Irish Journal of Agricultural and Food Research

60th Anniversary Issue

Volume 61, No 1, 2022 ISSN: 07916833 EISSN: 20099029





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Irish Journal of Agricultural and Food Research

Celebrating 60 years of the Irish Journal of Agricultural and Food Research

This special issue of the *Irish Journal of Agricultural and Food Research* (IJAFR) marks the journal's 60th anniversary. To celebrate this occasion, the Editorial Board has published a special print edition.

The objective of this special issue is to highlight scientific advancements made over the last 60 years. Then we look to the future to see how current knowledge, methods and tools can help us to meet the grand challenges facing the sector and wider society, as well as identifying gaps in knowledge that need to be filled by new research.

The IJAFR is a peer-reviewed, open access scientific journal published by Teagasc (Agriculture and Food Development Authority, Ireland). The journal was first published in October 1961 as the *Irish Journal of Agricultural Research*, evolving over the years to the current title, *Irish Journal of Agricultural and Food Research*, in 1992, which is an amalgamation of the *Irish Journal of Agricultural Research*, *Irish Journal of Agricultural Economics and Rural Sociology* and the *Irish Journal of Food Science and Technology*.

This special issue consists of 12 papers, compiled in 2021 – the journal's anniversary year, providing an overview of the wide range of research undertaken by Teagasc. These papers provide a great source of reference for those interested in Irish agricultural and food research. Topics include forestry, potato breeding and production, pig production, milk quality and processing, meat processing, ruminant nutrition, ruminant breeding, the Agricultural Catchments Programme, grassland, animal health and welfare, and the role of social science in agri food research.

Irish agriculture is in an ever-changing environment. Farmers and food processors are faced with challenges including climate change; pressure to reduce inputs including pesticides, fertiliser and antibiotics; increased animal welfare concerns; requirements to improve water quality, reduce methane emissions and increase biodiversity and carbon sequestration; as well as remaining profitable. Research that provides farmers and food processors with technical solutions to meet these challenges in a sustainable manner is as important as it ever was.

Cattle breeding in Ireland has evolved over the years. Now we have the Economic Breeding Index (EBI) for dairy, which allows farmers to select not just based on production but also on factors influencing the sustainability of our systems including health, longevity and fertility. Similar indexes have been developed for beef cattle and sheep.

Grazed grass is our cheapest feed source and is the foundation of the competitiveness of our ruminant livestock industries. Grassland also plays, and will continue to play, an important role in promoting and protecting biodiversity and in carbon sequestration.

Animal health and welfare are important areas of research across all the livestock enterprises, with research addressing important topics including antimicrobial resistance and welfare of livestock on farms.

In Ireland we produce world-class milk and meat, primarily from grassland. Product quality and safety are hugely important research areas to safeguard consumer health, maintain the reputation of Irish food and ensure market access internationally.



Social science research has an important role to play in understanding the food system and how its sustainability (in the broad sense of economic, environmental and social aspects) changes over this and the factors that influence it, monitoring the impact of key policies and trade relations, and adding rigour to systems-based research approaches through transdisciplinarity and the "multi-actor approach".

We welcome you to delve into this rich source of knowledge on Irish agricultural and food research.

Professor Frank O'Mara Director of Teagasc

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Special Issue article • DOI: 10.15212/ijafr-2020-0152 IJAFR • 61(1) • 2022 • 1-11



Irish Journal of Agricultural and Food Research

Irish Grassland Research — main achievements and advancements in the past 60 yrs and where to progress to next

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Abstract

In the last 60 yr Irish grassland production has increased substantially in no small part due to high-quality fundamental grassland research. Increased production from grassland has arisen from improved understanding (research and practice) of soil and plant nutrition, plant physiology and variety improvement, while improved understanding of feed evaluation, ruminant nutrition, grazing management and silage technology has contributed to increased utilisation of grassland. Annual grass DM production varies from 12.7 to 15.0 t DM/ha based on Department of Agriculture, Food and the Marine grass variety trials. More recent data from PastureBase Ireland indicate that average annual grass production (2020) on efficient dairy and dry stock farms is 13.5 and 10.0 t DM/ha, respectively. Ireland is now one of the world leaders in grassland research, particularly in the area of grazing utilisation, the development and use of grassland databases, decision support systems and grass selection indices for grass varieties. Future pasture-based systems must extend beyond food production to deliver additional benefits to farmers, to consumers and the wider society. Future systems will require more robust grazing animals with healthier functional traits, more diverse swards supporting improved animal performance and require fewer fertiliser and chemical inputs, and will support more biodiversity and enhanced carbon storage.

Keywords

Animal production • grass breeding • grassland • grassland management • grazing

Grassland science evolution

Increased production from grassland in the last 60 yr has arisen from improved understanding (research and practice) of soil and plant nutrition, plant physiology and variety improvement. At the same time, grassland utilisation has increased due to advances in feed evaluation, ruminant nutrition, grazing management and silage technology. Annual grass DM production varies from 12.7 to 15.0 t DM/ha based on Department of Agriculture, Food and the Marine variety trials (DAFM, 2021). More recent data from PastureBase Ireland (PBI) indicate that average annual grass production (2020) on efficient dairy and dry stock farms is 13.5 and 10.0 t DM/ha, respectively (M. O'Leary, Teagasc, personal communication). In the early 1960s, national stocking rates were less than 0.8 livestock units (LU)/ha. The first experiments demonstrated that if some fertiliser nitrogen (N) was applied for silage, it was possible to increase stocking rate to 2 LU/ha. Early experimental design consisted of self-contained farmlets using rotational grazing. These became blueprint systems

and were of great benefit to both advisors and farmers on how best to manage both livestock and grassland at farm level. By the mid-1970s, 2.47 LU/ha (or 1 LU/acre) or more became the norm on commercial grassland farms on dry soils. Over the next number of years, other factors influencing output per hectare were investigated including soil type/drainage, N fertiliser application rate, genetic merit of cows, concentrate supplementation and grass species/variety.

Research in the 1990s focused on the influence of grassland management on animal performance and this highlighted the importance of grass budgeting using decision support tools (DSTs) to aid grassland management. Additionally, the benefits of extending the grazing season in both spring and autumn, matching feed demand to grass supply and the importance of pasture-based animal genetics were identified. Forage legumes, particularly white clover (*Trifolium repens* L.), were highly regarded initially but their use declined mainly due to the low cost of N fertiliser (Gilliland *et al.*, 2009) which

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was used in increasing amounts. White clover is assuming much more importance in the last decade due to increasing restrictions on current and future N fertiliser use as a result of policies and strategies introduced to reduce N loss, for example, EU Water Framework Directive (2000/60/EC), the Nitrates Directive (SI 378 2006), EU Farm to Fork Strategy 2020 and Government of Ireland Climate Action Plan. Recognition of the environmental implications of grassland production systems has increased, especially over the last two decades. This includes the need to reduce nutrient emissions from agriculture and improve water quality, but also the role of grassland in biodiversity protection, carbon sequestration and landscape quality.

Key developments in grassland research

The objective of grassland research is to study the factors which can influence and increase the output of sustainable animal production and to incorporate this knowledge into a complete integrated system. Some key developments over the last 60 yr include:

- Research at Johnstown Castle quantified the effect of N, phosphorus (P), potassium (K) and lime on grass production. The first soil survey in the 1970s mapped the soils of approximately half the country. This provided information on the productivity of soils and showed that soil drainage was a significant determinant in the level of production achieved. It was estimated that over 1 million ha of lowland required drainage which led to the development of both shallow and deep drainage systems.
- Much of the early work carried out at livestock research centres (Moorepark [Dillon *et al.*, 2005], Grange [Drennan, 1999] and Athenry [Earle *et al.*, 2017]) quantified the effect of stocking rate on milk, beef and lamb growth rates. The influence of grassland system (rotational vs. set stocking), soil type, drainage and N fertiliser use was investigated. The application of this knowledge led to the development of "blueprints" for animal production systems. In all those systems, the whole management programme for both animal and pasture was specified. These systems are now widely used on farm.
- A key challenge in the early years was the availability of and quality of winter feed. There was a great dependence on hay. In 1958, only 160,000 t of grass were conserved as silage, whereas by 1976 this had increased to 10 million t. The reasons for this expansion included the development of simple unroofed silos in conjunction with polythene covering, use of cold fermentation process, self-feeding systems and elimination of the risk associated with saving hay due to weather conditions. Key innovations included knowledge on when and how to conserve grass

silage (Keating & O'Kiely, 1997), improved machinery mechanisation, assessment of its feeding value and how it should be supplemented.

Grassland management systems evolved placing greater emphasis on grazed grass rather than grass silage or concentrates in animal production. Key livestock production decisions like calving date (dairy, beef) and lambing date were targeted to maximise the use of grazed grass. This was only possible where grass-based animal genetics was used. Product quality also improved, and the benefits of grass-fed milk and meat were identified (e.g. Noci *et al.*, 2005; O'Callaghan *et al.*, 2016) giving Ireland a particular marketing advantage in production of "grass-fed" animal product.

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- The Teagasc grass and clover breeding programme was initiated in 1960 to breed varieties suited to the Irish environment. Initially greater emphasis was placed on yield, but the emphasis changed over the years to give greater emphasis on seasonality of yield and quality. Over the period 1973–2013, it is estimated that annual grass DM yield increased by 0.52% under conservation and 0.35% under simulated grazing (McDonagh *et al.*, 2016) in the Northern Irish evaluation lists. Over this period, there is no indication of any increase in herbage digestibility of the new varieties been released, but higher digestibility varieties have been released (McDonagh *et al.*, 2016).
- A lot of research investment, infrastructure and resources were used over the years to develop and strengthen capacity in grassland science. This facilitated a greater understanding on the influence of grazing management on animal performance. The importance of pre-grazing herbage mass (e.g. Wims et al., 2010, 2014; Curran et al., 2010), pre- and post-grazing height (e.g. Stakelum & Dillon, 2007; Ganche et al., 2015) as well as pasture allowance was identified (e.g. McEvoy et al., 2008; Curran et al., 2010). The use of markers to measure herbage intake helped greatly to understand the interaction between grazing management and animal nutritional requirements (Dillon, 1993). Knowledge gained from this work facilitated extending grazing season (spring and autumn) (e.g. Roche et al., 1996; Kennedy et al., 2005). Such advancements in grassland science have led to the development of decision-support "tools" which grass farmers now use (e.g. PBI) (Hanrahan et al., 2017).
- In the early 1980s, targets were established for milk and meat production. The milk production target was 6,820 L/cow (3.5% fat and 3.2% protein) and target live weight gain was 1,680 kg/ha for beef production both at a stocking rate of 2.47 LU/ha. In the current Teagasc Road Maps (Teagasc, 2020), dairy farmers nationally are achieving 5,484 L/cow at a stocking rate of 2.1 cows/ha (corrected for changes in milk composition), while current

research performance is 5,800 L/cow at a stocking rate of 2.70 cows/ha. In suckler calf to beef systems, the current national average carcass weight output is 241 kg/ha at a stocking rate of 1.6 LU/ha, and the current research carcass weight output is 321 kg/ha at a stocking rate of 1.6 LU/ha and 531 kg/ha at a stocking rate of 2.6 LU/ha.

Grassland management developments

The competitive advantage of Irish animal production systems is based on the efficient production and utilisation of grazed grass. Irish pasture has the potential to grow up to 15 t DM/ha per annum (O'Donovan et al., 2021), which is approximately 20% more than that produced in Western Europe (Peeters & Kopec, 1996). Although grazing systems have specific challenges such as unstable feed supply and reduced individual animal intake and performance, the principle benefit of improved grazing management has been to optimise the quantity and nutritive value of the forage consumed by grazing animals. Notwithstanding the substantial benefits of pasture-based systems, engaging more farmers in pasture measurement in support of more rapid and improved pasture management continues to be problematic. One of the key challenges in the future will be to further increase animal production per hectare by improving pasture growth and grass quality, increasing N use efficiency (NUE) and reducing greenhouse gas (GHG) and ammonia emissions. Two important themes that the Teagasc grassland research programme is focused on in terms of grassland management to optimise production and utilisation are grassland measurement tools and grass growth modelling.

Grassland decision support tools

Efficient grazing management requires anticipation and flexibility, and can be greatly facilitated by the development of dynamic tools with the capability to simulate different scenarios based on regular measurement of farm grass supply. One of the major deficiencies in grassland management at farm level has been the lack of a measurement capability. O'Donovan et al. (2002) introduced the concept of grassland measurement using visual assessment to dairy farms in Ireland. The rising plate meter has been used successfully in Ireland and this technology has been improved through the incorporation of GPS and smartphone technology allowing it to be integrated with web-based grassland management tools (McSweeney et al., 2018; Murphy et al., 2021a, 2021b). The development and use of DSTs at farm level was not a new phenomenon. The key objective of most DSTs is to increase the information available to help the decision-making process at farm level. The advancement of the internet and in particular the proliferation of smart phones have created

opportunities for the development and use of web-based DSTs that facilitated the collation of large quantities of data in a central data storage platform from different farms. The potential use of this information from a research perspective can be significant. Arguably, the most important step for the industry in the last 10 yr in grassland in Ireland has been the introduction of PBI (www.pbi.ie). PastureBase Ireland is an internet-based grassland management DST. In operation since 2013, PBI offers farmers grassland decision support and stores a vast quantity of grassland data from dairy, beef and sheep farmers in a central national database. The inclusion of the data storage function dramatically increases its functionality as it enables the development of longer-term research-based solutions established from data collected over a longer time frame across a large range of farms. PastureBase Ireland also provides an automated mechanism to benchmark farms across periods and across a range of farms. Figure 1 shows the average daily grass growth rates in 2018, 2019 and 2020, and the average growth rate from 2013 to 2020 (inclusive) recorded on PBI.

