses a growth prediction model to forecast expected grass yields 2 wk in advance. Therefore, although breeders desire cultivars that are successful over wide climatic ranges to maximise their sales volume, this is not where increased breeding effort is most required to improve livestock performance from grass.

**Breeding opportunities and challenges**

Given the considerable challenges posed by the breeding drivers discussed previously, questions arise as to what opportunities breeders have to effectively address them. The British Society of Plant Breeders was asked to survey its perennial ryegrass breeders for this paper. This survey was sent to all members operating in the UK market, which included both UK-based breeders and breeders from Denmark, France, Ireland and the Netherlands. The survey asked them to score their selection priorities for a total of 33 traits, across five groupings, as either A (very important to essential), B (somewhat important/important) or C (useful/irrelevant):

- **8 Productivity Traits**: Total herbage production; spring herbage production; summer herbage production; autumn herbage production; first-cut silage yield; second-cut silage yield; third-cut silage yield; overwinter/low temperature growth
- **9 Herbage Quality**: Spring grass quality; summer grass quality; autumn grass quality; digestibility; CP content; WSC content; fibre content; fatty acid profile; tannin content
- **4 Structural Parameters**: Lamina length; leaf area index; erect/prostrate habit; sward density
- **7 Resistance Factors**: Rust resistance; mildew resistance; Drechslera resistance; other diseases; persistence/longevity; drought tolerance; cold tolerance/winter kill
- **5 Specialist Characters**: Nitrogen use efficiency; phosphorus use efficiency; utilisation under grazing; livestock output measure; lower methane emissions

Only four traits were A-classed by all breeders (total and spring production, spring quality and digestibility), with a further six A-classed by a majority of breeders (first-cut silage yield, sward density, rust and Drechslera resistance, utilisation under grazing and persistence/longevity). Fatty acid profile and tannin content were C-classed as irrelevant by all breeders, but otherwise there was no clear consensus on the priorities of the remaining traits. Interestingly, one breeder had only a single “essential trait” (total yield), while another breeder listed 23 of the 33 traits as A-class priority. Overall, productivity and resistance traits retained high priority with herbage quality and structure less so, despite their importance to animal productivity as already described (Table 4). Specialist characters were also given a high priority, though there was little consensus on the priorities between breeders. A number of “additional” characters were reported by the breeders, each largely specific to an individual breeder. These included fibre or cell wall digestibility, re-heading, livestock wear, tillering, poaching/wear resistance and seed yield.

These results reflect the challenge of breeding for genetic gain in a crop that does not have a singularity of end-use and with the ultimate product depending on the efficiency of the ruminant “end user”. When viewed as a totality, they give some indication of the challenge of achieving a multifactorial improvement by targeting progress across a wide diversity of traits. All except one breeder reported that their germplasm resources were entirely either “elite/improved” (existing commercial cultivars) or “adapted” (of known favourable traits but not from existing cultivars). This one breeder was using between 1 and 5% of “unadapted” germplasm (of high genetic diversity without trait assessment, e.g. wild populations). So virtually all of the breeding effort is seeking to achieve improvements from within the gene pool of current cultivars and associated material.

There have been concerns expressed in some quarters regarding diversity bottlenecks due to this type of recurrent selection strategies (Yong-Bi, 2015), and there are knowledge gaps requiring more research into genetic diversity changes under plant breeding. However, as perennial ryegrass is allogamous, it requires several maternal plants of sufficient diversity to overcome the self-incompatibility genes (Klaas et al., 2011) and ensure commercially viable seed production capability. This implants a greater phenotypic variance within grass cultivars compared to autogamous or clonal cereals.

**Table 4**: Percentage of traits in each group assigned to one of three classes of importance: A = very important/essential; B = somewhat important/important; C = useful/irrelevant

| Perennial ryegrass trait group | A  | B  | C  |
|-------------------------------|----|----|----|
| Productivity                  | 55 | 30 | 14 |
| Herbage quality               | 35 | 35 | 30 |
| Structural parameters         | 32 | 46 | 21 |
| Resistance factors            | 52 | 38 | 10 |
| Specialist characters         | 54 | 11 | 34 |
This should make recurrent selection from existing cultivars successful and likely places perennial ryegrasses at a lower risk of entering a diversity bottleneck. Evidence of this comes from the statutory Plant Breeders’ Rights registration schemes in the UK. Table 5 shows the magnitude of differences between plants within registered cultivars for several characteristics measured on spaced plants in Distinctness, Uniformity and Stability tests of perennial ryegrass (data from AFBI Plant Testing Station, Crossnacreevy, Northern Ireland). These data are from registered cultivars, which are therefore “uniform” and so show that a difference in heading date between plants of 2.7–5.4 d can exist. Similarly, flag leaves can range between 3.6 and 6.1 cm in length and 1.2 and 2.2 cm in width, giving a leaf area range of 1.7–3.3 cm². Therefore, there is variance within registered cultivars that can be exploited to improve some traits that are important for animal performance and justifies breeders’ focus on using elite maternal germplasm. However, to make progress on a multifactorial basis may require more innovative approaches. It was notable that only one breeder reported using molecular selection methods in their current breeding programme, though several stated that they had future plans to do so. Genomic selection (GS) can facilitate multivariate selection to address the multifactorial resilience requirement, though grasses have lagged behind other crops in the use of these tools. This is partly due to allogamy, as it is harder to capture gene variants within cultivars that are effectively populations compared to autogamous or clonal crops. However, innovations such as the use of mixed models for genomic-wide selection (Bernardo & Yu, 2007) have been shown to enhance the efficiency of selective breeding (Lorenzana & Bernardo, 2009), and Yabe et al. (2018) have demonstrated the potential of GS for breeding by mass selection in a model allogamous species. Costs have, however, been prohibitive in the past and although now becoming cheaper still represent a significant investment. So, the following three recent examples of genomics in grass breeding have all involved investment from public or academic funders.

