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Developments in nutrition for pasture-based cattle and sheep systems in Ireland

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Abstract

For ruminant production systems, the requirement to meet specific nutrient targets in the animal's diet must be balanced with the aim of achieving high utilisation of forage in the overall feed budget. A focus of research and extension in an Irish industry context has been to meet these objectives using grazed pasture as the predominant forage source. This has prompted investigation to improve understanding of the components defining forage nutritive value, as well as the management factors affecting its intake and utilisation by animals. Similarly, quantifying the animal performance responses to varying type, rate and timing of dietary supplementation has been an important area of investigation. This review summarises some of the principal outcomes and developments over recent years across beef, sheep and dairy production systems. In addition, ruminant production systems are increasingly challenged to reduce potential environmental impacts by mitigating nutrient and gaseous emissions across their production cycles. Current and emerging research with regard to this issue, and enteric methane production in particular, is discussed.

Keywords

Grazing • nutrient balance • ruminants • supplementation

Introduction

Conversion of human-indigestible forage fractions to utilisable protein is the key contribution of ruminant production systems to global human food production (Laisse et al., 2018). Increasingly, however, international agri-environmental policy and the evolving preferences of consumers are placing additional technical demands on livestock farmers (Sidali et al., 2016; European Union (EU) Commission Farm to Fork Strategy, 2020). The primary challenges faced by the ruminant production sector in this regard are well documented and encompass minimising nutrient loss to the environment, reducing dependency on human-edible foodstuffs, addressing animal health and welfare considerations and satisfying consumer perceptions regarding sustainable food systems (Peyraud, 2017). These challenges must be met against a backdrop of often low and variable economic margins generated by primary agricultural production (Teagasc, National Farm Survey, 2019).

In Ireland, the agriculture sector has been traditionally dominated by cattle and sheep production enterprises. Pasture-based production models are characteristic, with land for grazing, hay and silage production accounting for 93% of utilisable agricultural area (Central Statistics Office [CSO], 2020). The evolution within, and interaction between, the various systems has been heavily influenced by EU agricultural policy. For example, the national dairy cow population declined from approximately 1.6 million (M) head at introduction of milk quotas in 1984 to 1.1 M in 2001, rising again in recent years to 1.6 M head with removal of milk quotas. On the other hand, the national beef cow population rose from 0.45 M head in 1984 to 1.2 M in 2001, coincident with both the introduction of coupled payments and the restrictions imposed by milk guotas, and has reduced to 0.95 M in 2020. The national population of breeding ewes has fluctuated in that time also, from 1.9 M in 1985, to a peak of 4.8 M in 1993, to a level of 2.8 M in 2020 (CSO, 2020).

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Furthermore, the sectors have diverged somewhat in structure with dairying developing larger-scale, seasonal pasture systems with greater grazing stocking intensities, beef systems having lower stocking intensities across a range of suckler and finishing models and the sheep sector having moderate farm scale with low grazing stocking densities relative to research benchmarks (Teagasc, National Farm Survey, 2019).

Globally, agriculture is estimated to account for 44% of methane (CH₄), 81% of nitrous oxide (N₂O) and 23% of total greenhouse gas (GHG) emission equivalents (Food and Agriculture Organization of the United Nations, 2020). In the pasture-based production model practised in Ireland, GHG emissions associated with production and transport of imported feeds, slurry handling and cropping are low relative to confinement-type systems (O'Brien et al., 2012). Enteric methane production therefore accounts for a higher proportion of total emissions, and was estimated at 58% of agriculturederived GHG in Ireland for 2020 (Environmental Protection Agency [EPA], 2021). When expressed per unit of product, the carbon efficiency of dairy production in Ireland, for example, compares well with international counterparts (Kelly et al., 2020). Nonetheless, total emissions have increased by 8% between 2014 and 2020 (EPA, 2021), reflecting a change in national herd output and structure. This has occurred in the context of a national climate policy in Ireland that has targeted a 20-30% reduction in GHG emissions from the agriculture sector before 2030 (Department of Environment, Climate Change and Communications, 2021). Clearly, nutritional mitigation of GHG, in efficiency and absolute terms, is a priority issue for the ruminant production systems nationally. At national level, these underlying factors have been important in framing the research themes and priorities for optimising nutrition management for each industry sector. There are a number of core issues that are common to each, including defining the quality of grazed pasture and conserved forages and its effect on animal performance, understanding the factors affecting productivity responses to feed supplements, nutrition effects on product quality, interactions with animal health and the potential for dietary mitigation of nutrient losses and GHG emissions. This paper presents an overview of some key research outcomes from recent years relevant to these themes, with a particular emphasis on pasture-based sheep, beef and dairy systems in Ireland.

Quantifying the nutritive value of pasture

The nutritive value of pasture is closely related to its digestibility due to the effect of digestibility on net energy concentration and ingestibility (Peyraud & Delagarde, 2013). Digestibility also affects the amount of ruminal fermentable carbohydrate that is available to support microbial protein synthesis and hence the supply of metabolisable amino acids (AAs; O'Mara et al., 1997). Pasture digestibility can be guite variable with a wide range being reported for the total-tract digestibility (TTD) in pasture-fed lactating dairy cows (72% to 84% organic matter TTD; Morgan & Stakelum, 1987; Rius et al., 2012; Garry, 2016). Many factors have been demonstrated to affect the digestibility of pasture such as pasture mass (Mambrini & Peyraud, 1994; Garry et al., 2021), nitrogen (N) fertiliser application (Delagarde et al., 1997; Peyraud et al., 1997), species and cultivar (Smit et al., 2005; Chen et al., 2019; Garry et al., 2020), morphological proportions (Beecher et al., 2015), environmental conditions (Van Soest, 1994) and seasonal variation (Roche et al., 2009b; Douglas et al., 2020). Over the past few decades, to understand and quantify pasture digestibility. Ireland has primarily focussed on the measurement of total-tract organic matter digestibility (OMD) using the in vivo total collection method in sheep and cattle (Morgan & Stakelum, 1987; O'Mara, 2000). A number of experiments have demonstrated that immature perennial ryegrass (PRG) can be highly digestible (Morgan & Stakelum, 1987; Beecher et al., 2014, 2018; Garry et al., 2020, 2021). The inclusion of white clover into PRG swards has been demonstrated to further increase the in vivo OMD of pasture-based diets (Peyraud, 1993; Hurley et al., 2021). This high OMD of immature pasture results in high concentrations of metabolisable or net energy per kg of dry matter (DM) (Bruinenberg et al., 2002; Institut National de Recherche Agronomique [INRA], 2018). Furthermore, the high concentrations of ruminal fermentable carbohydrate within immature pasture can support high microbial protein flows (Younge et al., 2004). Altogether, these attributes can allow high dry matter intake (DMI) and milk production performance to be achieved from pasture-based diets (Buckley et al., 2000). While an accurate measure of TTD can be achieved from the total collection method, an understanding of the ruminal kinetics of digestion and passage and the digestive compartment in which digestion might occur cannot be attained. This reduces our ability to understand mechanisms regulating DMI, the effect of a suboptimal ruminal environment on digestibility (Huhtanen et al., 2006) and the profile of nutrients available for absorption by the ruminant (e.g. volatile fatty acids, AAs from microbial protein). To attain a greater understanding of the site of digestion and nutrient supply in Irish pasture-fed lactating dairy cows, digesta flow studies incorporating duodenal or omasal sampling were performed (O'Mara et al., 1997; Younge et al., 2004; Dineen et al., 2020, 2021a). These studies have highlighted a number of key characteristics in regard to the nutritive value of pasture; immature pasture is highly digestible with the majority of digestion occurring prior to the omasum/ duodenum; extensive ruminal digestion of immature PRG N/ AA occurs suggesting that cows consuming such diets exhibit a large dependence on microbial AA to support metabolisable

AA supply; measurement of the rumen pool size of cows fed highly digestible immature pasture indicates that rumen distension does not limit DMI; and consumption of immature pasture stimulates high ruminal liquid passage rate which may affect microbial metabolism and protein synthesis.

The use of omasal sampling has been extremely limited in pasture-fed lactating dairy cow experiments when compared with the large body of literature that exists for indoor feeding systems (Broderick *et al.*, 2010; Huhtanen *et al.*, 2010). The omasal sampling technique conveys a number of advantages over duodenal sampling such as less invasive sampling, reduced variability of measurement (Huhtanen *et al.*, 2010) and increased capability of characterising the different sources of AA flows (i.e. feed, endogenous and microbial populations; Ahvenjärvi, 2006). Incorporating the omasal sampling technique into future studies is imperative to strengthen our understanding of the factors governing ruminal digestion and passage kinetics, DMI and milk production performance of pasture-fed lactating dairy cows.