Grass growth modelling

Another key area in terms of grassland management DSTs is grass growth modelling. Increasing the predictability of grass growth increases confidence in short-term feed budgeting. The development of the Moorepark St. Giles Grass Growth Model (MoSt GG model; Ruelle *et al.*, 2018) has been a major advancement in terms of grass growth modelling on farm. For a grass growth prediction model to become a valuable grassland management DST, the model must be easily adaptable to a range of soil types and management conditions. To increase the likelihood of farm level use, few input data should be required. The model must respond to the main factors that influence grass growth including defoliation, N fertiliser application, N returned to soil from livestock faeces and urine and soil water content.

The MoSt model is a dynamic model capable of accurately simulating grass growth at field scale in a pasture-based system developed based on the adapted Jouven model (Jouven et al., 2006a, 2006b; Hurtado Uria, 2013) through the addition of soil, plant N and soil water sub-models. The MoSt model is now used to predict grass growth on grassland farms across Ireland. Information required to complete the predictions includes grassland measurements and fertiliser management which are recorded in PBI, as well as meteorological data provided by Met Éireann (www.met.ie). The MoSt model predicts the trend in grass growth (increase, decrease, static) weekly. This information is very valuable for short-term feed budgeting for farmers who operate grass-based feeding systems; the directional trend change in grass growth as well as the absolute value predicted are important, and the directional trend takes precedence.

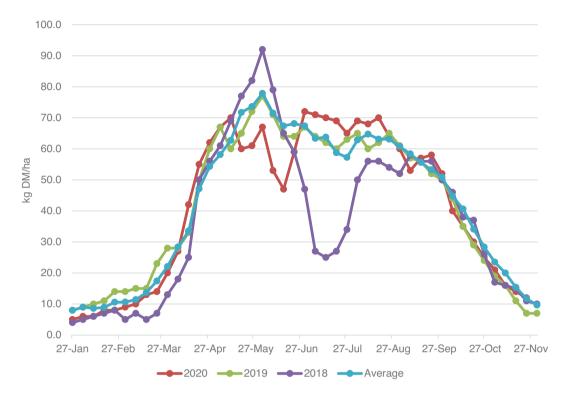


Figure 1. Daily grass growth rates (kg DM/ha) in 2018, 2019 and 2020 and the average growth rate from 2013 to 2020 (inclusive) recorded on PastureBase Ireland.

The model is currently (2021) predicting grass growth weekly on 50 commercial farms with the plan being to roll it out to all farms currently recording in PBI.

One of the main limitations of the MoSt GG model is that it does not consider pasture species other than perennial ryegrass or nutrients other than N. While this increases the model usability by minimising the inputs required, it does limit the model functionality.

Clover and other sward species

White clover (*Trifolium repens* L.) is the most important sown legume species in grazed grassland in temperate regions including Ireland (e.g. Peyraud *et al.*, 2009). The incorporation of white clover in grazing swards takes advantage of its capacity to fix atmospheric N and make it available for plant growth allowing the reduction in chemical N fertiliser (Egan *et al.*, 2018; Enriquez Hidalgo *et al.*, 2018). White clover has high digestibility and has a high energy value which is attributed to its low fibre concentration which reflects the absence of structural components such as stems and sheaths (Ayres *et al.*, 1998). A particular advantage of white clover is the reduced rate of digestibility decline in the mid-season compared to perennial ryegrass (Ulyatt, 1970).

Increased production performance as a result of increasing the sward white clover proportion has been observed in dairy cows (Egan et al., 2018; McClearn et al., 2020), beef steers (Thomas et al., 1981) and sheep (Orr et al., 1990). The results depend on the proportion of sward white clover content. Egan et al. (2017, 2018) found that cows grazing a grass-white clover sward (20%+ clover content) had greater milk yield and milk solids yield than cows grazing a grass-only sward. Research in the areas of incorporating white clover into grassland swards to optimise their contribution and persistence is a significant focus of ongoing research efforts. At a time when white clover inclusion in grassland swards in Ireland is low, despite the well-documented benefits in terms of herbage and animal production and reduced N fertiliser requirement, the development of a Carbon Profit Index, similar to the Pasture Profit Index (PPI) (McEvoy et al., 2011; O'Donovan et al., 2016), will provide farmers with confidence in selecting the appropriate white clover varieties for their system.

Other sward species such as other legumes and herbs are being investigated to examine their role in reducing the use of chemical fertilisers and pesticides, improving soil quality and enhancing biodiversity, while maintaining or increasing herbage production and quality, and animal performance from grazed pasture. In the future, the development of selection indexes for other grassland species may also be important for the industry.

Sward nutritive value

Animal performance at grass is highly influenced by the voluntary grass DM intake (VDMI) of the animal and the organic matter digestibility (OMD) of the grass ingested (Stakelum & Dillon, 2007). Accurate measurements of grass VDMI and OMD are difficult at grazing where pre-grazing herbage mass is a major factor affecting both the VDMI and OMD (Wims *et al.*, 2010). Grass OMD is higher when grass is maintained at a low herbage mass, which should result in greater grass VDMI.

Organic matter digestibility remains the best single predictor of ruminant animal production from high forage diets. Grass quality, measured as OMD, is a key driver of animal performance in grazing systems and is associated with overall farm profit. Herbage mass has a substantial effect on the OMD of a sward (Stakelum & Dillon, 2004; McEvoy *et al.*, 2010). The chemical composition of a perennial ryegrass sward shows large variations from the top to the base of the sward, with decreasing OMD as depth increases in the sward (Delagarde *et al.*, 2000). Perennial ryegrass varieties can vary in *in vitro* OMD due to differences in ploidy (Wims *et al.*, 2013; Beecher *et al.*, 2015) and heading date (O'Donovan & Delaby, 2005), as well as sward structure (McEvoy *et al.*, 2010).

There are opportunities to increase the productivity and efficiency of grass-based systems by strategically modifying the nutrient supply to the cow. To select the optimal strategy, quantitative knowledge of how the diet interacts with the ruminant, the nutrients it supplies and the metabolic requirements of the cow is crucial. Recent research using new feed chemistry demonstrates that the neutral detergent fibre fraction of immature pasture comprises a large potentially digestible pool that degrades rapidly in the rumen allowing for higher milk production performance to be achieved from grass-only diets (Dineen *et al.*, 2021a). Autumn-grass was shown to contain a lower proportion of digestible material which degrades at a slower rate when compared with spring and summer grass (Dineen *et al.*, 2021a; 2021b).

Harvesting and grazing management have to deal with the trade-off between grass quantity and quality. For silage conservation, grass should be cut at the beginning of the grass heading period to maximise net energy and protein harvested per hectare. At grazing, increased frequency of defoliation results in high-quality but a decrease in net herbage accumulation whereas infrequent defoliation leads to greater herbage production, but decreased grass feed value (Tunon, 2013). High biomass yield (kg DM/ha) at grazing will limit animal performance through digestive

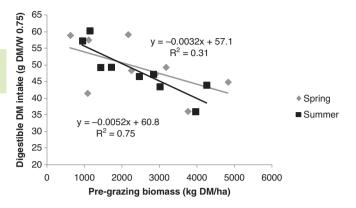


Figure 2. Effect of pre-grazing biomass on digestible DM intake measured in sheep (data from Beecher *et al.*, 2017).

constraints (low intake of poorly digestible matter), but highquality swards (low pre-grazing yield) can also limit animal performance through behavioural constraints if the time required to graze the required grass quantity of grass is too great (Baumont et al., 2004). The effect of pre-grazing yield at grazing may also vary across the grazing season. Tunon (2013) found no effect of pre-grazing herbage mass up to 2,300 kg DM/ha (>4 cm) on milk yield from April to July, but observed a reduction in milk fat plus protein yield compared to swards with pre-grazing herbage masses of 1,000 and 1,500 kg DM/ha from July to October. This agrees with Beecher et al. (2017) who observed no difference in OMD between swards with a pre-grazing mass <1,500 kg DM/ha and >2,000 kg DM/ha in the May to July period, but in the July to October period observed that increasing pregrazing yield resulted in a significant decrease in OMD and digestible DM intake (Figure 2).

Forage breeding advances

The Teagasc forage breeding programme was established at Oakpark in 1960, although it was not until 1985 that the breeding of commercial varieties became the primary focus. The majority of resources in forage breeding programmes in northwest Europe are committed to the improvement of perennial ryegrass given it is the main forage species sown in this region. White clover and red clover, the principal legumes for temperate grassland, are subject to significantly less breeding effort. In Europe, varieties cannot be sold without first undergoing and passing a National List or Recommended List (RL) evaluation system. The first Irish RL was published in 1976. The RL is highly influential with almost all seed sales in Ireland today consisting of RL varieties (Grogan & Gilliland, 2011). Given their importance, breeders' trials tend to mimic the RL trials and are not motivated to select for traits not measured in the RL trials (Stewart & Hayes, 2011).

Traditionally, the core target traits for improvement have been production and adaptation traits such as forage yield, persistence and disease resistance reflecting the traits measured in RL trials. The genetic gain in annual DM yield of perennial ryegrass and white clover has been estimated at 4%–6% per decade (Brummer & Casler, 2014; Gilliland *et al.*, 2021). This is modest in comparison with the 10%–15% per decade genetic improvement in cereal seed yield. The lag in the genetic gain of forage species is due to several biological factors and limited seed industry investment as forages are minor species in terms of global seed sales (Annicchiarico *et al.*, 2016).

Genetic improvement for nutritional value traits in perennial ryegrass has been modest with DM digestibility (DMD) increasing by 5–10 g/kg DM (0.5%–1%) per decade (Gilliland *et al.*, 2020). This may be attributed to limited breeding effort, as nutritional value is a relatively new addition to the RL. Grass DMD value was first added to the Ireland RL in 2009. Nutritional value is now a core trait for improvement in most grass breeding programmes but given that it typically takes 15–20 yr to develop, test and release a new variety, the effects of this increased breeding effort is only starting to be realised in new varieties.

Breeding methods

While animal production is not directly measured in RL trials, animals are often used to apply a grazing pressure in evaluation trials, particularly for legumes. This facilitates selection for grazing resilience (Gilliland *et al.*, 2021). Taking this a step further, Teagasc Moorepark began measuring the residual grazed height of RL trials after grazing with dairy cows. From this, a new grazing utilisation trait was created (Tubritt *et al.*, 2020) which was first added to the Ireland RL in 2021. The Teagasc breeding programme began measuring the residual post-grazing height of perennial ryegrass families in 2018.

Grass and clover breeding systems are based on recurrent restricted phenotypic selection and among-and-within-family selection (Conaghan & Casler, 2011). Selection is practiced on spaced plants and sward plots. The use of sward plots is less efficient than spaced plants as the selection intensity is lower and breeding cycle longer. Sward plots are necessary as not all traits, particularly forage yield, can be improved using spaced plants (Conaghan & Casler, 2011).

Grass variety selection indices

Perennial ryegrass variety economic selection indices such as the PPI in Ireland and the Forage Value Index (FVI) in New Zealand and Australia have been developed to aid variety selection decisions within the grassland industry. These indices utilise data from evaluation trials (O'Donovan *et al.*, 2016; Chapman *et al.*, 2017) expressing superior variety performance based on a total merit index (i.e. expressed as an increase in net profit per year). These indices increase the value of the information supplied to the end user, creating a communication tool expressed in a language (i.e. profit) that users more readily relate to. The relative difference between varieties for all traits is expressed in economic terms indicating the additional profit generated by one variety against another (O'Donovan *et al.*, 2016). Farmers can use the PPI to select varieties based on their total economic merit (sum of all traits) or by focusing on individual traits deemed to be of greater importance (McEvoy *et al.*, 2011).

Grazing efficiency of perennial ryegrass varieties influences the amount of herbage which can be utilised (Byrne et al., 2017). Swards that are consistently grazed to low post-grazing sward heights (<4 cm) support the highest utilisation levels (McCarthy et al., 2013). Hanrahan et al. (2018) reported that utilisation was one of the single largest (controllable) variables affecting profitability of ruminant systems with each additional tonne of DM utilised increasing profitability of dairy farms by €173/ha. Utilisation is a function of herbage production and harvesting by the animal which can be influenced by perennial ryegrass varieties. Herbage production is already captured in the PPI, but relative differences between varieties for grazing efficiency are not included as yet. Byrne et al. (2018) reported a 0.3-cm difference between diploids and tetraploids in achieved post-grazing sward height with the increased digestibility and lower tiller density of these varieties, compared to diploids, responsible for the grazing difference. Varietal grazing efficiency evaluation protocols have been developed by Tubritt et al. (2020) which, in agreement with Byrne et al. (2018), have found important differences between varieties in their ability to be grazed by cattle. The results from these protocols have provided the data necessary to develop a grazing efficiency sub-index within the PPI.

Future of grass breeding

Today, forage breeders are challenged by the difficulty of addressing contrasting demands by farmers (higher animal production potential) and society (reduced environmental and climatic footprint).

Genetic variation for the trait of interest is vital for breeding gain but suitable variation for new traits may not be available in the predominate species of today. This variation may be found in novel species that offer functional diversity in grassland (e.g. Caucasian clover [*Trifolium ambiguum*], birdsfoot trefoil [*Lotus corniculatus*], lotus [*Lotus pedunculatus*], sainfoin [*Onobrychis viciifolia*], chicory [*Cichorium intybus*], plantain [*Plantago lanceolata*] and interspecific hybrids). Increasing the number of species bred reduces the breeding effort per species although the magnitude of such depends on the breeding methodology and trait selection. The Teagasc forage breeding programme presently conducts four breeding programmes in parallel: diploid and tetraploid perennial ryegrass, white clover and red clover.