- The forage grass breeding programme of the Institute of Biological, Environmental and Rural Sciences in Wales (www.aber.ac.uk/en/ibers) exploits its academic links within the University of Aberystwyth to conduct “public good” breeding and attract funding from the Government (Defra, www.gov.uk/government/organisations/department-for-environment-food-rural-affairs) and research funders such as the Biotechnology and Biological Sciences Research Council (BBSRC) (www.bbsrc.ac.uk), the Technology Strategy Board (www.gov.uk/government/organisations/technology-strategy-board) and a seed industry company.
- Teagasc, Oakpark, Ireland, for a medium-sized genomics screening capability, required Government (Department of Agriculture, Food and the Marine [DAFM]) funding (www.teagasc.ie).
- DLF A/S, in Denmark, linked with Aarhus University (www.au.dk/en) for a genomics programme in 2011 and after 5 yr had examined around 1,800 ryegrass families, all with phenotypic data and had identified 1.8 million DNA markers (approximately 1% of the 2.7 Gb ryegrass diploid genome). This was an “Industrial PhD studentship” at AU, jointly run by DLF A/S and supported by public funding from the Danish Ministry of Education, through the Council for Industrial PhD Education (11–109967), (http://ufm.dk/en/research-and-innovation/funding-programmes-for-research-and-innovation/find-danishfunding-programmes/programmes-managed-by-innovation-fund-denmark/industrial-phd). The work demonstrated the potential for GS in perennial ryegrass (Fè et al., 2015) and has been further supported through a “public good” methane emissions study, partnered with Tystoftefonden (www.tystofte.dk) and

| Character name | Flowering date | Spring angle | Spring height | Spring width | Spring shape |
|----------------|----------------|---------------|---------------|--------------|--------------|
| Units          | days           | degrees¹      | cm            | cm           | cm           |
| Maximum        | 5.4            | 12.4          | 11.7          | 11.3         | 0.28         |
| Minimum        | 2.7            | 7.1           | 3.9           | 6.8          | 0.10         |
| Average        | 3.8            | 9.8           | 8.6           | 9.1          | 0.18         |

| Character name | Tiller height² | Plant width³ | Flag leaf length | Flag leaf width | Flag leaf area |
|----------------|---------------|--------------|------------------|----------------|---------------|
| Units          | cm            | cm           | cm               | mm             | cm²           |
| Maximum        | 13.6          | 12.7         | 6.1              | 2.2            | 3.3           |
| Minimum        | 9.0           | 7.7          | 3.6              | 1.2            | 1.7           |
| Average        | 11.6          | 10.3         | 5.0              | 1.7            | 2.6           |

¹Angle from ground level
²At ear emergence

Table 5: Magnitude of range within perennial ryegrass cultivars for spaced plant characters
funded under the Green Development and Demonstration Program, Ministry of Environment and Food, Denmark (www.mst.dk/service/om-miljoestyrelsen).

Other grass breeders, such as DSV, target specific traits, seeking causal genes for characters in quality traits (e.g. lignin synthesis) and plant structure (e.g. lamina length). There is a growing body of scientific evidence and experience in cytogenetics, genotyping, next-generation sequencing and bioinformatics to support further progress in this area. Evidence of synteny across genera in the Gramineae (or Poaceae), such as Brachypodium, rice (Oryza sativa), sorghum (Sorghum bicolor) and more recently the barley (Hordeum vulgare) genome (Mayer et al., 2011), novel approaches such as Targeting Induced Local Lesions in Genomes (TILLING) (Manzanares et al., 2016), or categorisation of specific quantitative trait loci, for example, cell wall degradability (Bolwell, 2000; Barrière et al., 2003) are opening new opportunities. Therefore, these examples indicate that new opportunities to breed for greater resilience and to expect breeding progress on a multifactor are no longer such an unattainable goal. However, the challenge for breeding business models is to find funding streams where they cannot entirely self-fund genomic breeding.