As many factors with endless combinations can affect the digestibility of pasture-based diets, in vivo experiments to describe their effect are neither practical nor cost effective. Therefore, laboratory feed evaluation techniques and mathematical models are used to estimate the supply of energy and AA from a diet. In addition, laboratory analysis to characterise the nutritive value of pasture pre-grazing provides superior management data in comparison to using historical tabulated values (Doughlas et al., 2021). A number of in vivo digestibility trials were conducted in Ireland from 1981 to 1984 to provide data for the evaluation of three in vitro laboratory procedures to predict in vivo digestibility (Morgan & Stakelum, 1987). The three in vitro procedures (neutral detergent cellulase [Dowman & Collins, 1982], rumen fluid pepsin [Tilley & Terry, 1963] and pepsin cellulose [Jones & Hayward, 1975]) were demonstrated to have moderate accuracy in predicting in vivo OMD when combined with regression equations (Stakelum et al., 1988). Morgan et al. (1989) subsequently modified the neutral detergent cellulose digestibility procedure for use with the "Fibertec" system which has since been routinely used in Ireland to predict in vivo OMD. The regression equation developed by Stakelum et al. (1988) to predict in vivo OMD was recently evaluated. Beecher et al. (2015) using an independent dataset of in vivo OMD found that predictions of OMD from the Morgan et al. (1989) in vitro procedure were significantly different from those of the in vivo measurements. The authors highlighted that a small sample size and the narrow range of in vivo OMD in the independent dataset may have contributed to the poor prediction capability. Garry et al. (2018) expanded the dataset and derived updated regression equations with a moderate capability to predict in vivo OMD, with a similar accuracy to the equation developed by Stakelum et al. (1988).

In a comprehensive evaluation incorporating 177 samples and utilising the pepsin cellulose method (Aufrère et al., 2007), a moderate capability to predict in vivo OMD of fresh grasses and permanent grasslands was also demonstrated (R² = 0.78; root-mean-square error [RMSE] 2.9; INRA, 2018). Altogether, there seems to be little scope to further increase the accuracy and precision of predicting in vivo OMD from the in vitro OMD procedures. This may be due, at least in part, to a number of in vitro OMD procedure limitations such as the use of cellulolytic enzymes, large pore size filtering apparatus and single fermentation time points. Cellulolytic enzymes do not degrade neutral detergent fibre (NDF) as efficiently as rumen microorganisms (Van Soest et al., 1978), large pore size filtering apparatus has been demonstrated to underestimate the recovery of components of the plant cell wall and overestimate digestibility (Udén, 2006; Raffrenato et al., 2018) and finally, a single fermentation time point can reduce the procedures' ability to adequately describe the dynamic and heterogeneous nature of NDF digestibility (Ellis et al., 2005; Huhtanen et al., 2008).

Nousiainen (2004) evaluated the ability of indigestible NDF (iNDF) concentration, measured after 12 d of in situ fermentation (Huhtanen et al., 2006), to predict in vivo OMD. The author reported a high capability to predict in vivo OMD at the forage specific level ($R^2 = 0.89-0.99$). This was recently supported by the findings of Garry et al. (2021) who demonstrated a close relationship among iNDF and in vivo OMD in sheep consuming PRG ($R^2 = 0.92$). However, the in situ procedure, like in vivo OMD, is quite laborious involving multiple handling of cannulated cows. Raffrenato et al. (2018) developed an in vitro method utilising rumen fluid, a small pore size filter paper and multiple fermentation time points to generate a comprehensive in vitro description of NDF digestibility. The authors demonstrated a strong relationship among undigested NDF (uNDF; measured after in vitro fermentation for 240 h) and iNDF ($R^2 = 0.89$; Raffrenato et al., 2018). This highlights the potential of the in vitro NDF digestibility procedure to increase our ability to predict in vivo OMD of pasture-based diets. Crucially, the procedure can be performed in a commercial laboratory setting and is repeatable and adaptable for routine feed evaluation.

Near-infrared reflectance spectroscopy (NIRS) technology can be utilised to expedite the feed evaluation process. In regard to forage digestibility, NIRS technology has been demonstrated to successfully predict iNDF concentration (Nousiainen *et al.*, 2004; Krizsan *et al.*, 2014). However, these NIRS calibration equations require sample preparation of drying and grinding which are laborious, time consuming and expensive. Murphy (2020) recently demonstrated the capability of NIRS calibration equations, developed from fresh pasture samples, to predict the concentrations of DM and crude protein (CP). While accurate estimations of DM were achieved, further development of the CP calibration models is required in addition to other chemical components such as iNDF/uNDF. Future work should focus on real-time estimation of the nutritive value of pasture-based diets through the development of fresh NIRS calibration models and other rapid technologies such as hyperspectral sensing (Pullanagari *et al.*, 2012).

Developments in nutrition of dairy cows

The predominant feeding strategy underpinning dairy production systems in Ireland is to maximise utilisation of grazed pasture in the diet of the lactating herd (O'Donovan *et al.*, 2011). This has proven economic (Hanrahan *et al.*, 2018), product quality (Alothman *et al.*, 2019) and environmental (O'Brien *et al.*, 2012) benefits in an Irish context. The typical annual pasture growth pattern in Ireland results in supplementation being most required during the spring (February/March) and autumn (October/November) grazing rotations, which typically coincide with the early postpartum and late lactation periods, respectively.

Pasture utilisation is a systems efficiency metric that encompasses annual pasture growth and feed demand patterns, supplementary feed and milk output, and is positively associated with profitability per unit area. Milk productivity per cow tends to increase profit only if derived from greater pasture utilisation. Indeed, Ramsbottom et al. (2015) concluded that production costs increase by approximately 1.5 times the rate of direct cost of supplementary feed purchase due to associated capital expenses. At the daily operational level, pasture utilisation for the optimal synthesis of milk requires consistent provision of high-digestibility, high leaf content swards, grazed at the optimal growth stage to the correct residual, by cows of a suitable genotype (Hennessy et al., 2020). Hence, the role of feed supplementation within the system has become tactical in nature, being employed to address deficits in pasture supply and quality, or to deliver specific limiting nutrients.

Achieving high levels of pasture intake while balancing feed demand variation due to stocking rate, with the impact of supplement feeding on pasture and total nutrient intake, is a key consideration for dairy grazing systems (McCarthy *et al.*, 2010). Daily intake of pasture is a limited by the combined effects of bite rate, bite mass and number and duration of grazing bouts (Dillon, 2006). This is of course predicated on the provision of a requisite daily DM allowance such that grazing behaviour and animal intake capacity are first-limiting on herbage intake (Bargo *et al.*, 2003). However, the objective of increasing daily pasture intake must be balanced with a requirement to achieve a post-grazing residual that maintains sward quality for subsequent grazing (Stakelum & Dillon, 2007). In addition, marginal increases in grazing stocking

rate may elicit a milk yield response on a per-hectare basis, despite a reduction in individual cow DMI and milk productivity (McCarthy *et al.*, 2010). The scale of milk responses to such changes in individual feed allowances may be genotype dependent (McCarthy *et al.*, 2007). McDonald *et al.* (2011) demonstrated that the impact of stocking rate on individual cow DMI and milk productivity resulted in a quadratic effect of stocking rate on dairy farm profitability per unit area.

The sward characteristics that maximise intake may differ with grazing management regime, for example, optimal pregrazing sward height may be lower for continuous versus rotationally grazed swards (Dillon, 2006). Dry matter intake is higher for swards with higher proportion of leaf content and greater OMD (Peyraud & Delagarde, 2013). Nonetheless, DMI and fat-corrected milk yield of grazing dairy cows is lower than that of cows offered total mixed diet formulated to maximise nutrient density and DMI (Kolver & Muller, 1998; O'Callaghan *et al.*, 2016). This is due to the physical limitations to intake imposed by grazing, in combination with higher and more variable NDF content in pasture, and lower non-structural carbohydrate content.

Numerous lactating dairy cow studies have characterised the influence of digestibility on variables such as DMI, rumen pool size, rumination and milk production performance (Oba & Allen, 1999; Cotanch et al., 2014; Zontini et al., 2015). Beecher et al. (2018) demonstrated, in an investigation with sheep, that the in vivo NDF digestibility of PRG was a better predictor of DMI than in vivo OMD. Dineen et al. (2021b) recently highlighted that when a more accurate characterisation of NDF digestibility is combined with the Cornell Net Carbohydrate and Protein System, a greater understanding of the nutrient supply and milk production performance of grazing dairy cows can be achieved. This increased understanding of pasture nutritive value, in regard to rumen turnover, metabolisable energy (ME) supply and post-ruminal AA flows, can aid in the development of future nutritional strategies to increase the efficiency and productivity of pasture-based systems. Such nutritional strategies could include development of improved pasture management practices (O'Donovan et al., 2002), optimisation of concentrate supplementation (Baudracco et al., 2010), selection of superior plant genetics (Lee et al., 2012) and the development of binary or multi-species pastures (McCarthy et al., 2020).