Gilliland et al. (2021) identified 33 potential traits for selection in perennial ryegrass. The authors noted that instances of breeding for novel traits are isolated. Breeders are conscious that, for a given level of genotypes evaluated, the higher the number of selected traits, the smaller the genetic gain for each trait. As it is necessary to assess all important traits in each generation of selection in order to produce improved varieties without major faults (Wilkins & Humphreys, 2003), selecting for more traits has an exponential effect on the breeding effort (Annicchiarico et al., 2016). Potential novel traits include protein and mineral content, fatty acid profile, anthelmintic and bloat safe properties, N-fixation rate, root architecture, N and P use efficiency, methane emissions and mixture compatibility, to name but a few. Selecting for novel traits can offer varieties a unique marketing advantage but only if farmer appreciation is high. This can be difficult to achieve if the trait is not measured on the RL, the variety ranks low in other traits on the RL and the main market for seed is from intensive farmers who consider production traits foremost. Changes to the RL, including a specialist variety and trait category, would encourage breeders to select for novel traits.

Despite considerable investment worldwide in molecular breeding technologies over the past two decades, markers have contributed little to the development of any forage varieties to date (Annicchiarico et al., 2016). The development of genotyping-by-sequencing procedures at a very low cost per data point may change that. Genomic selection (GS), based on the use of genome-wide markers to develop prediction equations for traits, enables selection of plants at an early developmental stage and replaces the need to phenotype the target trait for one or more selection cycles. Genomic selection may accelerate genetic gain by (i) shortening the breeding cycle, (ii) increasing the number of selection cycles per unit time, (iii) increasing selection intensity and (iv) utilising within-family additive genetic variation (Annicchiarico et al., 2016). Genomic selection is especially attractive for improving traits that require labour-intensive, expensive and multi-year evaluations. The application of GS may allow breeders to select for more traits while maintaining comparable selection intensity and genetic gain for each trait. The successful application of GS requires high-quality phenotypic data on a reasonably sized population to build a high-confidence, robust model. Characterising plant phenotypes is a major bottleneck in the process. High-throughput phenotyping using advances in machinery, optical sensors and machine learning is necessary to fully exploit GS. Genomic selection does not eliminate phenotyping. Phenotyping must continue on an annual basis to allow frequent updates and improvements

to the GS model (Brummer & Casler, 2014). Thus, GS will increase the total cost of the breeding programme but this should be recouped in greater genetic gain. While theoretical models indicate a two- to three-fold increase in genetic gain with GS (Pembleton *et al.*, 2018), they are largely untested in forages for key traits such as DM yield and nutritional value (Arojju *et al.*, 2020; Faville *et al.*, 2020). Critical parameters for GS in forages are gradually being elucidated.

Future grassland research direction

Ruminant production systems in Ireland are and will continue to be pasture-based and so the focus of research must continue to focus on evaluation under grazing.

- (1) The movement of grassland research onto grassland farms aided by PBI allows a greater understanding of the performance of grass and white clover varieties in an on-farm scenario including variation in management, stocking rate, soil type and fertility, and grazing pressure as well as the interaction with grazing, persistence, grazing season length and multiple years data. One of the main limitations of much grassland research is the lack of long-term datasets; the key to understanding grass variety or clover persistence is multi year's data.
- (2) The use of grass growth modelling to examine and understand the effects of climate limitations, soil type, climatic variables and their impacts in the longer term, as well as effects of soil fertility and sward species composition on grass growth.
- (3) The use of the MoSt model to better manage N use and requirements across the grass growing season will be key in promoting fertiliser management change for the grassland industry. The use of predictive real-time data for N management and a move away from date-bound decisions to more informed decision making based on real-time data is a key prerequisite of better N management for the industry.
- (4) Future developments with the MoSt will include the incorporation of other pasture species (especially white clover) and other nutrients to increase the model's functionality and usefulness.
- (5) The continued use of the grazing system experimental approach with the application of decision/management rules. While the use of component research is useful, it does not give the entire complexity of the treatment within the system. The use of multiple sites for research is important.
- (6) In grassland nutrition, strategies including improved grassland management, optimisation of concentrate supplementation and selection of superior plant genetics are still major avenues of research focus. Ruminants consuming grass-based diets exhibit a large dependence on microbial amino acids to support metabolisable amino

acid supply; how and when (season) this can be balanced is an area that requires further research to increase our understanding and knowledge.

- (7) The creation of high-quality, high tannin, low methane emission swards is now a key aspect of grassland research. Perennial ryegrass is invariably low in tannin content, so the pursuit of high tannin species can be complimentary to the focus of reducing methane emissions of grazing ruminants.
- (8) The use of more grazing in plant species evaluations; there is currently limited work completed. For example, in recent years, the benefits of multispecies swards under cutting/mowing have been documented but little to no grazing evaluation has taken place. There is a requirement for the grassland science, plant breeding and grass evaluation to be more proactive in moving to more intensive evaluations under grazing.
- (9) Grass breeding needs to focus on more grazing traits in the future, specifically grazing utilisation, mid-season quality and DM production over time rather than sward ground score.
- (10) Understanding the factors affecting establishment and persistence of white clover in grasslands is of key importance in developing protocols for over-sowing and reseeding to deliver productive persistent white clover swards that allow chemical N fertiliser use to be reduced.
- (11) The role of multispecies swards in our pasture-based systems must be evaluated and defined. Suitable species and combinations of species need to be evaluated. The research must focus on the added value aspect of specific species to the overall DM production, persistence, N fixation, canopy morphology and sward quality of the swards. Added benefits these may bring in terms of environmental benefits (e.g. reduced N loss, increase soil C content) to grazed pasture must be quantified.
- (12) A deeper understanding of the role of grasslands in delivering ecosystem services and addressing environmental challenges such as improvements in water quality, above and below ground biodiversity, and reductions in GHG emissions.
- (13) The uptake of DSTs in grassland continues to be slow; however, their role in the improvement of grassland production and utilisation can be immense. The role of peer-to-peer learning and the creation of grasslandfocused discussion groups will assist this process.

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Special Issue Article • DOI: 10.15212/ijafr-2020-0148 IJAFR • 61(1) • 2022 • 12-37



Irish Journal of Agricultural and Food Research

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 guotas. 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 quotas, 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 quite 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 (*R*² = 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 guite 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 guality, 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-quality 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-quality 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 guality 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 yield 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 vield 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 quality, 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 yield 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 quality. 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 CH,/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 yield 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; Guyader 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 quality, 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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Irish Journal of Agricultural and Food Research

The development of effective ruminant breeding programmes in Ireland from science to practice

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Abstract

A genetic improvement programme is a sustainable, cumulative and permanent approach to achieving year-on-year performance gains. Its success is predicated not only on an efficient and effective breeding programme but also on a vision of the traits of importance in the future. A single, industry-owned, centralised database for cattle and sheep has been the foundation for genetic improvement programmes in Ireland. While DNA information has been heralded as a breakthrough for accelerating genetic gain, the basic principles of a successful animal breeding programme still remain the same: (1) a pertinent breeding goal, (2) the appropriate breeding objective to deliver on the breeding goal, (3) an accurate genetic evaluation system, (4) an efficient and effective breeding scheme, and (5) a system to disseminate the elite germplasm to the end user; also of importance is a system for validating the underlying procedures and principles. The constituent traits and their relative emphasis within breeding objectives will continue to be contentious. Traits that will need to be considered more in future ruminant breeding objectives include environmental impact, product quality and animal well-being, including health; while not always explicitly included in Irish breeding objectives for cattle and sheep, indirect improvements for many are expected via the genetic improvement in traits like reproductive performance and survival as well as macro measures of quality such as milk fat and protein concentration and carcass merit. Crucial for the future sustainability of ruminant production systems is the co-evolution of management systems and breeding programmes so that the animal of the future is suited to the most sustainably efficient production system.

Keywords

Breeding programme • genetic • heritability

Introduction

Genetic improvement has been documented to contribute up to 90% of the gains in performance in livestock over time (Havenstein *et al.*, 2003); in reality, however, in ruminant production systems this is more like 50% (Berry, 2018). The cumulative, permanent and sustainable characteristics of genetic improvement dictate that benefits culminate over generations and the benefits that accrue can be permanent. On the other hand, any unfavourable trends realised through breeding, if not addressed, can deteriorate further with each advancing generation. An example of the latter in ruminants is the erosion of reproductive performance in both dairy and beef cattle (Lucy, 2001; Berry *et al.*, 2016a) as a consequence of aggressive selection for milk production and terminal characteristics, respectively. Such deterioration remains a threat especially for animal features not routinely measured

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(e.g. lifetime efficiency of feed use, environmental hoofprint). Projected genetic trends must also consider the production system (e.g. grazing or total mixed ration [TMR]) required to meet the demands of the ruminant; hence, the management systems and breeding programme must co-evolve.

The steps in a successful breeding programme are graphically illustrated in Figure 1 (adapted from Lopez-Villalobos & Garrick, 2005). The fundamentals of a successful breeding programme are to mate genetically elite individuals so that the next generation will, on average, be superior to the current generation; consideration must also be given to minimising the relationship among parents so as to avoid a rapid accumulation of inbreeding. This is because as well as having repercussions for animal performance (McParland *et al.*, 2007, 2008; Bjelland *et al.*, 2013), inbreeding also tends to

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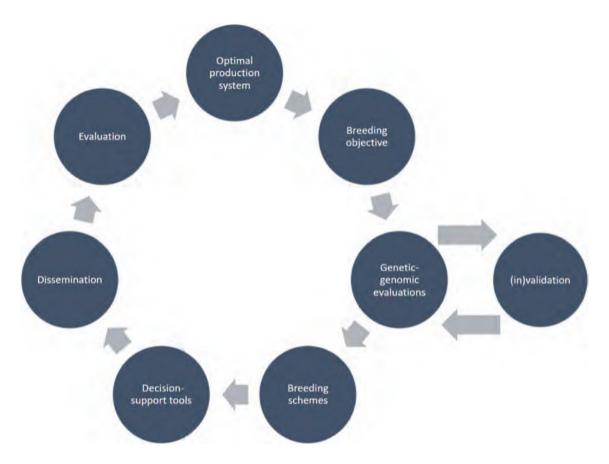


Figure 1. Components of a successful breeding programme.

erode exploitable genetic variability thus impacting long-term genetic gain (Berry, 2018). Validation of the benefit of genetic selection is required to instil confidence among end users thus ensuring high penetrance. This review focuses on the main scientific achievements that have contributed to genetic gain in Irish ruminant breeding programmes and the research undertaken to facilitate such performance gains; the review concludes with some thoughts on what gaps in knowledge currently exist, again with a particular attention on cattle and sheep breeding in Ireland.

Main scientific advancements

Genetic evaluations globally are generally based on a mixed model framework developed in the middle of the 20th century (Henderson, 1950). The best linear unbiased prediction procedure for predicting genetic merit of individuals does so by decomposing the observed performance of an animal (termed phenotype) into its genetic contribution, the contribution due to systematic environmental effects (e.g. herd, year, gender, age), and that remaining as unexplained variability (i.e. residual). Access to predictions of genetic merit for individuals enabled the exploitation of selection index methodology developed by Hazel (1943). Selection indexes are devised to maximise the correlation between animals ranked on the developed index and those ranked on an overall breeding objective. The breeding objective for a breeding programme is analogous to a mission statement for a company; it comprises a number of traits each appropriately weighted based on (perceived) importance. While observations for a given trait in a breeding objective are not necessarily required, data must exist for traits in the underlying selection index and thus much effort has been expended on strategies and the associated backend information and communication technology (ICT) infrastructure to capture and store such data.

While economic modelling is used to decide the weights on individual traits within dairy, beef and sheep breeding objectives in Ireland, some jurisdictions use economic modelling only as a guide with the final weights on individual traits often decided by a committee. Breeding objectives are routinely updated based on new information and knowledge both on the traits of likely importance in the future and on their associated (future) costs and value. Figure 2 demonstrates

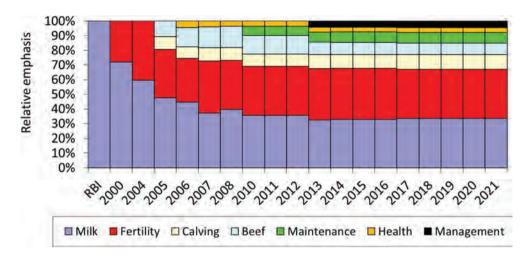


Figure 2. Change in emphasis on sub-indexes within the Irish dairy cow breeding objective, the economic breeding index (EBI) since its establishment in 2000; the relative breeding index (RBI) existed prior to 2000.

how the national dairy cow breeding objective in Ireland, the economic breeding index (EBI), has changed since its introduction in the year 2000; the changes observed reflect the addition of new traits as genetic evaluations became available but also the updating of the economic values as the expected prices and costs of production changed (Berry *et al.*, 2007). Because generation intervals tend to be particularly long in (dairy and beef) cattle (García-Ruiz *et al.*, 2016), breeding objectives in cattle especially must be very futuristic.