Cultivar evaluation opportunities and challenges

For many years, official evaluation schemes across Europe sought evidence of improvement in individual traits, the most important of which were DM yield and persistency, with resistance to any acute regional disease/climatic factor being a baseline requirement. Latterly, digestibility was introduced, but improvement continued to be required on a trait-by-trait basis, with “overall performance” only used for marginal pass/fail decisions. It was accepted that these traits were detached from the animal product as animal-based trialling demands resources beyond what most testing authorities can provide or breeders afford to fund. Hence, small plot field trials are expected to continue for large-scale cultivar evaluations to reduce candidate numbers to a smaller set of new elite performing cultivars (Conaghan et al., 2008). However, given the body of evidence presented previously showing the need for progress in characteristics that are now known to impact on animal intake, nutrition and environmental footprint, a more multifactorial approach to cultivar evaluation is clearly required. There are already a number of evaluation schemes that use indices to provide an overall performance indicator for perennial ryegrasses.

• The French small plot evaluation scheme (Reglement technique d’examen des varietes de plantes fourrageres et a gazon; www.gnis.fr/reglementation-mentions) applies an index rating to cultivars after they have passed the baseline evaluation criteria. Coefficients are applied to the yields (1–100% on measured values and 1–9 for notes) for a range of characteristics (total and seasonal yields, reheading, resistance to diseases, operational flexibility, flexibility of the foliage, persistency/sustainability and nutritional value – total N composition/acid detergent fibre [ADF] content/soluble sugar content), to give an overall rating. This allows for inferiority in some characters to be offset by favourable expression in others, but with an elimination threshold set for characters of major agronomic importance, such as reheading and rust resistance.

• Similarly, the Dutch Plantum index for grasses (Protocol Beslissingen Opmene en Afvoer Engels Raai Voeder 2019, Commissie Samenstelling Aanbevelende Rassenlijst; https://rassenlijst.info/ajax_frontoffice/manager/files/wp-uploads/2018/11/Engels-raaigrass-beslissingen-2019-def.pdf) assigns weighting and scale factors to total yield, first-cut silage yield, crown rust and ground cover, with minimum standards for winter hardiness and all but the first-cut yield.

These indices attempt to represent the overall value of a cultivar for animal production, based on the small plot characters, as listed. An alternative approach is to form indices based on the calculated financial value to the farm business of the herbage produced. So, DairyNZ uses the Forage Value Index (www.dairynz.co.nz/feed/pasture-renewal/select-pasture-species/about-fvi) in New Zealand. This is calculated from the economic value of the seasonal yields on a regional basis and each cultivar’s DM production level for each seasonal period. Cultivars are given a star rating to indicate an estimated annual value to the farm of −$78 to +$29 (1 star) up to +$351 to +$458 (5 star), using an online selection tool. In Ireland, Teagasc have developed a Pasture Profit Index (PPI; www.teagasc.ie/crops/grassland/pasture-profit-index) that provides predicted economic values for cultivars that have been recommended by the Government (DAFM). This research-based index (McEvoy et al., 2011; O’Donovan et al., 2016) assigns a financial value to each cultivar based on the seasonal (spring, summer, autumn) and total yield, persistency and digestibility of the herbage produced in small plot trials. In both of these financial-based indices, there has been a very strong engagement of farmers and an invigorated interest in grass cultivars, more production from grass and reseeding with better cultivars.

Teagasc have implemented a further level of farmer involvement by establishing a network of 66 farms to evaluate 11 currently recommended cultivars, sown in monoculture under intensive grazing systems (Byrne et al., 2017). The farmer monitors herbage production through weekly paddock cover estimations.
(O’Donovan et al., 2002) and uploads data into PastureBase Ireland (PBI), a farmer decision support tool and database (Hanrahan et al., 2017). Sward quality and ground score are measured by trained technicians at fixed periods during the season. In 2017, there was a range of 1.9 t DM/ha in total annual DM production, 44 g/kg DM for DMD and 0.7 for ground score. There are a number of implications of this scheme. It requires a large number of farmers who will commit and adhere to the evaluation scheme and incurs greater variances as not all cultivars are on all farms, sown in the same year and must account for regional conditions and farmer practice differences. It also cannot be conducted until after the initial small plot scheme has identified the few elite cultivars from among the many candidates. It does, however, produce performance data under actual farm grazing, across the actual range of farming conditions and greatly enthuses the “co-research” farmers (and their neighbours). The final phase in this PPI/PBI initiative is to adopt characters as described in earlier sections that enhance animal intake and utilisation and reduce nutrient losses to the environment, so that the indices and evaluations comprise a multifactorial calculation of key animal performance drivers. An unexpected implication has been that some of these co-research farmers are moving away from using mixtures to sowing single cultivars. As they have gained experience in using single cultivar swards and identified specific ones on which their livestock has optimised, they have sought to expand the area available to graze. Without this precision management experience, the loss in flexibility gained from mixtures may be detrimental to less grass-skilled farmers. If this became common practice, there would also be considerable problems for breeders and seed producers meeting the needs of a cultivar-demanding market that could change rapidly. However, the “milchindex” trademark has been successfully used by DSV to market cultivars of high digestibility and quality in Germany as a premium brand in an otherwise price-sensitive market. This typifies the potential benefits that breeders might gain if grass cultivars were more specifically defined for their animal performance potential to farmers.