Nutrition of early lactation dairy cows in grazing systems Supply of ME, and not metabolisable protein or specific AAs, is usually first-limiting for milk production in grazing systems (Kolver & Muller, 1998). This is primarily a function of physical/behavioural limitations to feed intake on highquality pasture, rather than large differences in nutrient density or digestibility per unit of DM (Bargo *et al.*, 2003). Given the positive associations between grazing season length and financial performance (Läpple *et al.*, 2012), nutrition research in an Irish context has orientated toward optimising intake and supplementation of pasture diets during extended grazing periods. The early spring period in particular presents the challenge of synchrony between low postpartum intake potential at the animal level and potentially challenging grazing conditions (Kennedy *et al.*, 2011; Patton *et al.*, 2012). A key objective has been to develop strategies that strike a balance between high grass utilisation, support of high milk solids yield derived primarily from pasture intake and promotion of metabolic health of the cow (Dillon, 2006).

To examine the efficacy of pasture as the primary forage source in early lactation, Kennedy et al. (2005) evaluated performance of cows fed pasture plus concentrate (3-4 kg DM) relative to herd-mates offered a total mixed ration (TMR) containing 0.6 of DM as concentrate plus moderate-guality grass silage, and reported similar solids-corrected yield (25.9 vs. 26.6 kg) and bodyweight change. No carryover effects were observed while milk protein content was improved through inclusion of pasture in the diet. Differences in concentrate feeding level were offset by superior intake and digestibility of grazed pasture relative to the forage silage component of the TMR. In contrast, O'Neill et al. (2011) showed significantly increased milk volume and total solids yield for a maize/grass silage/concentrate-based TMR relative to pasture for early lactation cows. This output difference resulted from greater daily DMIs for the TMR (19.2 kg vs. 14.5 kg) at comparable levels of dietary energy density. Differences in the biological performance of pasture and indoor diets are determined by the DMIs, nutrient densities and feed conversion efficiencies achieved within each system paradigm (Kolver, 2003). Such differences will ultimately determine the relative economic and environmental impacts for systems-level comparisons (Shalloo et al., 2004; O'Brien et al., 2012).

McEvoy et al. (2008), developing on the concept of optimising intakes in early season grazing scenarios, imposed a range of herbage allowances and concentrate supplementation rates in a factorial design. Early lactation milk production and grass utilisation were optimised where cows were offered 17 kg DM pasture plus 3 kg DM concentrate, or 13 kg DM plus 6 kg DM concentrate where pasture availability was limited. Negative residual effects on milk solids yield were observed for unsupplemented groups where daily DM allowances resulted in excessive (>0.4 units) body condition score (BCS) loss in early lactation. Ganche et al. (2013) also found a negative impact on milk solids yield and body condition of tightly restricting early postpartum intakes, albeit via differential herbage allowances at similar concentrate feeding rates. It was demonstrated that cows grazing to 2.7 cm residual heights had reduced intake and milk solids yield versus 3.5 cm or 4.2 cm, but there was little

evidence of carryover effects in the post-treatment period at common post-grazing residuals. While restricting nutrient intake in early lactation evidently curtails milk productivity, reducing grazing pressure in spring can result in progressive decline in sward digestibility, leading to a milk solids yield loss during summer rotations (Stakelum & Dillon, 2007). The management aims of high intake and sward conditioning for subsequent grazings must therefore be considered in tandem.

Supplement type and composition effects on dairy cow performance

Within the overall strategy of increasing grazed pasture in the lactating cow, there is a requirement to define the most suitable feed supplement for particular circumstances. The ideal feed supplement will increase intake of a specific limiting nutrient, minimise pasture substitution to elicit an economic response, have low risk of rumen upset and facilitate ease of storage and feeding (Kolver & Muller, 1998). Principal issues include rate and timing of supplementation, supplement type, production and health responses, effects on nutrient balances and the overall economic response.

The ingestibility or "fill value" of a forage is dictated by its fibre, protein and DM content and its physical properties (Faverdin et al., 2011) Inclusion of forage with higher ingestibility gives reliable milk responses where it replaces a lower-quality feed, for example, where maize silage replaces moderate-guality grass silage (Burke et al., 2007), or indeed where highdigestibility grass silage replaces lower-digestibility silage (Ferris et al., 2001). Maize may confer N-use efficiency (NUE) advantages compared to grass silage as a basal forage supplement (Burke et al., 2007). Milk responses to conserved silage supplements at grazing are usually limited by forage fill value and cow intake capacity however, particularly in scenarios of pasture allowances and quality are not limiting. For example, Morrison & Patterson (2007) compared maize silage, whole-crop wheat silage and concentrate as supplement options for mid-lactation cows grazing pasture. Concentrate supplementation produced a lower substitution rate and therefore greater total intake response relative to the forage supplements, resulting in superior milk responses; maize silage produced the greatest milk vield response of the forage supplements compared. Burke et al. (2008), on the other hand, found similar milk solids responses to 4 kg DM concentrate or maize silage in mid-lactation where supplements were offered in a scenario of restricted pasture allowance; the same study showed additional pasture allowance returning similar milk solids responses to either supplement type.

Concentrate feeding twice daily during milking is the predominant means of supplementation in pasture-based systems in Ireland, as it offers the advantages of simplicity of delivery, high energy and protein content and lower impact on pasture intake. It also provides a means of balancing macro and trace mineral deficiencies in pasture (Curran et al., 2016). Factors affecting variation in milk yield and body tissue accretion responses to concentrates are numerous and include pasture allowance and digestibility, stage of lactation and rate of supplementation (Bargo et al., 2003). Horan et al. (2005) also established an effect of cow genotype on marginal milk response to concentrate, which varied from approximately 0.5 to 1.1 kg solids-corrected milk between New Zealand and North American strains of Holstein Friesian, respectively. Milk responses to supplement feeding are governed to a large extent by substitution rate, defined as the differential between unsupplemented pasture intake and supplemented pasture intake, divided by supplement feeding rate. Therefore, while standard cereal-based concentrates may have net energy book values that are sufficient for up to 2 kg milk production per kg DM fed, the milk response rate is inevitably much lower (approximately 1:1) due to pasture substitution and the negative associative effect of concentrate on whole diet digestibility (Noziere et al., 2018). Developing more accurate real-time decision support on the likely responses to supplementation at pasture is an important objective (Ruelle et al., 2015).

Concentrate composition also impacts production and nutrient-use efficiency responses. A key aim for pasture feeding systems has been to reduce N surpluses and therefore urinary N excretion to the environment. Increasing pasture utilisation, grazing season length and milk solids yield are important factors (Ryan et al., 2012), while moderating CP inclusion levels in supplement can also play a role. On ryegrass diets, provision of a moderate allowance of highenergy, low-protein supplement can improve efficiency of microbial protein synthesis and duodenal AA flow (O'Mara et al., 1997). The N-efficiency effect of moderating supplement protein is dependent on specific composition and herbage N content. Reid et al. (2015) found no difference in milk solids yield or milk protein content, when pasture was supplemented with 3 kg DM of concentrate ranging from 90 to 277 g/kg DM. Feeding lower CP ration reduced blood urea N levels. Differences in urinary N excretion were minor across treatments however, which was attributed to high CP levels in the herbage and moderate level of supplementation. Whelan et al. (2012b), operating on lower pasture CP content, recorded a reduction in solids-corrected milk yield when concentrate protein was reduced from 180 to 150 g/kg DM. However, the effect was negated by replacing barley with maize meal as a starch source, or by inclusion of a methionine precursor (2-hydroxy-4-methylthio butanoic acid). Both strategies ensured improved supply of AA to the mammary gland despite the reduction in overall CP content. In that study also, a simple reduction of concentrate CP did not alter

urinary N excretion due to a reduction in milk N, whereas the modified low-protein diets improved N recovery rate. Burke *et al.* (2008) reported a reduction in urinary N, for no change in milk output, from feeding a lower CP concentrate (97 vs. 197 g/kg DM) with restricted pasture allowance. CP content remains widely used as a proxy for feed "quality" in dairy systems at industry level. However, there is significant scope to moderate N surpluses and lower costs of imported protein, by implementing strategies based on supply of dietary protein digestible in the small intestine (PDI), from pasture diets and supplements.

Choice of energy source for concentrate supplements may also affect milk yield and nutrient efficiency responses on pasture diets. Bargo et al. (2003), summarising studies involving early lactation cows grazing immature ryegrass swards, concluded a positive effect on milk yield by substituting digestible fibre sources (beet pulp, citrus pulp, soya hills) for starch-based energy supplements (barley, wheat). The benefits were less apparent in studies involving swards of lower digestibility however. Whelan et al. (2012a) demonstrated a milk response benefit to maize compared to barley as a concentrate energy source in early lactation grazing cows. In contrast, McKay et al. (2019), using late lactation grazing cows, showed a greater milk production response, and improved NUE, for a barley-based concentrate compared to a maize-based concentrate; pasture substitution was higher for the maize-based concentrate in that study. Higgs et al. (2013) similarly reported higher milk yield but lower milk fat content for starch-based compared to fibrebased concentrate supplements. Collectively, these studies indicate that optimal energy source for pasture supplements is dependent on basal forage guality, stage of lactation and proportion of concentrate offered in the daily diet.