Specific to the success of ruminant breeding programmes in Ireland was the establishment of the Irish Cattle Breeding Federation (ICBF) in 1997 (Wickham et al., 2012) followed in 2009 by the development of Sheep Ireland. The ICBF and Sheep Ireland are mandated by the Irish government to generate and distribute accurate national genetic evaluations to the respective industries. Prior to the establishment of the ICBF and Sheep Ireland, most stakeholders had their own system for data recording and storage, each with their own specific objectives but also potentially their own population demographics or geographical representations. For example, each cattle breed society herd book, of which there were 18 at the time ICBF was established, had its own computing system, while each milk recoding agency, of which there were 8 in 1998, also had its own computing system. Although creating a single version shared repository of verified data was an ambitious and arduous task for both the ICBF and Sheep Ireland, the developed infrastructure is now the epicentre of breeding (and many management) decisions made on Irish dairy, beef and sheep farms.

Annual genetic gain in any population for any trait or breeding objective can be easily represented by the breeder's equation (Rendel & Robertson, 1950):

$$\Delta G = \frac{i \cdot r \cdot \sigma_g}{L}$$

where ΔG is annual genetic gain, *i* is the intensity of selection, r is the accuracy of selection or, in other words, the accuracy with which the genetically elite animals can be differentiated from the genetically inferior, σ_a is the genetic s.d. (i.e. a measure of variability) and L is the generation interval (i.e. the average age of the parents at the birth of their progeny who in turn become parents). Hence, most of the effort in animal breeding research and development has focused on the exploration of technologies and approaches to improve each metric. In fact, most of the focus among geneticists has been on improving the accuracy of selection. The accuracy of selection is a function of the heritability of the trait and the quantity of information available; this is true irrespective of whether based on traditional genetic evaluations or genomic evaluations. Information in this context traditionally implied usable phenotypic data from the animal itself, its ancestors or its descendants. In more recent decades, approaches to supplementing this (observed) phenotypic information with genomic (i.e. DNA) information have been explored (Meuwissen et al., 2001; Berry et al., 2009). Nonetheless, the accuracy of selection irrespective of whether based on traditional genetic evaluations that exploit ancestry, or genomic information to infer relationships, is still a function of the heritability of the trait (Figure 3); the lower the heritability, the greater the number of progeny records required to achieve a given accuracy of selection.

The heritability of a trait is a measure of the proportion of the observed (i.e. phenotypic) variability amongst individuals that can be attributable to genetic differences (Visscher

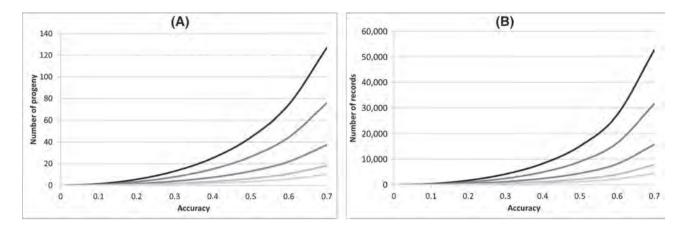


Figure 3. For heritability values of 0.35, 0.20, 0.10, 0.05 and 0.03 (in order of increasing darkness of lines), (A) the number of progeny required to achieve a given accuracy of selection using traditional ancestry-based genetic evaluations and (B) the number of records of phenotyped and genotyped animals to achieve a given accuracy of genomic evaluations (based on 1,000 effective chromosomal segments and 80% of the genetic variance accounted for by the genotyped markers). Note reliability which is used in cattle in Ireland is the accuracy squared.

et al., 2008), the latter usually being confined to differences that are directly transmissible from one generation to the next (i.e. additive genetic effects). All else being equal, the higher the heritability, the greater the accuracy of selection from traditional evaluations but also the fewer the number of genotyped and phenotyped animals required for a genomic evaluation reference population (Figure 3); nonetheless, high accuracy of selection can be achieved even for low heritability traits, and thus heritability has minimal impact on genetic gain in an efficient and effective breeding programme. Having said that, heritability is important for traits that are resource intensive to measure which is a likely feature of traits growing in importance in ruminant production systems such as environmental impact, product guality and animal well-being. Genomic selection (Meuwissen et al., 2001) using genotype information scattered densely across the entire genome has contributed to a transformational change in animal breeding programmes. This was particularly true for those species with long generation intervals and that assign considerable selection pressure to low heritability traits measured only in one sex; such characteristics typify modern dairy cow breeding programmes which, when coupled with the predominance of only one dairy breed in most temperate regions (i.e. Holstein-Friesian), is the reason for the rapid and ubiquitous uptake of genomic evaluations in dairy cattle. Whereas maternal breeding objectives in beef and sheep suffer also from comprising low heritability traits measured only on older females, traits constituting a large emphasis in the terminal indexes tend to be highly heritable, measured early in life and not sex limited. Genomic selection was an advancement on the previously advocated marker-assisted selection; the latter relied on just a few genetic markers but failed to deliver on promises of vastly improved accuracy of selection for quantitative traits across the population. The heralding of genome-wide enabled selection was possible with the commercial availability of (relatively) low-cost genotyping platforms (Boichard et al., 2012; Judge et al., 2016) that could rapidly and reproducibly (Berry et al., 2016c; Purfield et al., 2016; Marina et al., 2021) genotype animals simultaneously for tens of thousands of genomic variants. Ireland was the second country in the world to officially release national genomic evaluations in dairy cows (Berry et al., 2009) and the first country to release national genomic evaluations in a multi-breed population of beef cattle (Berry et al., 2016b); national multi-breed genomic evaluations for sheep now also exist in Ireland. Ireland also developed its own bespoke cattle genotyping platform, optimised in content for the Irish dairy and beef population while still being compatible with other commercially available platforms (Mullen et al., 2013); included on the Irish bovine genotype panel are variants to enable genomic evaluations and parentage testing among putative parent-offspring pairs genotyped using different variant types (McClure et al., 2013), as well as variants located within major genes (including those conferring congenital defects) and variants of research interest. Genomic variants included on the ovine panel are those to enable genomic evaluations and parentage testing/discovery as well as including several causal mutations and putative causal mutations associated with performance metrics.

Irish national cattle and sheep breeding objectives

The suite of traits included in Irish national dairy, beef, beefon-dairy and sheep breeding objectives in 2021 is shown in Figure 4, along with their respective relative emphasis. The

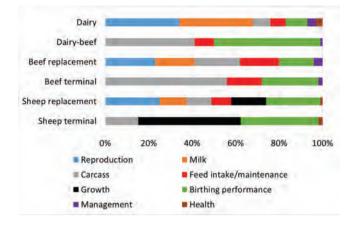


Figure 4. Relative emphasis on suites of traits within the Irish dairy and dairy-beef indexes as well as the beef and sheep replacement and terminal indexes.

partial correlation (i.e. adjusted for breed) among the beef terminal, beef replacement and dairy-beef index in 918 high-reliability artificial insemination (AI) beef bulls with progeny in Ireland is 0.40–0.41. The partial correlation between the sheep terminal and replacement index in high accuracy rams is 0.41.

Reproductive performance including survival constitutes a large proportion of the relative emphasis within the different breeding objectives targeting female replacements ranging from 23% emphasis in beef to 34% emphasis in dairy (Figure 4); this is largely attributable to the importance of maximising the utilisation of grazed grass and realising mature animal performance, with reproduction being represented by the number of lambs born in sheep; no predictions of genetic merit exist for ewe survival in sheep, but this is an area of ongoing research. Both reproduction and milk production (represented by maternal weaning weight or growth in beef and sheep) combined represent 37%, 41% and 68% of the emphasis in the sheep replacement index, the beef replacement index and the dairy breeding objective, respectively (Figure 4). The relative emphasis on calving or lambing performance (both direct and maternal) across all six breeding objectives was, on average, 27% varying from 10% in the dairy breeding objective to 49% in the dairy-beef index; calving performance here includes actual calving difficulty as well as both gestation length and perinatal mortality. Progeny slaughter performance represents just 8% of the emphasis in the dairy breeding objective but 12% and 21% in the sheep and beef replacement indexes; carcass traits (including age at slaughter for sheep) represent 41%-63% of the emphasis in the three terminal breeding objectives (Figure 4).

Fundamental to a successful breeding program, whatever the species, is routine access to high-quality data (with recorded ancestry and other ancillary information) for the traits of interest representing the germplasm being used in the population. Figures 5 and 6 illustrate the quantity of data recorded (including ancestry information) in Irish cattle and sheep populations, respectively. Two main points can be made – the extent of recording, especially in cattle, is very large and has been increasing in the past two decades and there is a relatively good recording of sire information, although room for improvement exists.

Genetic gain in s.d. units for each of the six breeding objectives is presented in Figure 7. Genetic gain in the sheep and beef breeding objectives was low (between 0.37 and 0.84 units) over the 20-yr period which is considerably slower than the genetic gain of 2.79 units for the national dairy index over the same 20-yr period. Year-on-year genetic gain in dairy animals has been relatively constant each year since 2002. Using the parameters proposed by Schaeffer (2006) for a successful dairy cow breeding program, a genetic gain of 0.215 genetic s.d. per year should be possible; this would increase to 0.47 for a successful genomic selection breeding program. Hence, genetic gain in the Irish dairy breeding programme is considerably less than what should be possible. Despite this, clear phenotypic differences between animals genetically divergent for the Irish dairy cow breeding goal (i.e. the EBI) are evident (O'Sullivan et al., 2019). In 2015, a DAFM-funded scheme used monetary incentives to encourage the use of the replacement index in beef herds which was then followed by the introduction of genomic evaluations in 2016 (Berry et al., 2016b). This has resulted in a genetic gain of 0.2 genetic s.d. units per year in the replacement index since the introduction of this scheme; this is similar to the annual genetic gain observed in dairy. Genetic gain was lowest for the dairy-beef index (0.17 units over the 20-yr period), which is an artefact of the dairy-beef breeding objective only being available to herd owners since 2019 (Berry et al., 2019). All in all, genetic gain has been achieved and the mass of validation studies undertaken to date which verify the impact of such genetic gain on phenotypic performance clearly imply that phenotypic gains have also been achieved.

Animal health continues to be poorly represented in the different breeding objectives, being only present in the dairy breeding objective (i.e. mastitis, somatic cell count and lameness) and both sheep breeding objectives (i.e. mastitis, lameness and dagginess); yet, the emphasis in all indexes is \leq 3%. Although currently not included in breeding objectives, stand-alone genetic evaluations for tuberculosis (Ring *et al.*, 2019) and liver fluke (Twomey *et al.*, 2016) in beef and dairy cattle are available nationally; further research is ongoing on increasing the suite of health traits with genetic evaluations.

The reasoning for the perceived low emphasis on health traits within the breeding objectives is because the definition of an economic value is the change in profit per unit change

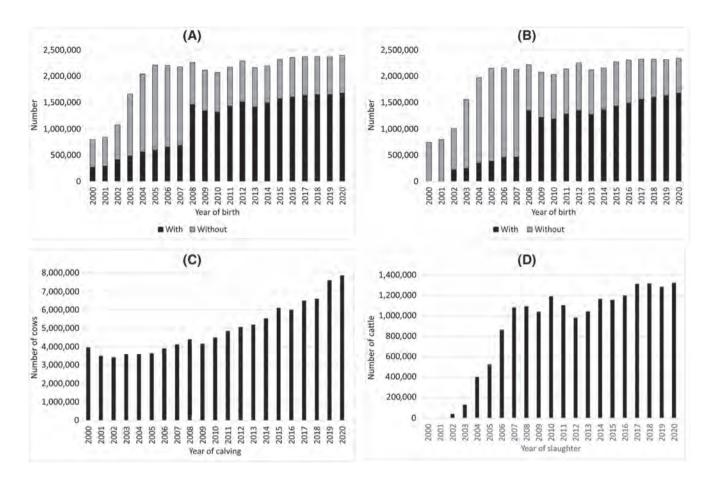


Figure 5. Number of (A) calves born with or without a sire recorded, (B) calving events with or without a recorded calving difficulty score, (C) dairy cows milk recorded and (D) prime cattle carcass records all recorded within the Irish Cattle Breeding Federation national database.

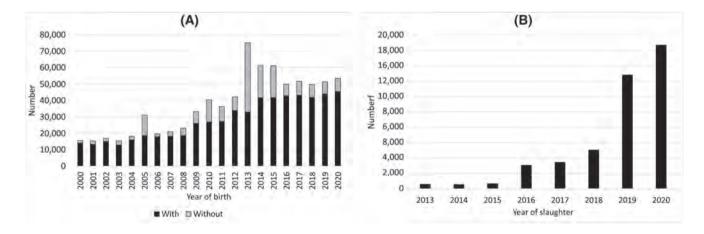


Figure 6. Number of (A) lambs born with or without a sire recorded and (B) lamb carcass records all recorded within the Sheep Ireland database.