Concluding remarks

It is widely accepted that improved efficiency of animal production from grass is the ultimate goal of forage grass breeding for European temperate regions (Wilkins & Humphreys, 2003), and identifying cultivar characteristics that can be highly utilised and influence animal performance is important from all aspects of grassland (Wims et al., 2013). Grass breeders must, as always, seek to be at the forefront of such grassland improvement. Today, this is increasingly driven by the twin need to fulfil leading grassland farmers’ requirements for quantifiable animal performance at grass and the regulatory imperatives to reduce GHG loses to the atmosphere and nutrients to ground waters. As overviewed in this paper, there is ample research evidence of grass characteristics that will enhance animal intake, metabolic utilisation and so livestock production from home-grown grazed and conserved perennial ryegrass. These traits will equally help lower the environmental impact of ruminant farming. It is also clear, however, that in assessing the evidence for such “animal performance” characters, there are often qualifications needed regarding repeatability, accuracy, magnitude of the value, interaction with and independence from other characters, as alluded to. Notably, the evidence from Smit et al. (2005b) of inconsistent animal performance responses to the expressed differences in grass structural traits indicates that it will be incumbent on farmers to manage their swards with sufficient precision to fully gain from any such breeding advances. Leading grassland farmers are, however, already operating at this level of expertise. Therefore, none of this should be an impediment to grass evaluators now actively adopting novel characteristics, particularly as the use of indices provides scope to account for any uncertainties, while still delivering a multifactorial assessment of the animal value of new cultivars. With these in place, breeders will be able to target improvement in multiple traits, which the straw poll indicated is within their current capability either by conventional methods or through their ambitions around GS. There is, however, some evidence that developing cultivars with high animal-value characters could lead to more use of single cultivar swards with implications for the business models of breeding companies and seed producers. Taking the available evidence overall, it is clear that published grassland research has identified a number of opportunities to improve animal performance from grass by adopting intake- and digestion-supporting traits into candidate cultivar listing procedures. For these traits, further research in not necessary nor are sources of new diversity required, beyond that currently available among commercial breeding stocks. The challenge is therefore for cultivar evaluators to adopt these traits into their listing decision processes. Even where the benefits are difficult to quantify, indices and expert panel weightings can be used to promote candidate cultivars with high expression of these characteristics. This will then encourage and challenge breeders to include these traits in the selection of their elite synthetics and drive genetic gain towards enhanced livestock productivity from perennial ryegrass. Evidence of cultivars with improved animal performance and reduced environmental footprint potential will be highly valued by leading farmers and government policy regulators. The benefit to breeders is that once grass cultivars are individually recognised for their financial contribution to farm efficiency and profitability, the opportunity to broker a seed price that better reflects their true
value and which can better offset the cost of development becomes an attainable goal. This should also act as a catalyst for continued research into new means of enhancing the livestock production potential of perennial ryegrass to the benefit of all the stakeholders.

References

Advisory Committee on Releases to the Environment (ACRE). 2007. Managing the footprint of agriculture: towards a comparative assessment of risks and benefits for novel agricultural systems. Report of the ACRE subgroup on wider issues raised by the farm scale evaluations of herbicide tolerant GM crops. London, DEFRA, page 90.

AFBI. 2017. “More from Grass. An Agri-Food and Biosciences Institute Occasional Publication”. Available online: www.afbini.gov.uk/publications/more-grass-afbi-loughgall.

Aldrich, D.T.A. and Elliott, C.S. 1974. A comparison of the effects of grazing and cutting on the relative herbage yields of six varieties of perennial ryegrass. Proceedings of the XII International Grassland Congress, Cornell University, United States of America, 3: 17–24.

Anon. 2016. “Delivering Our Future, Valuing Our Soils: A Sustainable Agricultural Land Management Strategy for Northern Ireland”. DAERA occasional publication, ISBN 978-1-84807-708-9. Available online: www.daera-ni.gov.uk/topics/land-and-landscapes/soil.

Barre, P., Moreau, L., Mi, F., Turner, L., Gastal, F., Julien, B. and Ghesquière, M. 2009. Quantitative trait loci for leaf length in perennial ryegrass (Lolium perenne L.). Grass Forage Science 64: 310–321.