A particular issue for grazing diets is the potential effect of sward type and carbohydrate composition of concentrate supplements on the risk of sub-acute ruminal acidosis (SARA). This disorder is generally defined on the basis of mean rumen pH with values below 5.8 considered confirmative, and has been associated with reduced milk solids yield, milk fat depression and health issues such as lameness and liver abscesses (Abdela, 2016). The risk of SARA is elevated where diets contain increased levels of non-fibre carbohydrate and reduced structural/forage fibre, which has led to some concerns regarding the potential role of grazing higher digestibility swards. Lewis et al. (2010) examined the effect of pre-grazing herbage mass across a wide practical range (1,200, 1,600 and 2,200 kg DM/ha) and found no significant effect on ruminal pH however. O'Grady et al. (2008) classified commercial dairy herds for SARA risk based on rumen pH profiles measured by rumenocentesis. Higher-risk herds were found to be grazing swards with higher acid and NDF contents while there was no difference in milk fat or milk fat to protein ratio between herds classified as high

or low rumen pH around threshold of 5.8. Enriquez-Hidalgo et al. (2014) reported higher mean rumen pH for cows grazing ryegrass-white clover swards compared to ryegrass only swards in autumn, despite lower NDF content in the sward containing clover; no differences were observed during spring and summer periods. In terms of concentrate type at pasture, including greater fractions of digestible fibre and/or more slowly degradable starch at pasture may be beneficial for rumen pH (Stakelum & Dillon, 2003); however, consistency of milk production responses can be difficult to quantify given the multiplicity of diet, sward and animal factors involved (Kolver & de Veth, 2002). Overall, it may be an over-simplification to assume definitive causation between provision of high-quality pasture at optimal pre-grazing mass and the risk of SARA. Further work is warranted to clarify the potential role in milk fat depression of temporal changes in rumen bio-hydrogenation of polyunsaturated fat content (Schroeder et al., 2004), particularly in immature grazed pasture.

Interactions between nutrition status and fertility in dairy cows

Throughout the 1990s and early 2000s, the issue of declining dairy cow pregnancy rates while milk production per cow increased was widely reported internationally (Lucy, 2001). Mee (2004) quantified this trend in an Irish context as a decline in first-insemination conception rate of approximately 0.9 percentage points per year annually over a 10-yr period, and a resultant increase in annual empty culling rates. The economic cost of suboptimal dairy herd fertility includes reduced milk production, culling and replacement costs and veterinary intervention. The cost is exacerbated in pasture-based systems due to the loss of synchrony between pasture supply and herd feed demand (Shalloo *et al.*, 2014); therefore, solutions to impaired dairy cow fertility have been an important research objective in recent decades.

Numerous contributing factors to declining dairy herd fertility have been posited including changes to herd scale and structure, reproductive management protocols and disease/ immunity burdens (Crowe *et al.*, 2018). Antagonism between genetic selection for milk productivity in early lactation and resumption of ovarian function and establishment of pregnancy has emerged as a predominant causal mechanism. More specifically, this has been characterised as being mediated through changes in the severity and duration of early lactation negative energy balance, that is, the differential between dietary nutrient intake and demand, rather than changes milk yield *per se* (Lucy, 2019).

A more severe dietary energy deficit in early lactation results in a more rapid BCS loss. Many studies have associated such accelerated rates of BCS loss with disimproved fertility outcomes (Buckley et al., 2003; Berry et al., 2003; Roche et al., 2009a). While it is recognised that dairy breeding indices rewarding high milk production at the expense of body tissue mobilisation elicited this trend (Lucy, 2019), various nutritional interventions have been attempted to arrest the impact on fertility. In a pasture system context, these intervention options are effectively constrained to an economically feasible rate and type of supplement fed in addition to pasture; studies investigating the fertility outcomes of changing type and rate of parlour-fed concentrates have predominated as a result. For example, Coleman et al. (2009), in a genotype by supplement rate study, found no difference in conception rate, embryo mortality rate or final pregnancy rate in grazing cohorts offered 3.4 kg compared to 0.4 kg DM of starch/fibre-based concentrate through the breeding season. Genetic index for fertility on the other hand delivered marked improvement in fertility metrics. In a similarly designed experiment, Vance et al. (2013) examined the effect of annual concentrate supplementation rate (530, 1,092 and 1,667 kg DM/cow) and genotype (Holstein, Holstein Jersey F1 hybrid) on milk productivity and fertility parameters. Concentrate feeding rate did not impact timing of postpartum resumption of ovarian cyclicity, conception rate or proportion of cows pregnant by end of breeding. In contrast, the Jersey/Holstein hybrid genotype had superior performance to the Holstein genotype across all these metrics; no genotype by feeding system interactions were detected. These trends were consistent with the findings of comparable work by Horan et al. (2004) and point to the limited capacity of simple changes in concentrate supplement rates to correct fertility issues where pasture quality and DM allowance are not limiting.

A further area of potential dietary intervention to improve fertility has been manipulation of the late gestation and peripartum diet, with the objective of creating a smoother transition to lactation and ultimately improved cow health. Strategies investigated have included alteration of pre-partum protein content (Murphy, 1999), inclusion of starch supplementation to condition rumen papillae to lactation diets and/or reduction in dietary energy density across the dry period to limit body tissue accretion (McNamara et al., 2003; Ryan et al., 2003; Butler et al., 2011). The broad conclusion from such studies has been that dairy herd health and fertility will not be compromised where dry period feeding programmes deliver optimal BCS at calving (3.0-3.25); a daily protein (PDI) intake of 610-630 g in late gestation; and a mineral status (dietary cation-anion balance, Ca, P and Mg content) that minimises (sub) clinical hypocalcaemia at calving. The options to achieve such outcomes are manifold and can generally be achieved using relatively simple grass silage-based dry cow diets (Mulligan et al., 2006).

A key development in thinking around potential for dietary manipulation of fertility has been the demonstration of

genetic control over peripartum nutrient partitioning and metabolic status, which effectively dictates metabolic status and immune function responses to diet in early lactation. For instance, Dechow et al. (2017) found that cows with a genetic tendency to be thin also had elevated growth hormone, B-hyroxybutyrate and non-esterified fatty acid profiles in early lactation; this had negative impacts on fertility. Moreover, Moore et al. (2014) reported that, on typical pasture-plusconcentrate diets, high economic breeding index (EBI) cows had increased blood insulin, insulin-like growth factor I and glucose levels, and maintained high BCS, compared to low EBI herd-mates. Postpartum uterine health and interval to resumption of ovarian cyclicity were also improved, while vield of milk solids was similar across the genotypes. Using the same animal model, Moran et al. (2016) identified strainmediated differences in expression of key metabolism, fertility and immunity-related genes in liver and muscle tissue across early- and mid-lactation time points; high fertility cows had clear advantages in capacity to favourably partition nutrients to health and fertility functions.

Therefore, while prudent nutritional management is important for establishing the conditions for good herd fertility, it is clear that improved genetic selection for energy balance and reproductive traits has been the primary factor in reversing negative herd performance trends in recent years (Cummins *et al.*, 2012; Berry *et al.*, 2016; Lucy, 2019). This has been delivered through the EBI in an Irish context; calving rates and milk solids yields have increased simultaneously in the national dairy cow population in line with their inclusion as selection objectives (Ring *et al.*, 2021). Changes to herd breeding values for fertility have facilitated simplified management of energy balance in early lactation.

Developments in nutrition of sheep

Prime lamb production in Ireland is grass-based with lambing concentrated in March to coincide with grass growth. The mean stocking rate is 7.6 ewes per hectare on lowland farms whilst the mean number of lambs reared per ewe joined is 1.3 (National Farm Survey, 2019). Grass, both grazed and conserved as silage, can account for up to 95% of total annual DMI in well-managed grass-based systems (Keady & Hanrahan, 2007).

Systems studies in Ireland have shown that 485–500 kg of lamb carcass can be produced per hectare from grass-based production models (Keady *et al.*, 2009; Hanrahan, 2010). More recently, from a 12-yr study in which only triplet reared lambs were offered concentrate pre-weaning, and grazing sward height management was as described by Keady (2010). Keady *et al.* (2018) reported that all lambs were slaughtered (mean carcass weight 19.9 kg) prior to the end

of the grazing season. To achieve this level of performance, mean daily live weight gains of 386, 302 and 275 g/d, for lambs reared as singles, twins and triplets, respectively, were required. Supplementing a triplet-rearing ewe and her lambs with approximately 90 kg concentrate resulted in triplet lambs having the same performance as lambs born and reared as twins (Keady *et al.*, 2018).

Each 0.5 kg increase in lamb birth weight (BW) increases subsequent weaning weight by 1.7 kg (Keady *et al.*, 2007; Keady & Hanrahan, 2009a, 2009b, 2018, 2021). Increased BW *per se* accounts for 53% of the increase in weaning weight (Keady & Hanrahan, 2009b). Birth weight also affects lamb mortality and thus the number of lambs reared per ewe joined. For twins and triplets the optimum BW is 0.93 and 0.78 times that of singles (Hanrahan & Keady, 2013). Each 1 kg reduction in ewe weight loss between mid-pregnancy and post-lambing reduces lamb mortality by 0.2 percentage units (Keady & Hanrahan, 2013b).