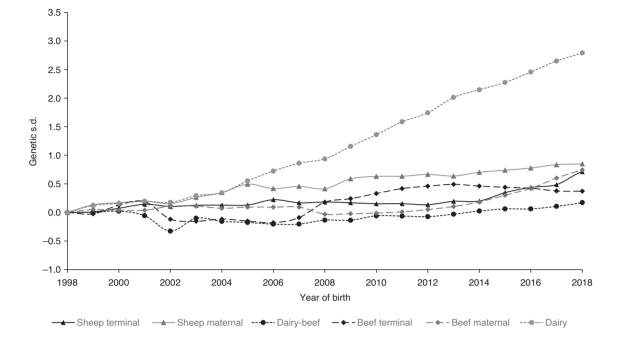


Figure 7. The genetic trend from 1998 to 2018 for the six breeding objectives in Ireland: sheep terminal index (triangles, solid black line; s.d. = $\in 0.65$), sheep maternal index (triangles, solid grey line; s.d. = $\notin 2.44$), dairy-beef index (circles, dotted black line; s.d. = $\notin 21$), beef terminal index (diamonds, dashed black line; s.d. = $\notin 32$), beef maternal index (diamonds, dashed grey line; s.d. = $\notin 40$) and the dairy index (circles, dotted grey line; s.d. = $\notin 60.65$).

in the trait in question holding all other traits in the breeding objective constant. Compromised animal health is known to influence other performance metrics (Sayers, 2017). Hence, animals with a genetic predisposition to poor health (or whose descendants are more likely to succumb to poor health) are also likely to have substandard predictions of genetic merit for performance traits; thus, the breeding objective values of these animals will be penalised via their poor predictions of genetic merit for these performance traits. The definition of economic values is also pertinent when explaining how the change in emphasis on certain traits may differ from expectation as prices and costs change (Figure 2). For example, when milk price is predicted to reduce, there may be an expectation that the emphasis on milk production in dairy breeding objectives should increase in the pursuit of maintaining profit; however, the increase in profit per unit increase in the yield trait has reduced and thus the emphasis, in turn, reduces. Moreover, economic values do not consider the accuracy of selection. Given the low heritability of health traits (Pryce et al., 1997; Berry et al., 2011; Ring et al., 2018) coupled with the generally lack of available data, the actual emphasis on health traits is therefore often even lower. Key therefore is not just to record more data on health events, but to ensure that data are communicated to the national database for use in genetic evaluations. Moreover, by decomposing (observed) broad health events like mastitis or lameness into their subclinical measures, or even more granular descriptors of the underlying pathogens, some of the random error should be removed thus increasing the heritability – the outcome is a higher accuracy of selection (and thus greater emphasis) for the same number of records, be it traditional genetic evaluations or the now more common genomic evaluations. Technological advances in sensing and associated communication systems have the potential to aid in this shortcoming.

Validation

Fundamental to the uptake of any technology is sound (ideally independent) evidence that the technology will deliver on promises. Breeding is not exempt from such demands. Ireland is, by far, the most prolific in studies investigating the relationship between genetic merit and subsequent phenotypic performance; this is true of dairy cattle (Ramsbottom *et al.*, 2015; O'Sullivan *et al.*, 2019; Ring *et al.*, 2021), beef (Clarke *et al.*, 1999; McHugh *et al.*, 2014; Connolly *et al.*, 2019; Twomey *et al.*, 2020) and sheep (McHugh *et al.*, 2017, 2020). Validation strategies to demonstrate the merits of breeding include controlled studies (Macdonald *et al.*, 2008; Clarke *et al.*, 2009; Coleman *et al.*, 2009; McCabe *et al.*, 2020) and cross-sectional analysis of either animal-level data (Crews *et al.*, 2006; Connolly *et al.*, 2019; Berry & Ring, 2020b;

Twomev et al., 2020) or herd-level data (Ramsbottom et al., 2015; Kelly et al., 2021). Each approach in itself has its own shortcomings, but when consensus is arrived at across all three strategies, then confidence will ensue. Many Irish controlled studies across a range of ruminant species have verified that genotypes of different genetic merit perform differently (Clarke et al., 2009; Coleman et al., 2009; McCabe et al., 2020; Fetherstone et al., 2021); while the extent and depth of measurement in such studies is generally highly precise, and the environmental noise is strongly controlled. such controlled studies can be hampered by a lack of statistical power, a lack of genetic diversity represented, and a caution of extrapolating to production systems not directly represented in the controlled study (hence their general inclusion as fixed effects in the statistical models). Cross-sectional analyses of large databases of individual animal records (Crews et al., 2006; Connolly et al., 2019; Twomey et al., 2020; Ring et al., 2021) do not generally suffer from a lack of statistical power (and thus the likelihood of Type II errors) or genetic diversity, but errors undoubtedly exist within the data; the hope is that the large number of experimental units will lessen the impact of such errors if occurring relatively randomly across genotypes. For example, Purfield et al. (2016) reported a sire parentage error of 13% in Irish (dairy and beef) cattle, while Berry et al. (2016c) reported an equivalent statistic of 10% in Irish sheep; because the assigned genetic merit of an animal is dictated, in part, by the sire, such errors undoubtedly influence confidence in the results. Similarly, assignment of animals to the appropriate contemporary group for inclusion in the statistical model is problematic (McHugh et al., 2017). Cross-sectional analyses of large databases of herd-level data (Ramsbottom et al., 2015; Kelly et al., 2021) suffer from similar issues to those of animal-level analyses with the added complication of how to appropriately account for inter-herd differences in technical efficiencies. The statistical approach taken in these studies (Ramsbottom et al., 2015; Kelly et al., 2021) was to attempt to adjust for inter-herd differences in technical efficiency through the adjustment of financial performance metrics for other available measures of technical efficiency such as stocking rate, herd size and concentrate input. While the objective of most such studies is to validate the gains achievable from breeding, also of interest is likely non-linear effects plus any repercussions for other (correlated) traits; the latter is particularly of interest in smaller controlled studies where deeper phenotyping for resource-intensive measures (e.g. feed intake, methane emissions) is possible.

Complementary decision-support tools

Gains in performance are achieved through a combination of strategic breeding and management decisions. The goal of (herd) breeding programmes is to shift the mean of the distribution of animals in the favourable direction; this can also be achieved by culling the lower performing animals. Decisionsupport tools for dairy (Kelleher et al., 2015) and beef (Dunne et al., 2020b) enterprises have been developed specifically for Ireland to value the expected remaining lifetime profit of each female in a herd. This information can be used to identify mature females for culling but also heifers for graduation into the mature herd (Kelleher et al., 2015; Dunne et al., 2020b). Both tools are built on the principles of selection indexes populated by what are termed production values which are the sum of both the additive genetic merit (used in breeding decisions) and non-additive genetic effects; also considered are non-genetic effects (e.g. permanent environmental effects) as well as other phenotypic factors like cow age and expected calving date. Similar to the national genetic-based breeding decision-support tools, the culling management tools provide the user with a single figure index value; this data-driven metric ultimately provides the user with confidence when making decisions that will have a substantial impact on the performance of the herd. A similar decision tool has been developed to value a calf assuming it is destined for beef production (Dunne et al., 2020a); taken in conjunction with the ranking tool of beef females to identify heifers suitable for the mature herd, comparison of values from both tools can aid in the decision as to the most appropriate fate of a given beef heifer. Such a tool may also be useful in the future to allocate a carbon cost to a given unit of product; while management strategies (e.g. source of energy and protein ingested) contribute to the carbon cost, so too do animal-level features such as days to slaughter and daily feed intake or daily methane output.

Despite lists of males ranked on total merit index being readily available to producers, deciding on which male to mate to which female can become unwieldy, especially in large herds and flocks. Sire mating advice tools are available for suggesting matings between dairy bulls and cows (Carthy *et al.*, 2019), but no such tools exist, in Ireland at least, for suggesting beef bulls matings with either beef females or dairy females; the same is true for sheep. While consideration of coancestry is important in the sire advice systems for dairyon-dairy or beef-on-beef matings, no such worry exists for beef-on-dairy matings (Berry, 2021).

Genetic evaluations work by decomposing the observed phenotype into an additive genetic effect (termed best linear unbiased predictions [BLUPs]) and environmental effects (termed best linear unbiased estimates [BLUEs]). Although focus until recently has been on the BLUP, there is growing interest in the BLUEs for individual herds or flocks and how the response to selection differs by BLUE (Dunne *et al.*, 2019; Kenny *et al.*, 2021). In a study of 1,058 Irish dairy herds, Dunne *et al.* (2019) reported that when herds were stratified based on their BLUE for milk production, the phenotypic realisation of increasing an animal's genetic merit by 1 unit for milk production was 20% greater in the herds with the best BLUE relative to the worst BLUE herds. Given that BLUEs are routinely generated alongside BLUPs, very little additional computational cost is required to incorporate such information into the decision-support tools currently available. BLUEs have the potential to tailor the estimates of an animal's phenotype based on the environment they will actually be performing in, rather than assuming an average production environment (Dunne et al., 2019; Kenny et al., 2021). Apart from the potential benefit BLUEs offer in tailoring breeding and management decision-support tools (Bastin et al., 2009). BLUEs can also be employed within advisory tools as a metric of the herd's environmental contribution to the overall phenotypic performance. Utilising both BLUEs and BLUPs combined can assist in the identification of potential weakness in the herd/flock, and in doing so, it can lead to the appropriate resolving measures to be put in place.

Knowledge gaps

Despite considerable research having been completed and deployed, particularly in the past two decades in Ireland, many gaps in knowledge and tools still exist. These include what will constitute the future ruminant breeding objectives and what relative emphasis is on each suite of traits, the most optimal methods for evaluating the genetic merit of animals (i.e. accuracy, speed of calculation), breeding scheme design to ensure long-term genetic gain and finally, the support mechanisms that collapse all the available data and downstream calculations into usable information for producers that can be acted upon.

Future breeding objectives

Factors dictating whether a trait should be included in future breeding objectives include (Shook, 1989):

- Its importance importance here was traditionally dictated by monetary value associated with an improvement in the trait; opinion is, however, changing to consider public good type measures with no current monetary reward for improvement.
- Extent of genetic variability logically without genetic variability, genetic improvement will not be possible. Genetic variation, no matter how small, exists for most traits. It is often incorrectly assumed that a low heritability translates to little genetic variability which may not be the case as a small proportion of a large phenotypic variance still translates to large (exploitable) genetic variability.
- Data availability individual animal data linked to ancestry and known contributing environmental influences are key to being able to differentiate genetically elite from genetically inferior animals. Although genomic evaluations mitigate the necessity for phenotypic data on an animal itself or

its descendants for achieving moderate to high accuracy, phenotypic data are still required on a relatively large population in order to calibrate the prediction equations (Figure 3). The requirement for data on the objective traits themselves can be circumvented by having data on correlated heritable traits, for example, using somatic cell count as a predictor of a clinical mastitis goal trait.

An additional factor which impacts the decision of what trait(s) to focus on for inclusion in a breeding objective is the associated cost-benefit. This is particularly important in light of growing pressures to consider traits associated with the social cost of ruminant production (i.e. use of human-edible energy and protein sources and environmental hoofprint). While there is much interest in improving the efficiency of production through the measure of daily feed intake (Crowley et al., 2010; Berry et al., 2014a, 2014b; Pryce et al., 2015; Hurley et al., 2017), the measurement of such performance traits is resource intensive and a return on investment may not actually be obvious; the same is true for carbon/methane intensity. Faster gains in such metrics may actually be achievable by exploiting more readily available phenotypes such as age at slaughter in terminal animals (Santos et al., 2015; Berry et al., 2017) and lifespan or survival in cows (McHugh et al., 2014; De Vries, 2020; MacNeil et al., 2021; Ring et al., 2021).

While not always explicitly included in breeding objectives, in some instances, much of the variability in (detailed) product quality, efficiency, environmental load, as well as animal health and welfare is already captured via correlated traits. For example, the inclusion of milk output (positive weight) and live weight (negative weight) in the dairy cow EBI is similar to milk solids per kilogram live weight which is correlated with feed conversion efficiency in dairy cows (Hurley et al., 2016). Similarly, residual feed intake is completely captured via its component traits within the Irish beef breeding objectives (Van der Werf, 2004). Although (residual) feed intake is included within the beef and beef-on-dairy breeding objectives, the phenotype is from animals fed indoors; evidence is not clear as to whether this actually translates to feed intake in grazing animals (Lahart et al., 2020) where, in fact, a greater intake capacity may be favourable. No feed intake genetic evaluation currently exists for sheep in Ireland due to a paucity of individual animal phenotypic records. Whereas genetic evaluations exist for milk fat and protein content in dairy cows (Sneddon et al., 2015) and meat organoleptic properties in cattle and sheep (Swan et al., 2015; Berry et al., 2021), the desire for genetic evaluations on more granular measures such as micronutrient content (Soyeurt et al., 2011; de Marchi et al., 2014; Frizzarin et al., 2021) or amenability to easier processing (de Marchi et al., 2014; Visentin et al., 2015) may intensify. Despite the collection of gold standard observations for such traits in large populations of animals for genetic evaluations not being feasible, mid-infrared spectroscopy of milk samples can be

used to accurately predict such traits (de Marchi *et al.*, 2014; Visentin *et al.*, 2015; McDermott *et al.*, 2016), and genetic evaluations of mid-infrared predicted traits are possible (Bastin *et al.*, 2011; McParland *et al.*, 2015). Similarly, while measures of carcass weight, conformation and fat score are used in cattle and sheep breeding objectives, potential exists to decompose these further into the individual primal cuts (Sarti *et al.*, 2013; Judge *et al.*, 2019), aligning more closely with the downstream processing industry and consumers. Potential may also exist to use non-destructive spectroscopybased approaches to predict meat quality (Herrero, 2008).

As genetic trends for longevity improve in dairy cows (García-Ruiz *et al.*, 2016; Berry, 2021), cows are expected to get older. Risk to different ailments including lameness, mastitis and other health problems is known to increase with age (O'Connor *et al.*, 2019) although strategies to mitigate this may be possible, for somatic cell count at least (Williams *et al.*, 2022). Hence, it is likely that the importance of functional conformation and animal health will become more important in the future but also the ability of the mature cow to maintain high performance (and low somatic cell count in the case of dairy cows) with advancing parity (Williams *et al.*, 2022). A similar dilemma exists for beef and sheep.