Barrière, Y., Guillet, C., Goffner, D. and Pichon, M. 2003. Genetic variation and breeding strategies for improved cell wall digestibility in annual forage crops. A review. Animal Research 52: 193–228.

Beecher, M., Hennessy, D., Boland, T.M., McEvoy, M., O’Donovan, M. and Lewis, E. 2015. The variation in morphology of perennial ryegrass cultivars throughout the grazing season and effects on organic matter digestibility. Grass and Forage Science 70: 19–29.

Bernardo, R. and Yu, J. 2007. Prospects for genome-wide selection for quantitative traits in maize. Crop Science 47: 1082–1090.

Bolwell, G.P. 2000. Biosynthesis of plant cell wall polysaccharides. Trends in Glycoscience and Glycotechnology 12: 143–160.

Byrne, N., Gilliland, T.J., McHugh, N., Delaby, L., Geoghegan, A. and O’Donovan, M. 2017. Establishing on-farm phenotypic performance of grass varieties on Irish grassland farms. Journal of Agricultural Science 10: 1633–1645.

Byrne, N., Gilliland, T.J., Delaby, L., Cummins, D. and O’Donovan, M. 2018. Understanding factors associated with the grazing efficiency of perennial ryegrass varieties. European Journal of Agronomy 101: 101–108.

Cashman, P.A. 2014. Differential productivity and persistency responses to simulated and animal grazing of perennial ryegrass genotypes. PhD thesis, Queens University Belfast.

Chang, J., Viovy, N., Vuichard, N., Ciais, P., Campioli, M., Klumpp, K., Martin, R., Leip, A. and Soussana, J.-F. 2015. Modeled Changes in potential grassland productivity and in grass-fed ruminant livestock density in Europe over 1961–2010. PLoS One 10: 30, doi:10.1371/journal.pone.0127554.

Conaghan, P. and Casler, M.D. 2011. A theoretical and practical analysis of the optimum breeding system for perennial ryegrass. Irish Journal of Agricultural and Food Research 50: 47–63.

Conaghan, P., Casler, M.D., McGilloway, D.A., O’Kiely, P. and Dowley, L.J. 2008. Genotype × environment interactions for herbage yield of perennial ryegrass sward plots in Ireland. Grass and Forage Science 63: 107–120.

Cooper, J.P. and Breeze, E.L. 1971. Plant breeding: forage grasses and legumes. In: “Potential Crop Production” (eds. P.F. Wareing and J.P. Cooper), Heinemann Educational Books, London, pages 295–318.

Delagarde, R., Faverdin, P., Baratte, C. and Peyraud, J.L. 2011. Grazeln: a model of herbage intake and milk production for grazing dairy cows. 2. Prediction of intake under rotational and continuously stocked grazing management. Grass and Forage Science 66: 45–60.

Dillon, P., Roche, J.R., Shalloo, L. and Horan, B. 2005. Optimising financial return from grazing in temperate pastures. In: “Proceedings of the Satellite Workshop 20th International Grassland Congress, Cork, Ireland. Utilization of Grazed Grass in Temperate Animal Systems” (ed. J.J. Murphy), Wageningen Academic Publishers, Wageningen, the Netherlands, pages 131–147.

Downing, T. and French, P. 2009. Improved understanding of fiber digestibility in ryegrasses. Journal of Extension 47: 1–7.

Easton, H.S., Amyes, J.M., Cameron, N.E., Green, R.B., Kerr, G.A., Norross, M.G. and Stewart, A.V. 2002. Pasture plant breeding in New Zealand: where to from here? Proceedings of the New Zealand Grassland Association 64: 173–179.

EASAC. 2018. European Academies’ Science Advisory Council, Extreme Weather Events in Europe. Report on March 2018, publisher Schaefer Druck und Verlag GmbH, Teutschenthal, Germany, pages 8. Available online: https://easac.eu/fileadmin/PDF_s/reports_statements/Extreme_Weather/EASAC_Statement_Extreme_Weather_Events_March_2018_FINAL.pdf.

Fé, D., Cericola, F., Byrne, S., Lenk, I., Ashraf, B.H., Pedersen, M.G., Roulund, N., Asp, T., Janss, L., Jensen, C.S. and Jensen, J. 2015. Genomic dissection and prediction of heading date in perennial ryegrass. BMC Genomics 16: 921. doi: 10.1186/s12864-015-2163-3.

Ferris, C.P., McCoy, M.A., Patterson, D.C. and Kilpatrick, D.J. 2010. Effect of offering dairy cows diets differing in phosphorus concentration over four successive lactations: 2. Health, fertility, bone phosphorus reserves and nutrient utilisation. Animal 4: 560–571.
Flores-Lesama, M., Hazard, L., Betin, M. and Emile, J.-C. 2006. Differences in sward structure of ryegrass cultivars and impact on milk production of grazing dairy cows. *Animal Research* **55**: 25–36.