Lamb BW is influenced by many factors. Grass silage digestibility affects both intake and nutritive value of silage and, consequently, is the most important factor influencing grass silage feed value (FV). Form a review of the literature, Keady et al. (2013a, 2013b) concluded that each 10 g/kg increase in digestibility increased lamb BW and ewe weight at lambing by 52.3 g and 1.3 kg, respectively. Keady & Hanrahan (2021) reported that the proportional increase in silage intake due to increasing silage FV was similar during mid and late pregnancy, thus increasing the intakes of ME and digestible undegradable protein (DUP) by 53% and 28%, respectively. During the final 6 wk of pregnancy, ewes offered high FV grass silage (DM digestibility [DMD] = 788 g/ kg, silage intake potential = 92 g/kg W0.75) gained 0.15 units BCS whilst those offered medium FV silage (DMD = 698 g/kg, silage intake potential = 82 g/kg W0.75) lost 0.35 units BCS (Keady & Hanrahan, 2021). Furthermore, increasing silage FV offered to ewes during mid and late pregnancy improved their progeny weaning weight by 1.9 kg, thus reducing age at slaughter by 16 d.

Whilst chop length has no effect on silage intake, or on the performance of beef cattle (Steen, 1984) or dairy cows (Gordon, 1982), it affects the intake characteristics of silage when offered to pregnant ewes (Chestnutt, 1989) and finishing lambs (Fitzgerald, 1996). Using a precision chop harvester relative to single chopping to reduce chop length increased silage intake and, consequently lamb BW by 0.25 kg whilst reducing ewe weight loss during pregnancy by 4.9 kg (Chestnutt, 1989).

Increasing the DM concentration of maize at harvest alters chemical composition of the resulting silage, due to reduced concentrations of acid detergent fibre and CP, and increases starch and ME concentrations (Keady *et al.*, 2003, 2008a, 2013a; Keady & Hanrahan, 2013b, 2021). Increasing the

DM of maize at harvest (DM from 180 to 259 g/kg) offered to ewes during mid and late pregnancy increased total DM and ME intakes by 31% and 43%, respectively, and ewes were 4.2 kg heavier at lambing and had a significantly higher BCS, but lamb BW was not altered (Keady & Hanrahan, 2021), indicating partitioning of ME to BCS rather than to foetal growth. However, lambs from ewes that had been offered the silage made from the higher DM maize gained more weight from 5 wk to weaning and were 14 d younger when drafted for slaughter relative to lambs from ewes that received low DM maize silage (Keady & Hanrahan, 2021).

The effect on ewe and lamb performance of replacing grass silage with maize silage is influenced by the FV of the grass silage and the maturity of the maize crop at harvest. The intake of ME is increased by replacing medium FV grass silage with maize silage but is reduced when high FV silage is replaced by maize silage (Keady & Hanrahan, 2021). Previously, Keady *et al.* (2008a) observed, with dairy cows, that partially (40%) replacing medium FV and high FV grass silages with maize silage resulted in total daily DMI increases of 2.25 and 0.51 kg/cow, respectively. Similarly, Keady *et al.* (2003) observed that, with grass silages of low (ME 10.2 MJ/kg DM), medium (ME 11.0 MJ/kg DM) and high (ME 12.0 MJ/kg DM) FV, replacing of 40% of the grass silage with maize silage resulted in a response in daily total DMI of +1.85, +1.45 and -0.10 kg/cow, respectively.

The response to concentrate feed level in late pregnancy is dependent on forage FV, and thus a substitution effect. Keady & Hanrahan (2021) reported substitution rates of 0.18 and 0.75 kg silage DM per 1 kg increase in concentrate feed level for medium and high FV silages, respectively. Thus, increasing concentrate feed level from 15 to 25 kg during the final 6 wk of pregnancy did not increase ewe or lamb performance as the response in ME intake was only 26% of the response from increasing silage FV (Keady & Hanrahan, 2021). Previously, it was reported that increasing concentrate feed level from 15 to 25 kg during late pregnancy improved the BW of lambs born to ewes offered low FV grass silage (DMD = 660 g/kg DM) but had no significant effect on BW of lambs from ewes offered high FV grass silage (Keady & Hanrahan, 2010).

The ingredient composition of concentrate offered to pregnant ewes affects lamb body weight at birth and subsequent growth performance. Keady & Hanrahan (2012) concluded that replacing rapeseed, maize distillers and maize gluten with soyabean meal as the main protein source in concentrates which were iso-energetic and iso-nitrogenous increased lamb BW by 0.36 kg, equivalent to increasing the feed level of the non-soya-based concentrate by 75%, that is, 16–28 kg during late pregnancy.

Initial studies (Keady et al., 2007, 2009; Keady & Hanrahan, 2009a) indicated that, relative to ewes that were housed

unshorn and offered silage-based diets, ewes extended grazing (offered set allowances of deferred herbage) produced lambs that were heavier at birth (0.7 kg) and weaning (2.4 kg). The effects of extended grazing on lamb BW varied with stage of pregnancy when extended grazing had occurred. Relative to ewes that were housed and unshorn, ewes that were extended grazed during mid (Keady & Hanrahan, 2009a, Keady et al., 2007), late (Keady et al., 2007) or during both mid and late pregnancy (Keady et al., 2007; Keady & Hanrahan, 2009a) produced lambs which were 0.18, 0.37 and 0.59 kg heavier at birth. Ewes that were shorn at housing or extended grazed during mid and late pregnancy produced lambs with similar BWs (Keady & Hanrahan, 2009a), indicating that the response to extended grazing was attributable to reduced heat stress outdoors rather that any nutritional benefit from extended-grazed herbage which has an FV similar to medium or low FV grass silage (Keady & Hanrahan, 2007).

Feeding concentrate to lambs at pasture

The lamb performance response to concentrate supplementation at pasture depends on grass supply and its FV, and on the level of concentrate offered. From the results of four consecutive grazing seasons in set-stocked grazing systems, Grennan & McNamara (2005) concluded that offering 300 g concentrate daily to lambs grazing to a low residual sward height (5 cm) resulted in the same level of lamb performance pre-weaning as that for lambs grazing to a high residual height (6 cm) without concentrate supplementation. While concentrate supplementation reduced the age to slaughter by 28 d, increasing grass height from 5 cm to 6 cm reduced the age at slaughter by 13 d, equivalent to feeding 16.3 kg concentrate per lamb from birth to slaughter.

Increasing forage FV or concentrate feed level increases dressing proportion (Keady & Hanrahan, 2013b, 2015) and thus drafting weight, to achieve a given carcass weight, is reduced. Ad libitum concentrate feeding results in the highest level of lamb performance. Keady & Hanrahan (2013b, 2015) reported daily gains of 267 and 228 g, respectively - which were at least 30% greater than forage-based diets. Whilst shearing lambs, offered a wide range of dietary treatments, increased intakes of DM and ME, lamb carcass gain was not altered; thus, efficiency of conversion of ME to carcass gain was reduced (Keady & Hanrahan, 2015). Each 10 g/kg increase in silage digestibility increases lamb carcass gain by 9.3 g/d (Keady et al., 2013b). As concentrate feed level increases, the response to silage digestibility declines due to the reduction in the proportion of forage in the diet (Keady & Hanrahan, 2013a, 2013b, 2015). The response to concentrate feed level varies with silage FV and thus substitution rate. Keady & Hanrahan (2015) reported linear and quadratic growth rate responses to increasing concentrate feed level with medium and high FV grass silages, respectively. Previous authors (Steen *et al.*, 2002; Keady *et al.*, 2008b) have shown that increasing silage FV increases ME intake and also increases the efficiency of utilisation of ME for carcass gain. The response to replacing grass silage with maize silage depends on the FV of the grass silage (Keady *et al.*, 2003, 2008a, 2008b; Keady, 2005; Keady & Hanrahan, 2013a, 2013b). For example, replacing medium and high FV grass silage with maize silage altered forage DMI of finishing lambs by +19% and -25%, respectively (Keady & Hanrahan, 2013a, 2013b).

In a survey of herbage mineral content, 80%, 73%, 23% and 11% of Irish sheep farms were considered to be deficient for I, Co, Se and Zn, respectively, and the concentrations of Cu, I, Co, Se and Zn vary by month with highest concentrations generally occurring in the spring and autumn (Hession, 2021). In the case of Se, 89% of farms were classified as marginal, whilst herbage on all farms met the dietary requirements for Cu. Sixty-nine percent of Irish sheep producers supplement their flocks with minerals and vitamins; drenching and mineral buckets are the most preferred supplementation methods for lambs and ewes, respectively (Hession et al., 2018a). Supplementation with Co, either by drench or bolus, had no effect on ewe BW, litter size, number of lambs reared per ewe joined or on lamb BW at birth or weaning (Hession et al., 2018b). Keady et al. (2017) reported that supplementing lambs with Co post-weaning increased weight gain in a rotational system and reduced the age at drafting for slaughter. Response to mineral supplementation depends on herbage mineral availability and supplementation decisions should be evidence based.