Environmental traits like methane emissions and nitrogen use efficiency are also likely to grow in importance in the future. Although the acquisition of (accurate) measures for such traits is resource intensive, the costs are incurred by few but the benefits are realised by many. For example, assuming that the output from the Irish dairy, beef and sheep sectors is 8 billion kg of milk, 550,000 tonnes of beef meat and 55,000 tonnes of sheep meat, then the charge per kilogram output per €1 million cost of phenotyping animals for a breeding programme would be just 0.013, 0.18 and 1.8 cents, respectively. Methane data are currently being collected in dairy, beef and sheep in Ireland with the anticipation of generating sufficient data for the development of national genetic evaluations as well as identifying the most optimum strategy for recording such data; one example of the latter is the extent of genotype-byenvironment between methane measured indoors on animals fed a mixed ration versus methane measured outdoors in grazing animals.

Developments in agri-tech and the growing accessibility of sensing systems for measuring a whole plethora of metrics (Greenwood *et al.*, 2016) open up opportunities as well as create challenges for future animal breeding programmes. The opportunities include the generation of vast quantities of objective measures not only on the animal itself, but also reflections of the prevailing environmental conditions (for use in the statistical model). Data on non-animal features are also useful in potentially improving the precision of genetic evaluations through the consideration of genotype-by-environment interactions (BLUEs; Dunne *et al.*, 2019).

Sensing systems which can be deployed on the animal include those based on accelerometers, magnetometers, gyroscopes, visual, sensors, audio sensors and location sensors as well as equipment to measure temperature. gastrointestinal function, heart rate and respiratory rate (Greenwood et al., 2016; Halachmi et al., 2019). Thermal imaging or actual cameras to measure things in multiple dimensions are feasible. Detailed reviews of the agri-related technologies available are discussed by both Greenwood et al. (2016) and Halachmi et al. (2019). The greatest benefit, however, from such technological advances will be when the vast array of information sources are combined and complemented with available information on ancillary animal and environmental features like animal age, prevailing weather and genetic merit. Of concern, however, is the potential disputes on the ownership of the data and the ability to use these data in national genetic evaluations; this could potentially lead to the development of proprietary genetic evaluations or even genetic evaluations within herds or groups of herds. Such sensing systems will likely have greatest impact for low heritability traits where vast quantities of data are required to achieve accurate predictions of genetic merit but also where combining different data sources including information on influencing systematic environmental effects could contribute to a higher heritability and, by extension, a greater accuracy of selection for the same number of phenotypic records.

Though there is much commentary on agri-tech and its contribution to extensive phenotyping via sensing systems and downstream analytics, the value of (subjective) producer-scored data cannot be ignored. Despite being subjective in nature, these traits are clearly heritable (O'Brien *et al.*, 2017; Ring *et al.*, 2018) and constitute a large proportion (i.e. up to 36% of the emphasis in the breeding objectives) of the relative emphasis of Irish cattle and sheep breeding objectives. Moreover, many are strongly correlated with the goal trait; in an analysis of predicted primal cut data from >100,000 carcasses on Irish beef cattle, Pabiou *et al.* (2012) reported a genetic correlation of 0.49 between farmer-scored weanling quality and the proportion of the eventual carcass of the animal classified as very high-value cuts.

Methodology

Many genetic evaluations now incorporate genomic information (Pimentel & Konig, 2012; Meuwissen *et al.*, 2016); the Irish dairy, beef and sheep genomic evaluations all include genomic information. Over-estimation of genetic merit in animals with no performance or progeny information is of growing concern (Koivula *et al.*, 2017). Many possible contributing factors to this bias exist including: (1) there always was bias even in traditional pedigree-based genetic evaluations (e.g. McHugh *et al.*, 2014; Twomey *et al.*, 2020; Ring *et al.*, 2021), (2)

selective genotyping of animals may occur whereby not all available animals are genotyped, (3) preferential treatment of females in the genotyped reference population may exist, and (4) the small bias per generation culminates over multiple generations before self-correction of the animal through phenotypic data on the animal itself or descendants. Confidence in genomic predictions can be impacted when the realised benefits are less than expected based on published genomic evaluations. Hence, this shortcoming is an area of particular interest (Dassonneville et al., 2012; Koivula et al., 2017). Being able to generate genomic predictions that accurately transfer across generations and breeds is also of particular interest (Olson et al., 2012) especially in Ireland given the large diversity in breeds and their crosses; it is likely that sequence data coupled with advanced computational approaches such as machine learning could help deliver better outcomes (Liu et al., 2019). While phenotypic and genomic data are rapidly amassing on routinely recorded traits, the speed with which data on more difficult-to-measure traits are accumulating is not as fast. Such traits of particular relevance to the modern era are those associated with environmental load, efficiency of feed use, and product quality; these are all difficult-to-measure traits and thus the required dataset sizes to achieve accurate genomic predictions using traditional approaches may not be possible (Figure 3). Algorithms to account for the smaller phenotyped (and genotyped) reference population may also be required especially where (imputed) sequence data are available; procedures for the optimal construction of a small reference population are also important. Finally, the accuracy with which the phenotype of an animal can be predicted based on its additive genetic merit is limited by the narrow-sense heritability (i.e. proportion of phenotypic variance attributable to additive genetic effects). Being able to predict non-additive genetic effects (i.e. intraand inter-locus effects) would be advantageous in improving the predictive ability of performance from genomic information with the benefits realised in decision-support tools.

Breeding schemes

The ruminant breeding schemes in Ireland (e.g. McParland *et al.*, 2009) do not actively exploit recent advances in reproductive technologies (with the exception of Al). Four pathways contribute to genetic gain (Robertson & Rendel, 1950): sires to produce sires (i.e. bulls/rams to sire the next generation of elite [AI] bulls/rams), sires to produce dams (i.e. Al and natural mating bulls/rams used by producers to generate female replacements), dams to produce sires (i.e. elite cows/ewes to produce the next generation of young elite [AI] bulls/rams) and dams to produce dams (i.e. cows/ewes in commercial herds). Much of the genetic gain currently achieved is in the sire to produce progeny pathways; simulating an efficient dairy cattle breeding programme,

Schaeffer (2006) documented how over 80% of annual genetic gain in such a breeding programme is achieved via the sire to produce progeny pathways. Much of the further genetic gain will therefore likely be achieved through the dam to produce offspring pathways; this can be realised through a combination of improved selection intensity and reduced generation interval with the improvement in accuracy of selection being achieved mainly through genomic evaluations although more extensive phenotyping, especially as heifers/ewe lambs, could improve the accuracy of selection further. Accurate data collection on individual candidate dams has huge potential to increase the accuracy of selection, especially for high heritability traits. By its very nature, more accurate data collection is likely to be less influenced by random noise, thus possibly contributing to an even higher heritability in itself. Accurate phenotypic data could also, of course, imply deeper phenotyping. One example is the interval from calving to the commencement of luteal activity versus the interval from calving to first service. From a review of the cattle literature, Berry et al. (2014b) reported a mean heritability of 0.149 for the interval to commencement of luteal activity versus a mean of 0.052 for the interval to first service; some of the observed difference could be due to less accurate recording of the latter (e.g. missed oestrus) but also conscious decisions by the producer not to serve a cow even though she was on oestrus. The same principles would exist for activity meters on females. For mass selection, where the animal is selected on the basis of its own phenotype, the accuracy of selection is the square root of the heritability; so, for example, based on a heritability of 0.35 (e.g. milk yield), the accuracy of selection on a single record from an individual would be 0.59 (i.e. $\sqrt{0.35}$); assuming a repeatability of 0.50 (e.g. milk yield), the accuracy of selection for an animal with two or three records would be 0.68 and 0.73, respectively. Moreover, not only would such information on individual females be useful for breeding purposes but it also can have considerable use in day-to-day management decisions.

Opportunities to improve selection intensity in cattle in particular include the use of targeted sexed semen and embryo production. Sexed semen can contribute to genetic gain through increasing selection intensity by only needing to mate a proportion of the genetically elite females in the herd/ flock to generate replacements (Sørensen et al., 2011). The mean of the top 25% of females in a herd/flock is 2.54 s.d. units higher than the mean of the top 75% of females in the herd/flock; based on mean s.d. across Irish dairy and beef herds of €32 (25,549 herd-year between 2016 and 2018) and €25 (56,756 herd-years between 2016 and 2018) for the dairy and beef replacement index, this equates to a difference in the respective index between the top 25% and top 75% of €81 and €64, respectively. All else being equal, this should increase the rate of genetic gain from this pathway by the same amount and that of the entire population (assuming

no changes to other selection pathways) by 11% using the population parameters reported by Schaeffer (2006) for dairy cows. These selected females who become parents of the next generation will also tend to be the younger females (i.e. heifers and ewe lambs); this will contribute to an additional benefit in reducing the generation interval. Combined, the increased selection intensity and a reduction in generation interval of the dam to produce dam selection pathway by 1 yr could accelerate genetic gain by a factor of 1.24 over and above the status quo.

Selection intensity and generation interval can also be improved, particularly in the dams to produce sires selection pathway, with embryo production coupled with genomic selection of the generated embryos. Traditional strategies of multiple ovulation embryo transfer are now being replaced by ovum pick-up combined with in vitro embryo production (OPU-IVP; Pontes et al., 2011); efficient procedures now exist to generate high-quality implantable embryos without the necessity for any hormonal treatment of either the donor or the recipient. One of the main bottlenecks and costs of such breeding schemes are those associated with the recipients. Carefully selecting the implanted embryos based on their genotype can increase the intensity of selection further and reduce the requirement for recipient females. Nonetheless, as selection intensity in particular improves with the exploitation of such reproductive technologies, the risk of inbreeding also intensifies. Genome-derived inter-animal relationships can, however, help mitigate against rapidly accumulating inbreeding. More importantly, genomics can also help focus on the location of homozygosity in the genome and its impact, if any, on subsequent performance (Pryce et al., 2014); this is because inbreeding is unlikely to have an impact on regions of the genome not controlling performance. Several lethal mutations have, for example, been discovered (Cole et al., 2016; Braiek et al., 2021), so caution should be taken when mating carriers. Moreover, given the impact of climate change on weather conditions (and downstream effects like exposure of naive populations to exotic organisms), maintenance of genetic diversity will be key to ensure a robust population; inbreeding erodes genetic diversity.

Although developments in reproductive technologies enable faster genetic gain in the female to progeny pathway, it also provides opportunities to be more selective in the sires used on the females not chosen to be parents of the next generation. Dairying in particular can reap the benefits of increasing the value of calves through the use of beef bulls on the dairy females (Berry & Ring, 2020b) exploiting tools like a dairy-beef index (Fogh, 2016; Berry *et al.*, 2019) to identify such sires. The same is true for beef cows in that sires with more terminal characteristics can be mated to females not destined to become parents of the next generation. Care, however, should be taken of any likely increase in the risk of calving dystocia (Berry & Ring, 2020b) but also the potential impact of beef sires on subsequent dairy cow performance even in the absence of any degree of calving difficulty (Berry & Ring, 2020a).

Decision support

Developments in sensing systems and their use in agriculture will naturally lead to increased volume, velocity, variety, veracity and value (i.e. big data). Decomposing these data into value-creating decision-support tools with crosscompatibility across other such tools will be a major challenge: greater interaction with end-user focus groups will be of utmost importance to ensure that the tool is not only fit for purpose but also reaps a sufficient return on investment for all actors. Artificial intelligence will undoubtedly contribute to the analytical systems underpinning such tools; explainable artificial intelligence (XAI) systems will also have a major role in demonstrating how the solutions have been arrived at and thus can be readily understood (and therefore more accepted) by the end user. It is also likely that more use will be made of federated learning to deal with heterogenous data sources while preserving privacy and security of the data owners.

Whereas many decision-support tools, especially those based on mating advice, tend to predict the expected mean performance, the variability in predictions of the associated risk will also become important. For example, in the development of a sire mating advice system for mating dairy bulls to dairy females, Carthy et al. (2019) predicted the expected progeny merit for the different combinations of male-female matings. With growing access to genomic information, however, it is possible to accurately construct the phased haplotypes of all animals. Such knowledge can be used to calculate the expected variance in progeny genotype (Santos et al., 2019) which can then be used to generate the distribution in expected (total or additive) genetic merit for all evaluated traits (and overall breeding objective). Such a tool could be particularly useful in establishing the risk of calving dystocia for a given mating, especially for beef-on-dairy matings (Berry, 2021). In such circumstances, dairy producers may opt for bulls with a slightly greater mean predisposition to calving difficulty but with a greater likelihood of producing more homogenous calves and thus fewer very large calves which may require veterinary intervention during calving. Growing information on genetic variants with large effects including those associated with infertility (Cole et al., 2016) will also play a pivotal role not only in mating advice programmes but also in personalised management systems.

Personalised management is where the management is optimised to the genotype of the individual. While often heralded as the future, the practice of personalised management or nutrition is well established; a good example of such is the different feeding management in late gestation sheep depending on the number of lambs *in utero* or indeed the differential in

feeding levels and dry length period of cows differing in body condition score. However, generation of predisposition metrics (called polygenic scores in the human sciences; Torkamani et al., 2018), which incorporate both genetic and non-genetic features coupled with more automation on farms, will make personalised management more achievable. Prediction of genetic merit for certain traits can also influence decision rules used in decision-support tools, implying that the decision process is bespoke to the animal. For example, a somatic cell count in dairy cows of >200.000 cells/mL may cause an alert in primiparous cows, but this threshold may lowered to >150,000 if the cow in guestion is known to have genetic predisposition to mastitis: this is akin to patients being asked about family history of certain diseases by doctors when trying to more accurately diagnose ailments. Decision-support tools and personalised management can, however, complicate genetic evaluations. Such personalised management may involve feeding to yield thereby impacting the foundational assumptions of a contemporary group; another example could be the prediction of likely mastitis in which case the producer may try to advert a clinical case and, if successful, no mastitis event will enter the database for use in genetic evaluations. Such personalised management could also be at the level of the herd exploiting herd BLUEs to tailor not only the breeding goal to the herd but also the expected response to selection for each trait given the herd BLUE for that trait (Craig et al., 2018; Dunne et al., 2019; Kenny et al., 2021).