Gill, F.L., Dewhurst, R.J., Evershed, R.P., McGeough, E., O’Kiely, P., Pancosta, R.D. and Bulla, I.D. 2010. Analysis of archaeal ether lipids in bovine faeces. *Animal Feed Science and Technology* **166–167**: 87–92.

Gilliland, T.J., Barrett, P.D., Mann, R.L., Agnew, R.E. and Fearon, A.M. 2002. Canopy morphology and nutritional quality traits as potential grazing value indicators for Lolium perenne varieties. *Journal of Agricultural Science* **139**: 257–273.

Gowen, N., O’Donovan, M., Casey, I., Rath, M., Delaby, L. and Stakelum, G. 2003. The effect of grass cultivars differing in heading date and ploidy on the performance and dry matter intake of spring calving dairy cows at pasture. *Animal Research* **52**: 321–336.

Hanrahan, L., Geoghegan, A., O’Donovan, M., Griffith, V., Ruelle, E., Wallace, M. and Shalloo, L. 2017. PastureBase Ireland: a grassland decision support system and national database. *Computers and Electronics in Agriculture* **136**: 193–201.

Hanrahan, L., McHugh, N., Hennessy, T., Moran, B., Kearney, R., Wallace, M. and Shalloo, L. 2018. Factors associated with profitability in pasture based systems of milk production. *Journal of Dairy Science* **101**: 5474–5485.

Humphreys, M.O. 1989. Water-soluble carbohydrates in perennial ryegrass breeding. I. Cultivar and hybrid progeny performance in cut plots. *Grass and Forage Science* **14**: 237–244. Available online: https://doi.org/10.1111/j.1365-2494.1989.tb01932.x.

Humphreys, L.R. 1997. “The Evolving Science of Grassland Improvement”. Cambridge University Press, Cambridge, United Kingdom, ISBN 978-0-521-49567-7, page 280.

Humphreys, M.O. 1999. The contribution of conventional plant breeding to forage crop improvement Grasslands 2000. In: “Proceedings of the XVIII International Grassland Congress”, Volume 3 (eds. J.G. Buchanan-Smith, L.D. Bailey and P. McCaughey), Saskatchewan Agriculture & Food, Winnipeg, Manitoba and Saskatoon, Saskatchewan, Canada Extension Service, pages 71–77.

Humphreys, M.W. and Thomas, H. 1993. Improved drought resistance in introgression lines derived from *Lolium multiflorum × Festuca arundinacea* hybrids. *Plant Breeding* **111**: 155–161.

Hynes, D.N., Stergiadis, S., Gordon, A. and Yan, T. 2016a. Effects of concentrate crude protein contents on nutrient digestibility, energy utilization and methane emissions of lactating dairy cows fed fresh-cut perennial grass. *Journal of Dairy Science* **99**: 8858–8866.

Hynes, D.N., Stergiadis, S., Gordon, A. and Yan, T. 2016b. Effects of nitrogen levels in concentrate supplements on animal performance and nitrogen utilization of lactating dairy cows fed fresh-cut perennial grass. *Journal of Dairy Science* **99**: 8111–8120.

Lorenzana, R.E. and Bernardo, R. 2009. Accuracy of genotypic value predictions for marker-based selection in biparental plant populations. *Theoretical and Applied Genetics* **120**: 151–161.

Irwin, R. 2019. “Investing in Grassland Management Yields Dividends for Beef Farmers”. *Farm Week*, 3 May 2019. Available online: https://farmweek.com/investing-in-grassland-management-yields-dividends-for-beef-farmers/.

Jarvis, S.C., Wilkins, R.J. and Pain, B.F. 1996. Opportunities for reducing the environmental impact of dairy farming managements: a systems approach. *Grass and Forage Science* **51**: 21–31.

Klaas, M., Yang, B., Bosch, M., Thorogood, D., Manzanares, C., Armstead, I.P., Franklin, F.C.H. and Barth, S. 2011. Progress towards elucidating the mechanisms of self-incompatibility in the grasses: further insights from studies in Lolium. *Annuals of Botany* **108**: 677–685.

Kole, C. (ed.) 2013a. “Genomics and Breeding for Climate-Resilient Crops: Volume 1, Concepts and Strategies”. Springer Science and Business Media, Switzerland AG, ISBN 978-3-642-44096-0, page 520.

Kole, C. (ed.) 2013b. “Genomics and Breeding for Climate-Resilient Crops: Volume 2, Target Traits”. Springer Science and Business Media, Switzerland AG, ISBN 978-3-642-43571-3, page 490.

Lively, F. 2019. Beef from Grass – an evaluation of beef grazing strategies for the NI beef industry. *AgriSearch*, online report: https://www.agrisearch.org/beef/ongoing-beef/grassland-management-beef/491-b-22-16-beef-from-grass-an-evaluation-of-beef-grazing-strategies-for-the-ni-beef-industry.