Product quality

Carcass classification, as set out in EU Regulation 2137/92, is undertaken to improve market transparency. Hanrahan (2006) concluded that as lamb carcass weight increased from 16 kg to 22 kg, the proportion of intramuscular fat increased from 0.15 to 0.22, an increase of 50%. Using slaughter data from 250,000 lamb, Hanrahan (2006) concluded that most carcasses fall into three categories, 33.3% and 63.6% classified as conformation U and R, respectively, while 82.4% of carcass are assigned fat class 3. Using these data Hanrahan concluded that carcasses assigned to fat classes 2, 3 and 4 had intramuscular fat levels of 16.7%, 23.5% and 31.2%, respectively. On grass-based systems castrating male lambs reduced lamb weaning weight by 1.8 kg whilst increasing the age at slaughter by 16 d (Hanrahan, 1999). On grass-based systems, in which males were slaughtered prior to the end of the grazing season, leaving male lambs entire had no negative impact on meat flavour or eating quality but improved tenderness relative to meat from castrates (Keady et al., 2015).

Developments in nutrition of beef cattle

Feed is a primary input accounting for over 75% of direct costs of beef production. Consequently, converting feed into animal product as efficiently as possible is a major determinant of profitability (Taylor et al., 2018) and environmental sustainability (Fitzsimons et al., 2013; Taylor et al., 2020). Seasonality of grass growth dictates that pasture-based beef production systems consist of a grazing season and an indoor winter period annually, with grass silage providing the winter forage on most farms (McGee et al., 2014). Of the predominant feedstuffs available, grazed pasture is cheapest, purchased concentrate is the most expensive and grass silage and other conserved forages are intermediate (Finneran et al., 2012). Costings of annual grass consumed when the grazing and conservation areas are integrated, which is the norm on most beef farms, are much more complex (Finneran et al., 2011). The comparatively lower cost of efficiently produced grazed pasture means that the evolution of pasture-based beef production systems entailed optimising the contribution of high-nutritive value grazed herbage to lifetime intake of feed, and providing grass silage and concentrate as efficiently and at as low a cost as feasible. For example, within spring-calving suckler calf-tobeef research production systems, the composition of the annual feed budget on a DM basis comprises approximately 0.61 grazed grass, 0.31 grass silage and 0.08 supplementary concentrates (McGee et al., 2018b), with high individual and per-hectare animal output. Corresponding values for suckler calf-to-weanling systems are 0.73, 0.26 and 0.01, respectively. Consequently, these systems predominantly convert "human-inedible" forages into "human-edible" beef meat products.

Growing/finishing cattle at grass

Grazed grass intake of growing beef cattle grazing PRGbased swards typically ranges from 14.0 to 20.0 g/kg live weight across contrasting genotypes (Clarke *et al.*, 2009; Lawrence *et al.*, 2012). Differences in pasture species and grazing management influence the feeding value of herbage offered which, in turn, impacts performance of grazing beef cattle. In well-managed rotationally grazed systems and good grazing conditions, a target daily live weight gain of 1.0 kg throughout the grazing season should be attainable for steers without concentrate supplementation (Regan *et al.*, 2018); however, in commercial practice this is often not the case. Grazing excessively high or low pre-grazing herbage masses (Doyle *et al.*, 2019, 2021) and grazing too tightly (Doyle *et al.*, 2020; O'Riordan *et al.*, 2011a) negatively impacts beef cattle growth at pasture. Subsequent compensatory growth at pasture diminishes the growth advantage of early turnout to pasture in spring of "yearling" cattle compared to their counterparts offered grass silage plus supplementary concentrates and turned out 3–4 wk later (Gould *et al.*, 2011a; McGee *et al.*, 2014). Relatively high growth rates of cattle at pasture are often due to the expression of compensatory growth (McGee *et al.*, 2014). Furthermore, growth rates of cattle at pasture do not necessarily represent the true growth potential of the animals due to the fact that performance is usually considerably lower than that of similar animals finished indoors on highconcentrate diets (Lenehan *et al.*, 2015a).

Grazed grass herbage is characterised by high CP concentrations resulting in imbalances in the supply of carbohydrate and protein in the rumen of beef cattle and inefficiency of N capture (Owens *et al.*, 2008a), and consequently relatively low NUE (O'Connor *et al.*, 2019). Strategies to reduce urinary N excretion in grazing beef cattle include reducing fertiliser N application rate (O'Connor *et al.*, 2019), increasing grass regrowth interval (Owens *et al.*, 2008a) and supplementation with energy sources (O'Connor *et al.*, 2018). Reducing dietary CP is a primary strategy to mitigate N excretion and related emissions from beef cattle, and may reduce feed costs too.

The potential benefits of binary grass-clover (legume) swards compared to grass monocultures, in terms of herbage nutritive value, voluntary intake and performance of beef cattle, as well as the capacity of legumes to fix atmospheric N (and reduce requirement for fertiliser N inputs) are well recognised (Phelan *et al.*, 2015). Research is commencing on the evaluation of multi-species swards, including grasses, legumes and herbs/ forbs as a means to further increase the resilience of pasturebased beef production systems.

Early finishing of cattle at pasture in autumn is attractive as it eliminates the need for an expensive indoor finishing period. Due to accumulated animal growth and decreasing seasonal grass growth, herd feed demand usually exceeds supply in autumn on most beef farms. Consequently, there may be a role for strategic concentrate supplementation at pasture to enhance feed-nutrient intake, and thus subcutaneous fat deposition and carcass fat score especially of steers and bulls finished at pasture (Lenehan et al., 2017a; Regan et al., 2018). Carcass growth response to concentrate supplementation while grazing will primarily depend on the availability and quality of pasture and level of supplemented concentrate. Concentrate response is higher where grass supply is low and where grass quality is poorer, and declines as concentrate supplementation level increases. Substitution rates for finishing cattle grazing autumn pasture supplemented with concentrates range from 0.1 to 0.8, with marginal values at higher levels of supplementation in excess of 1.0 in some studies (French et al., 2001a; Lenehan et al.,

2017a). At adequate (~20 g/kg live weight) grass allowances in autumn, feeding ~0.50–0.75 kg of concentrate per 100 kg live weight resulted in carcass growth responses for steers between 30 and 110 g carcass per kg concentrate (Keane & Drennan, 2008; McNamee *et al.*, 2012). In practice, feeding this moderate level of concentrates will likely result in carcass growth responses at the upper end of this range. Responses of 82–88 g carcass per kg concentrate DM were obtained for suckler bulls (Marren *et al.*, 2015; Lenehan *et al.*, 2017a).

In autumn, the diet of grazing cattle is generally unbalanced because there is usually excess degradable protein in autumn grass (Owens *et al.*, 2008b). Therefore, dietary energy rather than protein is the limiting factor and, where supplementation occurs, concentrate energy sources are required. Animal performance is similar for starch-based (barley) or fibre-based (pulp) concentrates as supplements to autumn grass (Drennan *et al.*, 1997; French *et al.*, 2001b).

Growing/finishing cattle on grass silage diets

Intake is a major determinant of the performance of cattle consuming grass silage and mechanisms regulating intake are complex (McGee, 2005). Most of the variation in net energy content of grass silage is associated with its digestibility. Silage DMD must improve on beef farms; DMD values above 700 g/kg need to become the norm for growing and finishing cattle with values of circa 750 g/kg for topperforming animals (O'Kiely, 2015). This will require utilisation of highly productive swards within grassland management systems that optimise both grazing and silage production components. Additionally, much greater emphasis is needed on knowing the yield, digestibility and ensilability of crops pre-harvest, the quantity, nutritive value and preservation characteristics of silage conserved, as well as restricting losses during harvesting, ensilage and feed-out (O'Kiely, 2015). Nevertheless, beef cattle rarely consume sufficient grass silage to achieve their production potential and as a result, energy-rich concentrates are routinely supplemented in practice (McGee, 2005).

Performance of beef cattle increases with increasing grass silage digestibility and the impact of digestibility increases as the proportion of silage in the diet increases (McGee, 2005; Cummins *et al.*, 2007). For example, in finishing cattle, a 10 g/kg increase in silage digestibility was associated with an increase in carcass gain of circa 33 g/d where silage was the sole feed and 21–29 g/d when supplemented with concentrates at 0.20–0.40 of dietary DMI (McGee, 2005). Conversely, each 10 g/kg decline in digestibility requires an additional circa 0.33 kg concentrate DM daily to sustain performance (Keady *et al.*, 2013b). Substitution rate of concentrates for grass silage is

a function of silage digestibility and concentrate feed level – it increases with both. With high-digestibility grass silage, substitution rates for diets containing <0.5 or >0.5 dietary DMI as concentrates range from 0.29 to 0.64 and 0.55 to 1.15 kg silage DM per kg concentrate DM, respectively (McGee, 2005). Inclusion of cereal-based concentrates with grass silage generally has a negative effect on ruminal digestibility of NDF (Owens *et al.*, 2008c); consequently, total diet digestibility does not necessarily increase with supplementation.