Conclusions

The key steps of a successful animal breeding programmes include: (1) a pertinent and relevant breeding goal, (2) the appropriate breeding objective underpinned by a selection index with sufficient high-quality data from the relevant population (and production systems), (3) an accurate genetic/ genomic evaluation system, (4) an efficient and effective breeding scheme, and (5) a system to disseminate the elite germplasm to the end user; validation of genetic evaluations and breeding objectives is also key. While the current national breeding objectives in Ireland are extensive, suites of traits that will need to be considered more in future ruminant breeding objectives include environmental impact, product quality and animal well-being. Research on how best to incorporate such traits (i.e. phenotyping strategy, genetic evaluations, weighting factors) is underway.

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Special Issue Article • DOI: 10.15212/ijafr-2020-0150 IJAFR • 61(1) • 2022 • 55-86



Irish Journal of Agricultural and Food Research

Ruminant health research – progress to date and future prospects, with an emphasis on Irish research

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Abstract

This review addresses the progress that has been made in ruminant health research over the last 60 yr, with an emphasis on Irish research. The review focuses on the economically important infectious diseases of dairy and beef cattle and of sheep, calf diseases, regulated and non-regulated infectious diseases, lameness, mastitis and parasitoses. The progress to date, current knowledge and future challenges are all addressed. Paradigm shifts have occurred in many of these diseases, the most profound of which is the change from increasing antimicrobial usage (AMU) to the realisation of the challenge of antimicrobial resistance (AMR) and the current reduction in AMU. Another major change in thinking is the move away from focus on the pathogen exclusively towards a more holistic view of the roles of host immunity and adequacy of management. In the last 60 yr, many new diseases have emerged but in parallel many new technologies have rapidly evolved to monitor and control these threats to animal health. Irish research has contributed substantially to improved current ruminant health. The major future challenge is how to manage ruminant health in a OneHealth world where animal, human and environmental health and sustainability are intimately intertwined and interdependent.

Keywords

Beef • dairy • health • review • sheep

Introduction

Given that this is the 60th anniversary of the IJAFR, this paper reviews the progress we have made in ruminant health research over the past half-century, the state-of-the-art today and to horizon scan where developments might take us in ruminant health over the next half-century, where have we come from and where are we going? Both cattle enterprises (dairy and suckler-beef) and sheep are covered. The focus is on animal health, to the exclusion of animal welfare, which is included in the companion paper by Boyle et al. (2022). However, this publication dichotomy does not imply the authors believe these subjects are separate; on the contrary, the clear linkages between animal health, wellbeing and productivity are accepted and improvements in one domain improve other domains. Given the scale of the undertaking, reviewing 60-yr research and projecting forward, much of the focus is Irish or Euro-centric, though not exclusively. The

major, economically important ruminant health issues, as defined by a Delphi study of Irish agricultural stakeholders (More et al., 2010), are addressed in the alphabetical order: calf health (dairy and beef separately), infectious diseases (both regulated and non-regulated [brucellosis, bovine viral diarrhoea (BVD), bovine tuberculosis (bTB), infectious bovine rhinotracheitis (IBR), Johne's disease (JD) and the transmissible spongiform encephalopathies]), lameness and mastitis (with a focus on control; selective dry cow therapy and antimicrobial use), parasitoses (nematodes, liver and rumen flukes and external parasites) and sheep diseases (causes of mortality, lameness, maedi visna, mastitis, ovine pulmonary adenocarcinoma, pestiviruses and Q-fever). Given the importance of antimicrobial resistance (AMR), it is dealt with under the specific major disease of import separately: calf morbidities and mastitis.

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Calf health research

Given that most of the literature on calf health tends to be enterprise-specific, that is, dairy or beef, we have documented this research separately.

Dairy calf health research

In the interests of brevity, only salient issues are addressed here; for broader recently published narratives on dairy calf health, see Mee (2021a) and Lorenz (2021). Each topic is reviewed under current knowledge, future challenges and knowledge gaps.

Perinatal dairy calf health

Perinatal dairy calf mortality rates (death at full term, >260 d, within 48 h of birth) have improved (declined) in Irish dairy herds in recent years (Mee et al., 2008; Ring et al., 2018a). Though difficult to quantify, genetic selection against dystocia, stillbirth and prolonged gestation using functional genetic selection indices (Miglior et al., 2017) has contributed to a reduction in perinatal problems where selection pressure has been intensive enough (Mee, 2021b). In recent years, our knowledge of perinatal health has advanced beyond the peripartum period. For example, our current knowledge indicates that foetal programming and calfhood performance (e.g. Hayes et al., 2021) have significant impacts on lifetime productivity (Berry et al., 2008), reproductive performance (Cushman & Perry, 2019), health (Perry et al., 2019) and longevity (Berry et al., 2008). Sixty years ago, perinatal health research was confined to effects in humans, for example, the Barker hypothesis (Barker et al., 1989).

The day (Borchers *et al.*, 2017; Horvath *et al.*, 2021) and, to a lesser extent, the time (Titler *et al.*, 2015) of calving can now be predicted with commercially available technologies or algorithms (Fenlon *et al.*, 2017). However, these advances are not without problems with some of these technologies (Mee *et al.*, 2019; Voß *et al.*, 2021). While heretofore movement of cows to the calving unit was recommended within 1–2 d precalving (Mee, 2008), recent research has identified a sensitive phase during Stage 1 of calving when movement can be detrimental to cow and calf calving outcomes (Proudfoot, 2019). The behavioural needs of the cow pre-calving have now been incorporated into novel calving accommodation strategies which provide optional seclusion in group calving units to facilitate a more "natural" calving (Proudfoot, 2019).

Current knowledge of timed assistance (Schunemann *et al.*, 2011) suggests that early prudent assistance at calving may not be injurious to the calf or adversely affect the dam (Villettaz Robichaud *et al.*, 2017), though replication of such results is needed.

On the perinate side, the impacts of both calving duration and calving difficulty on perinate vitality have been elucidated (Villettaz Robichaud *et al.*, 2017; Mee, 2021c), and various methods of perinatal vitality biophysical profiling have been established (Murray & Leslie, 2013). Calf resuscitation policies have been evaluated (Mee, 2018a) using various techniques (Stilwell *et al.*, 2020), equipment (Ando *et al.*, 2013) and medications (Ravary-Plumioen, 2009) to revive/ resuscitate newborn calves; the simple stratagem of sternal recumbence is still paramount (Uystepruyst *et al.*, 2002). The epidemiology (Raboisson *et al.*, 2013), investigation (Mee, 2020a), immunology (Jawor *et al.*, 2020) and control (Szenci *et al.*, 2021), pathology (Mock *et al.*, 2020) and control (Szenci *et al.*, 2012) of perinatal mortality have all been advanced.

While congenital defects were traditionally documented as case reports (Mee, 1994), increasingly the epidemiology (Whitlock *et al.*, 2008; Romero *et al.*, 2020), pathology (Gehrke *et al.*, 2019) and aetiology (Mee, 1995; Reinartz & Distl, 2017) of such cases are presented so that our current knowledge has advanced from the singular to the population level. Current advances in genetic diagnostics (Sieck *et al.*, 2020) have added greatly to our understanding of the causes of some of these defects and ultimately their prevention. This area is continually evolving as new causes of congenital anomalies are discovered, for example, Schmallenberg virus (Collins *et al.*, 2019).

Our current knowledge of navel antisepsis in newborn dairy calves indicates that when compared to positive controls in recent randomised controlled trials (RCTs), iodine (7%) (the most commonly used product) performed similarly, though not better (Wieland *et al.*, 2017; Bruno *et al.*, 2018), and results were dependent upon environmental hygiene (Fordyce *et al.*, 2018).

Given the importance of colostrum to the health of the newborn calf and beyond the perinatal period, it is not surprising that there has been an explosion in "colostrology" (Lora et al., 2018) regarding, for example, colostrum quality (Quigley et al., 2013) and hygiene (McAloon et al., 2016a, 2016b, 2016c) over the last 60 yrs. In the early days of colostrum evaluation, a colostrometer (measuring specific gravity) was used (Geiger, 2020), but this has now largely been surpassed by the current optical or electronic Brix refractometers (Lopez et al., 2021). Current recommendations on the volume of colostrum to feed dairy calves are based on body weight, but baseline volume is now larger (4 L) than in the past (Geiger, 2020). This probably reflects larger Holstein calves and the need for higher serum Ig concentrations on modern intensive dairy farms. While traditionally suckling the dam was recommended, then nipple feeding, latterly oro-oesophageal feeding has become a recommended method of colostrum feeding (Godden et al., 2009; McAloon et al., 2021). Though laboratory-based tests for evaluation of passive immunity

have been available for decades (e.g. sRID test; McGee and Earley, 2019), recently more practical tests have been developed and compared (Dunn *et al.*, 2018), and thresholds for failure of passive transfer (FPT) are constantly being reevaluated (Lombard *et al.*, 2020). The development of artificial colostrum has been a qualified success with highly variable results (Mee *et al.*, 1996; Geiger, 2020). While the focus of this paper is on health, the companion paper by Boyle *et al.* (2022) has addressed welfare outcomes of FPT.

Currently, snatch calving (immediate removal of the newborn calf from the dam and calving environment) is a recommended management practice on dairy farms to reduce the risk of infection (especially from *Mycobacterium avium* subspecies *paratuberculosis* [MAP]) in the perinate from a contaminated calving environment (Mee, 2020b), though public perception is now causing a re-evaluation of this practice (Beaver *et al.*, 2019; Placzek *et al.*, 2021).

The future challenges in perinatal dairy calf health research stretch from genomics to farm blindness (Mee, 2020b). Given our current knowledge of the adverse effects of foetal programming, we need to be able to modify this programming so that its impacts are beneficial not detrimental. The impacts of environmental and nutritional factors on foetal development and calf survival have been reviewed recently (Mee, 2021a). Advances in genomics will need to target more refined adverse perinatal phenotypes, for example, weak calf syndrome. The enigma of the "unexplained stillbirth" (Mee, 2013) requires further exploration. Specifically, the role of factors not easily diagnosable at routine necropsy examinations need to be examined, for example, genetic, nutritional and management causes. We need reliable, cost-effective automated methods of monitoring both the dam pre- and intra-partum and her at-risk foetus during and immediately after birth. Translating advanced paediatric resuscitation into the calving pen is a real challenge. Routine low-cost screening for a wider range of deleterious inherited mutations should be a norm within both the beef and the dairy industries. Better preventive protocols for navel-ill are required. Cheaper, more consistent quality colostrum supplements/replacers are a requirement where natural colostrum quality can be variable.

Despite 60 yr of research on perinatal dairy calf health, there are still numerous knowledge gaps that we can now identify. The most pressing in the area of perinatal dairy calf health is the development of automated, reliable wearable technologies for calving cows and term/newborn calves and how we can replicate or augment the beneficial properties of natural colostrum.

Young dairy calf health

The major scientific achievements (as detailed hereunder) in young dairy calf health (calves up to approximately 6 mo

of age) over the last 60 vr have, though not exclusively. revolved around the two predominant causes of morbidity and mortality: calf diarrhoea and calf respiratory disease, both in housing and while at pasture. With our current knowledge. we now know that infectious calf diarrhoea is a result of compromised host immunity, infectious challenge and management failure. We have advanced from "white scour" caused by colibacillosis (Wood, 1955) to the recognition of parasites (Cryptsporidium spp., Eimeria spp.) and viruses (e.g. rotavirus, coronavirus) (Caffarena et al., 2021). This knowledge has meant that both preventive and therapeutic protocols are now more broadly based (Lorenz et al., 2011a), with more emphasis on management and less on microbes. This is particularly true of the management of diarrhoea in calves at pasture due to roundworm infestations where targeted selective therapy is now considered best practice (O'Shaughnessy et al., 2015). As in humans, oral electrolyte solutions (ORS) are considered more important than antimicrobial usage (AMU) (Wenge-Dangschat et al., 2020). While maternal vaccination has a role to play, its effectiveness is highly dependent upon colostrum management (Durel et al., 2017). Maintenance of a milk diet during diarrhoea is beneficial for recovery (Lorenz et al., 2011a) and not a cause of diarrhoea, as previously thought. With increasing knowledge of the gut microbiome, the developments of preventive medications (e.g. prebiotics, probiotics, vaccines, coccidiostats) have been major scientific achievements (Cangiano et al., 2020).

As with calf diarrhoea, we have moved on from calf pneumonia being attributed to a "virus" (Maier et al., 2020) to polymerase chain reaction (PCR) tests for specific viruses and bacteria (Hamad et al., 2019). This achievement has allowed targeted respiratory vaccination protocols to be developed for young calves, even in the presence of maternally derived antibodies (Richeson & Falkner, 2020). Calf-side diagnostics traditionally reliant upon clinical inspection, a thermometer and a stethoscope have been supplemented with transthoracic ultrasonography (TUS), (Cuevas-Gómez et al., 2021; Rhodes et al., 2021). The design of purpose-built calf housing, and latterly, calf hutches (first built in the 1970s) and their modification where necessary (e.g. installation of positive pressure ventilation tubes and adjacent preventives, e.g. calf jackets; Roland et al., 2016; Robertson, 2020) have been major advances, especially as herd and calf group sizes have increased (Nordlund & Halbach, 2019).