Long, D., Billings, P., Hindle, J. and Gilliland, T.J. 2010. Marketing of improved grass varieties, 171–183. In: “Grasses for the Future, Perennial Ryegrasses: Current and Future Genetic Potential” (eds. M. O’Donovan and D. Hennessy), Teagasc Occasional Publication, Fermoy, Co. Cork, Ireland, page 188.

Manzanares, C., Yates, S., Ruckel, M., Nay, M. and Studer, B. 2016. TILLING in forage grasses for gene discovery and breeding improvement. *New Biotechnology* **33**: 595–597.

Martin, C., Morgavi, D.P. and Doreau, M. 2010. Methane mitigation in ruminants: from microbe to the farm scale. *Animal* **4**: 351–365.

Mayer, K.F.X., Martis, M., Hedley, P.E., Šimková, H., Liu, H., Morris, J.A., Steuernagel, B., Taudien, S., Roessner, S., Gundlach, H., Kubaláková, M., Suchánková, P., Murat, F., Felder, M., Nussbaumer, T., Graner, A., Salse, J., Endo, T., Sakai, H., Tanaka, T., Itoh, T., Sato, K., Platzer, M., Matsumoto, T., Scholz, U., Doležel, J., Waugh, R. and Stein, N. 2011. Unlocking the barley genome by chromosomal and comparative genomics. *The Plant Cell* **23**: 1249–1263.

Mayne, S. 2018. Farmers must plan for a ‘rainy day’. *Farming Life*, 9th June 2018. Available online: https://www.farminglife.com/news/farmers-must-plan-rainy-day-1023526.

McDonagh, J. 2017. Improving the productivity of perennial ryegrass (*Lolium perenne*) pastures in dairy systems in Ireland: genetic gain, genotype by management interactions and grazing efficiency. PhD thesis, Queens University Belfast.

McDonagh, J., O’Donovan, M., McEvoy, M. and Gilliland, T.J. 2016. Genetic gain in perennial ryegrass (*Lolium perenne*) varieties 1973 to 2013. *Euphytica* **212**: 187–199.
McEvoy, M., O'Donovan, M. and Shalloo, L. 2011. Development and application of an economic ranking index for perennial ryegrass cultivars. *Journal of Agricultural Science* **94**: 1627–1639.

Meehan, E.J. 2016. “Grass and Clover Recommended Varieties for Northern Ireland 2016”. Department of Agriculture and Rural Development, Annual Publication, Belfast, Northern Ireland, United Kingdom, page 40.

Merry, R.J., Lee, M.R.F., Davies, D.R., Dewhurst, R.J., Moorby, J.M., Scollan, N.D. and Theodorou, M.K. 2006. Effects of high-sugar ryegrass silage and mixtures with red clover silage on ruminant digestion. I. In vitro and in vivo studies of nitrogen utilization. *Journal of Animal Science* **84**: 3049–3060.

Miller, L.A., Baker, D.H., Theodorou, M.K., MacRae, J.C., Humphreys, M.O., Scollan, N.D. and Moorby, J.M. 2001. Efficiency of nitrogen use in dairy cows grazing ryegrass with different water soluble carbohydrate concentrations. *Proceedings of the 19th International Grasslands Congress*, Llandysul, Wales, United Kingdom, pages 377–378.

Misselbrook, T.H., Gilhespy, S.L., Cardenas, L.M., Williams, J. and Dragosits, U. 2016 *Inventory of Ammonia Emissions from UK Agriculture 2015*. DEFRA Contract SCF0102, Inventory Submission Report, Oct. 2016.

O’Donovan, M. and Delaby, L. 2005. A comparison of perennial ryegrass cultivars differing in heading date and grass ploidy with spring calving dairy cows grazed at two different stocking rates. *Animal Research* **54**: 337–350.

O’Donovan, M., Dillon, P., Rath, M. and Stakelum, G. 2002. A comparison of four methods of herbage mass estimation. *Irish Journal of Agriculture and Food Research* **41**: 17–27.

O’Donovan, M., McHugh, N., McEvoy, M., Grogan, D. and Shalloo, L. 2016. Combining seasonal yield, silage dry matter yield, quality and persistency in an economic index to assist perennial ryegrass variety selection. *Journal of Agricultural Science* **155**: 556–568.

Osterburg, B., Isermeyer, F., Lassen, B. and Röder, N. 2010. Impact of economic and political drivers on grassland use in the EU. Grassland in a Changing World. *Proceedings of the 23rd General Meeting of the European Grassland Federation*, Kiel, Germany, 29 August–2 September, 2010. Grassland Science in Europe, **15**: 14–28.