Subsequent compensatory growth at pasture diminishes the advantage of concentrate supplementation of young "weanling" cattle offered grass silage; consequently, live weight gains of 0.5-0.6 kg/d through the "first" winter are acceptable for steers, heifers and suckler bulls destined to return to pasture in spring (Marren et al., 2013; McGee et al., 2014). This also applies to older "store" cattle in their second winter destined for subsequent finishing at pasture (Keane & Drennan, 2008; Keane & Moloney, 2009). However, a higher level of feeding is generally warranted during the first winter for "replacement" beef heifers (Heslin et al., 2020). The production response to concentrate supplementation is higher with lower-digestibility silage (McGee, 2005). For finishing cattle offered highdigestibility grass silage, the growth response to concentrate supplementation - increasing from ~2 to 10 kg/head daily - is generally curvilinear (McGee, 2005; Keane et al., 2006). Due to this progressive decline in growth response to concentrates, high-digestibility grass silage plus moderate concentrate inputs can achieve a large proportion of the carcass and lean tissue gain achieved with high-concentrate diets. Accordingly, in order to determine the optimum or breakeven level of concentrate supplementation per se, estimates of carcass efficiency (kg concentrates per kg carcass), silage substituted (kg DM per kg carcass gain) and the true costs of grass silage and concentrates are required (McGee, 2015). In addition to dietary feeding value, efficiency of feed utilisation primarily depends on weight of animal (decreases as live weight increases), potential for carcass growth (e.g. breed type, genetic merit, animal sex, compensatory growth potential) and duration (decreases as length increases) of the finishing period (McGee, 2015; McGee et al., 2018a). High-concentrate diets are predominantly used to finish bulls, including animals previously grazing (O'Riordan et al., 2011b).

Although barley is widely used as a supplement with grass silage, wheat (Drennan *et al.*, 2006), oats (McGee *et al.*, 2018b) or maize (Lenehan *et al.*, 2015b) can be equally effective. Similarly, by-product feed ingredients including molassed sugar-beet pulp (Keane, 2005), citrus pulp (Lenehan *et al.*, 2017b), palm kernel expeller meal (Magee *et al.*, 2016), corn gluten feed (Kelly *et al.*, 2018), maize-dried distillers grains (Magee *et al.*, 2015a) and soya hulls (Magee *et al.*, 2015b) can fully or partially replace rolled barley in concentrate rations as a supplement to grass silage without

negatively impacting animal performance. However, due to "associative effects" the relative feeding (and economic value) of by-product feed ingredients is contingent on concentrate feeding practices, such as inclusion level in the concentrate ration and the amount of concentrates fed.

The CP concentration of commercial "growing" and "finishing" concentrates for beef cattle in Ireland often seems excessively high in relation to animal requirements. Indeed, the general perception is that the higher the CP percentage, the "better" the concentrate. In most cases, diets are formulated with minimal consideration for current concepts of protein metabolism such as rumen-degradable or undegradable protein. The growth response in "weanling" cattle, even bulls, to additional protein above that supplied in a barley onlybased concentrate as a supplement to high-nutritive value grass silage is small (Lenehan et al., 2015c). For "finishing" cattle offered high-digestibility grass silage plus barleybased concentrates, increasing protein supply from either a rumen-degradable or undegradable protein source did not significantly affect animal growth (McGee, 2005; Kennedy et al., 2021), implying that concentrate CP concentrations of ~100 g/kg fresh-weight basis, which is 20%-50% lower than commercially available concentrate rations, may suffice under such conditions. Recent research is evaluating the role of indigenous protein feedstuffs, including faba beans and peas, in beef cattle rations (Kennedy et al., 2021) in order to increase self-sufficiency nationally.

Concentrate supplementation feeding strategies include feeding frequency, complete diet feeding/TMR, co-ensiling, concentrate distribution pattern and restricted feeding (McGee, 2005). Offering cereal-based rations comprising circa 0.50 dietary DMI in one as opposed to two daily feeds (Drennan et al., 2006) or mixing of grass silage and barleybased concentrates in a TMR compared to separate feeding (Keane et al., 2006) had no effect on animal efficiency or performance. Feeding weanling cattle a fixed total concentrate allowance offered at a flat daily rate or at a higher rate over the first half of the winter gave a better growth response than when offered at a higher rate over the second half of the winter (Keane, 2002). In finishing cattle offered grass silage feeding, a fixed total quantity of concentrates at a flat rate or varied pattern resulted in similar efficiency of feed energy utilisation (Cummins et al., 2007).

Suckler cow nutrition

In spring-calving grass-based calf-to-weanling and calf-tobeef systems, the cow-herd consumes approximately 85% and 50% or greater of total feed inputs, respectively (Lawrence *et al.*, 2013). Nutrition of spring-calving suckler cows generally involves feed energy restriction and mobilisation of body fat reserves during the indoor winter period when feed costs are high and deposition of body reserves on cheaper-produced pasture (Drennan & McGee, 2004). The robustness of cow genotypes to deal with such contrasting nutritional environments has implications for animal breeding programmes. A negative linear relationship exists between cow winter-weight loss and subsequent gain at pasture; indeed, a compensatory growth-like occurrence is evident (Drennan & McGee, 2004). These annual changes in body reserves, however, need to be within the boundaries of target BCS at key stages of the production cycle - late pregnancy, calving and breeding - in order to maintain good reproductive performance (Drennan & Berry, 2006), as well as avoiding nutritionally induced calving difficulty. As plane of nutrition is manifested through body reserves, BCS is a key practical tool for nutritional management of suckler cows.

Cows offered grass silage of reduced DMD during late pregnancy have lower DMI and greater weight loss compared to those offered higher DMD silage (Drennan & McGee, 2004) although calf BW is generally unaffected as energy partition is prioritised towards foetal growth. Suckler cows in good BCS (~3.0+, scale 0-5) at housing in autumn can be restricted to circa 75%-85% of feed energy requirements. This restriction can be applied through various approaches depending on silage digestibility, including offering moderate DMD (~660 g/kg) silage ad libitum (Drennan & McGee, 2004), restricting silage intake (McGee et al., 2005) or reducing dietary energy value through inclusion of straw (McGee & Earley, 2013). When offered moderate DMD grass silage ad libitum, DMI relative to live weight ranges from 11.0 to 15.0 g/kg across contrasting suckler cow genotypes in late pregnancy (McGee et al., 2005; Minchin & McGee, 2011). This ad libitum silagefeeding regime is practical as the forage characteristics result in self-regulation of intake and nutrient supply. However, because the annual national DMD of silage nationally ranges between 600 and 640 g/kg (O'Kiely, 2015), this means that concentrate supplementation for suckler cows is required on many farms to achieve an adequate plane of nutrition.

Multiparous cows in moderate BCS postpartum can tolerate the negative energy balance associated with consuming moderate DMD grass silage *ad libitum* in early lactation provided they are calving relatively close to commencement of grazing, but primiparous, thin and early calving cows require a higher plane of nutrition particularly to avoid delayed oestrous cyclicity. Maintaining a 365-d calving interval is critical to spring-calving suckler herds (Diskin & Kenny, 2014). McGee *et al.* (1998) showed that primiparous suckler cows offered grass silage supplemented with 2 kg of concentrates daily postpartum had less weight loss and greater milk yield resulting in greater early life calf growth than those offered only grass silage. Milk, a primary source of nutrients for the suckled calf in early postnatal life, remains a significant component of the diet until weaning, and thus, is a primary driver of calf pre-weaning growth (Sapkota *et al.*, 2020).

Early turnout to pasture in spring increases grazed grass in the annual diet of the cow. Restricted access grazing, when soil or weather conditions are poor, is a nutritional management strategy resulting in at least comparable cow performance, and transitory benefits in calf growth, compared to those housed indoors on grass silage-based diets (Gould et al., 2010, 2011b). Grazed grass DMI relative to live weight ranges from 17 to 24 g/kg for contrasting lactating suckler cow genotypes (Gould et al., 2011a; Lawrence et al., 2013; McCabe et al., 2017, 2019), which are comparable to zerograzed intakes (Murphy et al., 2008). Grass alone is generally sufficient to meet the nutrient requirements of single-suckling lactating cows in rotationally grazed systems when herbage supply is not limited (Drennan & McGee, 2009). Under these circumstances, cow live weight gains up to circa 100 kg during the grazing season are achievable, especially with low-milk yield genotypes and multiparous animals (McGee et al., 2005; Drennan & Berry, 2006). However, cows that are very highly stocked or offered low herbage allowances have lower live weight and/or BCS gains and, in more severe cases, lower milk yield resulting in lower pre-weaning growth of their progeny compared to those on low stocking rates (Drennan & McGee, 2008). Similarly, lactating suckler cows grazing to low residual sward heights (4.1 vs. 5.3 cm) gained less weight and body condition, and had lighter calves at weaning than those grazing to a higher residual height (Minchin et al., 2011). Live weight gains of spring-born single-sucking unsupplemented calves on well-managed rotationally grazed systems typically exceed 1.1 kg daily over the grazing season, although this is heavily influenced by dam milk yield (McGee et al., 2005; McCabe et al., 2019). Calf growth responses to "creep feeding" suckled calves at pasture in late lactation with energy-based concentrates can range from 60 to 190 g live weight per kg concentrate (McGee et al., 1996).