Parijs, F., Van Waes, C., Vandecasteele, B., Haesaert, G., Roldán-Ruiz, I. and Muylle, H. 2017. The optimal lignin quantification method to breed for an improved cell wall digestibility in perennial ryegrass. *Grass and Forage Science* **73**: 101–111.

Parsons, A.J., Edward, G.R., Newton, P.C.D., Chapman, D.F., Caradus, J.R., Rasmussen, S. and Rowarth, J.S. 2011. Past lessons and future prospects: plant breeding for yield and persistence in cool-temperate pastures. *Grass and Forage Science* **66**: 153–172.

Pérez-Prieto, L.A. and Delagarde, R. 2012. Meta-analysis of the effect of pregrazing pasture mass on pasture intake, milk production, and grazing behavior of dairy cows strip-grazing temperate grasslands. *Journal of Dairy Science* **95**: 5317–5330.

Price, R. 2015. “Pre-mow Grazing Helps Cows Yield 70% of Milk From Forage”. *Farmers Weekly*, 18 February 2015. Available online: https://www.fwi.co.uk/livestock/dairy/pre-mow-grazing-helps-cows-yield-70-milk-forage.

Sampouj, J.-P., Baudouin, P., Bayle, B., Béguierv, V., Bourdon, P., Chosson, J.-F., Denefoul, F., Galbrun, C., Ghéssiquière, M., Noël, D., Pieterszéke, W., Tharel, B. and Viguié, A. 2011. Breeding perennial grasses for forage usage: an experimental assessment of trait changes in diploid perennial ryegrass (*Lolium perenne L.*) cultivars released in the last four decades. *Field Crops Research* **123**: 117–129.

Shibata, M. and Terada, F. 2010. Factors affecting methane production and mitigation in ruminants. *Animal Science* **81**: 2–10.

Smit, H.J., Tas, B.M., Taweel, H.Z., Tamminga, S. and Elgersma, A. 2005a. Sward characteristics important for intake in six Lolium perenne varieties. *Grass and Forage Science* **60**: 128–135.

Smit, H.J., Tas, B.M., Taweel, H.Z., Tamminga, S. and Elgersma, A. 2005b. Effects of perennial ryegrass (*Lolium perenne L.*) cultivars on herbage production, nutritional quality and herbage intake of grazing dairy cows. *Grass and Forage Science* **60**: 297–309.

Talbot, M. 1984. Yield variability of crop varieties in the U.K. *Journal of Agricultural Science* **102**: 315–321.

Tas, B.M., Taweel, H.Z., Smit, H.J., Elgersma, A., Dijkstra, J. and Tamminga, S. 2005. Effects of perennial ryegrass cultivars on intake, digestibility, and milk yield in dairy cows. *Journal of Dairy Science* **88**: 3240–3248.

Tubritt, T., Gilliland, T.J., Delaby, L. and O’Donovan, M. 2018. Comparison of grass utilisation performance of perennial ryegrass varieties. *Proceedings of the 27th General Meeting of the European Grassland Federation: Sustainable milk and meat production from grasslands*, Cork, Ireland, 17–21st June 2018, *Grassland Science in Europe*, **23**: 54–56.

van Wijk, A.P.M. Den Nijs and A. Elgersma, Pudoc, Wageningen, pages 13–18.

Wilkins, P.W. 1989. Genotype/harvesting frequency and genotype/nitrogen level interactions for annual dry matter yield in *Lolium perenne* in relation to breeding. *Euphytica* **3**: 207–214.

Wilkins, P.W. and Humphreys, M.O. 2003. Progress in breeding perennial forage grasses for temperate agriculture. *Journal of Agricultural Science* **140**: 129–150.

Wilkins, P.W., Allen, D.K. and Mytton, L.R. 2000. Differences in the nitrogen use efficiency of perennial ryegrass varieties under simulated rotational grazing and their effects on nitrogen recovery and herbage nitrogen content. *Grass and Forage Science* **55**: 69–76.
Wims, C., Kennedy, E., Boland, T. and O’Donovan, M. 2009. Effect of evaluation protocol and cultivar on the classification of seasonal and total dry matter yield. *Irish Journal of Agriculture and Food Research* **48**: 266.

Wims, C.M., McEvoy, M., Delaby, L., Boland, T.M. and O’Donovan, M. 2013. Effect of perennial ryegrass (*Lolium perenne* L.) cultivars on milk yield of grazing dairy cows. *Animal* **7**: 410–421.

Yabe, S., Hara, T., Ueno, M., Enoki, H., Kimura, T., Nishimura, S., Yasui, Y., Ohsawa, R. and Iwata, H. 2018. Potential of genomic selection in mass selection breeding of an allogamous crop: an empirical study to increase yield of common buckwheat. *Frontier Plant Science* **9**: 1–12. doi: 10.3389/fpls.2018.00276.

Yong-Bi, F. 2015. Understanding crop genetic diversity under modern plant breeding. *Theoretical and Applied Genetics* **128**: 2131–2142.