Mitigation of rumen methane by nutrition management – developments and challenges

Methane gas is a by-product of the microbial fermentation of ingested feed by ruminant animals and is a notable energy loss to the animal (Johnson & Johnson, 1995). It is also an acknowledged potent greenhouse gas (GHG) and makes a significant contribution to anthropogenic GHG emissions (Martinez-Fernandez *et al.*, 2018). The development of dietary supplements to mitigate methane emissions from ruminant livestock either directly through inhibiting microbial methanogenic biosynthetic pathways or indirectly through limiting the availability of its precursor hydrogen to methanogenic archaea is a key focus of research worldwide.

Historically, halogenic compounds such as bromoform and chloroform have been studied for their efficacy as antimethanogenic compounds (Bauchop, 1967; Russel & Martin, 1984). However, they are currently mainly used as experimental controls (Martinez-Fernandez *et al.*, 2018) due to their strong anti-methanogenic albeit toxic and carcinogenetic qualities. This has also been the case for ionophores such as monensin (an antibiotic) which deplete the rumen microbiome and therefore inhibit methanogenesis. Antibiotics were previously fed to animals as growth promoters, particularly in the United States. However, they are now banned for use as growth promoters in the EU as of 2006 due to issues with resistance and human health concerns (EMA, 2007).

Hristov *et al.* (2013) listed the efficacy of various livestock dietary additives for reducing CH_4 emissions. This study highlighted the potential of lipid inclusion in ruminant diets, seaweed algae and 3-nitrooxypropanol (3-NOP) to substantially reduce methane emissions.

The addition of fats and oils as methane abatement compounds to ruminant diets has been promising. Lipids result in an antagonism in methane production as they are toxic to and therefore reduce methanogens and protozoa numbers (Beauchemin et al., 2009; Broucek, 2018). However, fat addition can negatively affect feed intake, carbohydrate digestion in the rumen and overall milk guality. There are also issues surrounding sulphide toxicity at high fat intake levels. As regards plant-based oil seeds, Kliem et al. (2019) found that only linseed-based supplements reduced methane emissions (across production, yield and emissions intensity) when comparing the administration of linseed, palm and rapeseed oil products to dairy cows. Similarly, Boland et al. (2020) reported an 18% decrease in emission intensity (g CH₄/kg milk) from pasture-fed dairy cows receiving linseed oil-based concentrates compared with cows receiving stearic acid- or soy oil-based concentrates.

There are also a range of industrially formulated products with the potential to reduce methanogenesis such as Mootral (a feed additive containing allicin from garlic and citrus extracts) and Agolin Ruminant (an essential oil blend). Studies have shown positive, albeit variable effects of both products on reducing the amount and rate of enteric CH_4 production in both dairy and beef cattle (Hargreaves *et al.*, 2019; Belanche *et al.*, 2020). Agolin Ruminant has also been shown to improve livestock productivity (particularly dairy), which could potentially reduce intensity of methane emissions. It is also cheap to buy rendering it a potential, affordable solution. However, both of these additives are in need of further trials under different dietary regimes (Roque *et al.*, 2019a).

Seaweed, in particular *Asparagopsis taxiformis* (Delile) Trevis. contains anti-methanogenic properties. Many studies have seen significant reductions in methane emissions from livestock receiving seaweed-based additives at various administration rates and concentrations (Machado *et al.*, 2016; Roque *et al.*, 2019b). Further work is required to understand the potential long-term effects on animal productivity and health. There are concerns surrounding the concentrations of both bromoform (a potential carcinogen) and iodine within red seaweeds, which could potentially carry through the food chain. However, this is not the case with brown seaweeds where there is still potential for safe use as a methane inhibitor, although this is in need of further research and validation (Antaya *et al.*, 2019). The supply, consistency and sustainable use of seaweeds may be an issue as regards the feasibility of growing seaweeds or the environmental impact of harvesting wild crops. Work is also ongoing to assess seaweed extracts for their anti-methanogenic capability.

The synthetic non-toxic compound, 3-NOP, is a promising methane inhibitor which has displayed consistent methane vield decreases of 20%-40% depending upon animal type, diet composition, dose and method of supplementing 3-NOP (Haisan et al., 2014, 2017; Martinez-Fernandez et al., 2014; Hristov et al., 2015; Vyas et al., 2016, 2018a, 2018b; Beauchemin et al., 2020). Many studies have reported the positive effects of 3-NOP in vitro (Anderson et al., 2010; Guvader et al., 2017) as well as in vivo in sheep (Martinez-Fernandez et al., 2014), dairy cows (Haisan et al., 2017) and beef cattle (Romero-Perez et al., 2014). Furthermore, a metaanalysis of in vivo studies concluded that dietary inclusion of 3-NOP does not compromise the productive performance of ruminant animals (Jayanegara et al., 2018). However, consumer behaviour will need to be considered before it is adopted as an on-farm mitigation option, that is, there may be issues surrounding the consumption of products that arise from animals fed on synthetic compounds (Beauchemin et al., 2020). Three meta-analyses have concluded that 3-NOP is effective in mitigating enteric methane emissions without negatively impacting animal performance (Dijkstra et al., 2018; Jayanegara et al., 2018; Kim et al., 2020). A review of growing-cattle studies showed that feeding 3-NOP had no effect on DMI but daily methane production and yield was decreased by 50% (van Gastelen et al., 2019).

Evidence from Teagasc work and elsewhere suggests that changes in microbial colonisation of the rumen during the early postnatal period may imprint the rumen microbiome with lasting effects on biochemical functionality including methanogenesis, which extend into later life (Jami *et al.*, 2013; O'Hara *et al.*, 2020). Work to date shows clearly that the first month of life presents a time-frame during which the rumen micobiome becomes established but is also susceptible to environmental influence, including diet. This presents a potential opportunity for manipulation of both the composition and functionality of the microbiome through strategic dietary supplementation. Recently, Meale *et al.* (2021) showed that early life administration (oral dose) of dairy calves with 3-NOP from birth to 14 wk of life resulted in a marked reduction in methane emissions, which persisted to 12 mo of age. This equated to a cumulative reduction of circa 150 kg of CO_2 eq per head in these cattle during the first year of life (Meale *et al.*, 2021).

Within grass-based production systems, the use of such feed additives is currently best suited to the indoor winter feeding periods. In order for 3-NOP or any other additive to be an effective option for methane mitigation on grass-based systems as in Ireland, a slow-release rumen bolus form of the additive is required for sustained effectiveness. Efforts are underway to produce inhibitors suitable for grazing-based systems and alternative formulations containing 3-NOP (Leahy et al., 2020). A slow release option has examined initial prototypes which were able to extend methane reduction from feeding time to 6-8 h with one small dose delivered in a supplemental feed. The new slow release formulations of 3-NOP were tested and showed potential to extend the time that 3-NOP is active in the rumen, based on gas emission profiles from cows (Muetzel et al., 2019). Further studies are planned to refine promising formulations and to establish their methane reduction potential for pasture-fed cattle.

Summary and conclusions

Ruminant-based agriculture faces increasing scrutiny as to its role in global food systems due to issues around environmental and social impact, land use efficiency and product quality. In such circumstances, the relative sustainability of ruminant systems may increasingly require leveraging of their utility as converters of indigestible plant material into high-value human-edible protein. In practice, this will mean maximising the contribution of highly digestible forage to the overall diet. Research across sheep, beef and dairy systems in Ireland has demonstrated the capacity for quality grazed pasture and conserved forages to deliver diets with high-nutrient content, good feed intake characteristics and excellent animal health and productivity potential. Improved understanding of the role of fibre fractions in determining nutrient supply has been of particular importance to development of feed and forage management guidelines. Furthermore, the refinement of protein nutrition guidelines to an AA content rather than N content has provided opportunities for greater animal performance and nutrient-use efficiencies. Where feed supplementation is practised, it has been demonstrated that factors such as basal forage guality, the animal's genetics and physiological state, as well as supplement rate and type, all contribute to physical and economic responses. Consideration must also be given to the likely effects on nutrient balances and potential losses to the environment. Inclusion of specific dietary factors to reduce gaseous emissions has shown promise but requires optimisation for grazing systems. Pasture management and

animal feeding can sometimes be viewed as unrelated or even competing disciplines at farm level. A continuing challenge for research and extension is to develop and embed the concept of excellent pasture and forage quality as a cornerstone of animal nutrition programmes. Further integration of prediction models for forage intake, animal response models and realtime analysis of feed and forage composition will enhance management decisions in this regard.

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