An apparent increase in abomasal disorders ("abomasal syndrome") in young dairy calves has occurred in the last 60 yr. While traditionally this was attributed to "stress", as in humans, our understanding has now improved and broadened to include multiple management factors, for example, total solid content and osmolarity of liquid diet (van Kruiningen *et al.*, 2009; Burgstaller *et al.*, 2017).

In addition to these well-recognised calf diseases, the last 60 yr have seen the emergence of "new" calf diseases. Examples include bovine neonatal pancytopoenia, congenital defects, cryptosporidiosis (first reported in 1971), haplotype cholesterol deficiency, Hobi-like mucosal disease, SBV-AHS (Mee, 2018b). Rapid advances in modern diagnostics have allowed us to determine the aetiology of these conditions and adopt ameliorative measures. Across all young calf diseases, there have been advances in the development of whole-calf scoring systems to more objectively assess the degree of morbidity (Boyle & Mee, 2021). More recently, wearable sensor technologies have become commercially available allowing, with variable accuracy, monitoring of health, behaviour, growth and disease (Carslake *et al.*, 2021).

At a farm level, the major future challenges in young calf health remain the same in 2021 (Mee, 2018b) as in the 1960s (Leech et al., 1968) with regard to calf diarrhoea and pneumonia. At an industry level, some challenges are global (e.g. AMR, evolving regulatory frameworks, shifting consumer expectations). At a research level, the genetics of calf diseases (Vinet et al., 2018), automated monitoring of health (Kour et al., 2018), "colostrology" (Lora et al., 2018), accelerated growth pre-weaning (Quigley et al., 2018), lifetime sequelae of calfhood diseases (Chuck et al., 2018) and calf welfare (Neave et al., 2018) are all future challenges. With herd size increases continuing in Ireland, calf rearing will become a specialized vertically integrated dairy enterprise for large units while smaller farms will continue with traditional management. This presents challenges for emerging contract calf rearers to maintain calf health at the standards of home-reared calves (Mee et al., 2018).

Rapid development of pen-side diagnostics (e.g. infrared pulse oximetry, real-time thermography, DNA/RNA sequencing) and wearable wellness (implantable) biosensors (e.g. accelerometers, calving sensors, ear fever tags, nanobiosensors; Costa et al., 2021) present a challenge to independent research to provide evidence-based results demonstrating the benefits or otherwise of such technologies. Similarly, 24/7 data collection and storage (the "calf cloud") on feeding, behaviour, welfare and intake via automatic feeders will facilitate pre-clinical diagnosis smart phone alerts of the individual calf and group deviations from expected norms of health and performance (farm-level "big data"; Morrison et al., 2021).

An overarching challenge is to shift the paradigm from disease therapies to better disease prevention.

Currently, we have major knowledge gaps around how to manage infectious calf diseases with diminished AMU. How to develop anti-parasitic immune-modulators or vaccines is a knowledge gap constraining progress in control of cryptosporidiosis and coccidiosis. We need to know more about how to evaluate and alter the microenvironment of calf housing to prevent respiratory disease. Our knowledge of the causal web (pathogenesis) for abomasal disorders is incomplete, a fact emphasised when we try to investigate outbreaks and solve group problems. Our ability to interpret and use the outputs from the multitude of precision livestock farming (PLF) data sources is hampered by the emerging nature of this discipline and our limited knowledge base of its evidenced-based benefits.

Beef calf health research

The most important diseases – diarrhoea and respiratory disease – of beef calves are addressed here. Underlying each of these morbidities is the suckler cow colostrum passive immunity.

Beef-suckler cows colostrum

Colostrum-derived passive immunity is central to the health, performance and welfare of neonatal beef-suckler calves, and economics of beef-farming enterprises. The IgG immunoglobulins are divided into two subclasses, IgG, and IgG_a. IgG1 is selectively transported by the udder from the circulation to the lacteal secretions and is the principal IgG for passive immunisation of the calf. IgG, is more homogeneous than IgG, and is found in high concentrations in bovine serum (McGee & Earley, 2019). The transfer of IgG, from blood to mammary secretions is greater for beef × dairy cows compared to most beef breed types (McGee et al., 2005). First-milking colostrum yield is higher for beef × dairy cows than for beef × beef and purebred beef breeds and higher for multiparous than for primiparous cows, but generally colostrum immunoglobulin concentration is relatively similar for each of the respective categories. Consequently, colostrum immunoglobulin mass (volume × concentration) production in beef cows seems to be primarily limited by colostrum volume (McGee et al., 2005, 2006).

The effect of maternal nutrition during late gestation on colostrum yield is not well documented; however, most studies provide evidence that colostrum immunoglobulin concentration is not adversely affected by under-nutrition (McGee & Earley, 2019). Colostrum immunoglobulin mass ingested relative to birth weight post-parturition is the most important variable determining calf passive immunity. From a practical perspective, research has shown that feeding the beef-suckler calf 5% of birth weight in colostrum volume using a tube feeder within 1 h post-calving, with subsequent suckling of the dam (or a second feed) 6-8 h later, ensures adequate passive immunity, equivalent to a well-managed suckling situation where the calf suckles "naturally" within 1 h after birth, with unlimited access to the dam subsequently (McGee et al., 2006). Compared to older cows, calves from younger cows, especially primiparous animals, have lower serum immunoglobulin concentrations.

Young beef calf health

In a recent study on calf health in Ireland, Todd *et al.* (2018) reported that 20.4% of suckler-beef calves were treated with antibiotics for disease by 6 mo of age. The leading cause of morbidity from birth to 6 mo of age was diarrhoea, accounting for 44% of the disease events. The second and third most frequent causes of morbidity in calves during the first 6 mo of life were bovine respiratory disease (BRD) and navel infection, respectively.

Calf diarrhoea

Calf diarrhoea is one of the main causes of calf morbidity and mortality in suckler-beef herds (Waldner & Rosengren, 2009). In Ireland, calf diarrhoea remains the number one cause of mortality in calves <1 mo of age (Department of Agriculture, Food and the Marine [DAFM], 2019) with rotavirus and Cryptosporidium being the two most commonly identified pathogens. Dehydration, acidosis, impaired growth rate or death are the major consequences (Gunn & Stott, 1998). Although the majority of incidences of calf diarrhoea occur in the first 2 wk of life (Clement et al., 1995; Bendali et al., 1999a, 1999b), diarrhoea can also occur in older calves due to a variety of different enteropathogens. A number of preventive measures have been adopted to control calf diarrhoea. However, changes in management practices, such as better management of colostrum feeding, can help lower the incidence of calf diarrhoea significantly (Clement et al., 1995; Lorenz et al., 2011a, 2011b).

Bovine respiratory disease

Bovine respiratory disease (BRD), a disease of the lower respiratory tract of cattle, has a multifactorial aetiology of infectious agents, host factors, environmental stress factors and their interactions, resulting in bronchopneumonia. Predisposing factors are those that affect the magnitude of the infectious challenge (e.g. overstocking, poor hygiene, inappetence, inadequate ventilation) and those that affect immuno-competence. These include stress, draughts and fluctuating temperatures, poor nutrition and/or concurrent disease. In most cases, it would appear that the primary infective agent is viral, producing respiratory tract damage that is subsequently extended by secondary bacterial infections. Viruses are unaffected by antibiotics; however, antibiotic treatment is usually administered to treat secondary bacterial infections. Vaccines against BRD are available, but their use is not mandatory and the timing of administration can vary.

Bovine respiratory disease is the most prevalent disease of recently weaned beef calves in Ireland, accounting for 34.3% of deaths in calves between 1 and 5 mo old (Murray *et al.*, 2017; DAFM, 2019). In addition, BRD is also the most prevalent disease of recently weaned feedlot cattle in Ireland (Murray *et al.*, 2017; Cuevas Gomez *et al.*, 2020) and

internationally (Delabouglise *et al.*, 2017; Hay *et al.*, 2017; Wilson *et al.*, 2017) and causes substantial economic losses due to decreased animal performance, higher mortality rates and increased costs associated with treatment (Cernicchiaro *et al.*, 2013; Blakebrough-Hall *et al.*, 2020) as well as negatively impacting animal welfare (Lynch *et al.*, 2011; Wolfger *et al.*, 2015a, 2015b; Earley *et al.*, 2017).

Early and accurate BRD diagnosis

Early and accurate diagnosis of BRD is essential to guide more prudent use of antimicrobials, lower relapse rates and reduce animal mortality. Nasal or deep nasopharyngeal swabs, transtracheal or bronchoalveolar lavage samples can be used for virology, bacteriology, cytology and parasitology (Lorenz et al., 2011b). Nonetheless, the diagnosis of BRD remains a challenge due to the lack of an ante-mortem "gold standard" diagnostic method, meaning that delayed and under-detection of BRD is a significant problem. Numerous methods such as auscultation, clinical respiratory score charts (including evaluation of nasal discharge, ear dropping, rectal temperature, cough and so on), and automated behaviour or temperature monitoring systems are used as diagnostic methods for BRD (Wolfger et al., 2015a, 2015b). However, these methods usually fail to detect lung lesions associated with BRD in animals of all ages, often resulting in a variable number of cases going undetected (Leruste et al., 2012).

Respiratory signs can be evaluated using the Wisconsin clinical respiratory score (CRS) (McGuirk & Peek, 2014). The CRS is based on the assessment of five clinical signs including elevated rectal temperature, cough, eye and nasal discharge, and ear position. Each clinical sign is partitioned into four levels of severity (from 0 to 3) where 0 indicates the lowest risk of being sick and 3 with the greatest risk of BRD. It is recommended to treat animals with the respiratory disease if the CRS is ≥5 and to observe calves with scores of 4. Calves with ≤3 are considered clinically healthy. Some of the drawbacks of using scoring systems alone include the subjective nature of ranking the severity of clinical signs as well as the inability to identify animals with sub-clinical BRD (sBRD) (White & Renter, 2009). The detection of sBRD in cattle with lung lesions without showing clinical respiratory signs can only be confirmed using TUS. The combination of CRS with TUS provides a better classification of BRD and sBRD. A recent study performed at Teagasc Grange showed that 18% (28/153) of recently weaned suckler-beef calves (Cuevas-Gómez et al., 2020) had lung lesions that were not detected using the Wisconsin calf respiratory scoring chart in the 28 and 30 d, respectively, post their arrival to the research centre. Beef HealthCheck is an Animal Health Ireland (AHI)led programme which was developed in collaboration with the Irish Cattle Breeding Federation, the DAFM, Meat Industry Ireland and Veterinary Ireland. Thus, for every batch of cattle

slaughtered at a Beef HealthCheck participating factory, farmers will receive a report indicating a disease score relating to any liver and lung conditions present at slaughter.

Novel diagnostics for BRD

New technologies are being used for the identification of viral and bacterial infectious agents causing BRD. Viruses and bacteria associated with BRD are generally diagnosed using culture on Petri dishes, quantitative PCR (qPCR) or mass spectrometry. However, these diagnostic techniques take between several hours and several days to return results and will not identify novel or unknown viruses which may be causing the disease. More recently, two new molecularbased diagnostic techniques for the identification of bacteria and viruses (both known and novel) causing BRD are being used (Johnston et al., 2017; McCabe et al., 2018). The first approach is called 16S rRNA gene amplicon sequencing. Using this technique, Mycoplasma and Pasteurellaceae have been identified, and in addition, a novel bacterium in the Leptotrichiaceae family was detected in lesioned lung tissue from BRD-affected calves (Johnston et al., 2017). The second approach is Oxford Nanopore MinION Sequencing, a molecular nucleic acid sequencing-based technique that is optimised for the diagnosis of viruses causing BRD. McCabe et al. (2018) tested the potential of untargeted nanopore sequencing on the MinION Mk1B for rapid simultaneous identification of a mixture of DNA and RNA viruses that are associated with BRD. McCabe et al. (2018) reported correct simultaneous identification of the combined DNA and RNA viral species involved in BRD by PCR-free rapid (10 min) tagmentationbased library preparation and nanopore sequencing on the portable Oxford Nanopore Technologies MinION Mk1B sequencer. The MinION has the capability of becoming a rapid point-of-care diagnostic test for the identification of viral and bacterial species causing BRD, directly on farm. These new diagnostic approaches will enable prudent antibiotic usage for the treatment of animals affected by BRD.

AMR and calf health

Antimicrobial resistance is currently recognised as one of the most challenging problems for human and animal health. The use and misuse of antimicrobials can contribute to the development of antimicrobial resistance (FAO, 2016; O'Neill, 2016). In a recent stakeholder survey in Ireland, AMR was ranked first by farmers and professional service providers with respect to the dairy and beef fattener/finisher sectors (Meunier *et al.*, 2020). A recent study quantified AMU and identified specific life stages, and diseases within calves, including dairy and beef animals (Earley *et al.*, 2019). A total of 123 (79 beef and 44 dairy) farms, comprising 3,204 sucklerbeef calves and 5,358 dairy calves, representing 540,953 and 579,997 calf-days at risk, respectively, were included in the

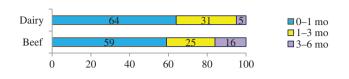


Figure 1. Proportion of antimicrobial treatments (%) for suckler-beef and artificially reared dairy calves from birth to 6 mo of age.

study. All calves were raised on farm of origin and most of the studied herds were closed herds. In this study, only animals showing signs of disease were treated with antimicrobials and no mass administration of antibiotics was practised. The highest risk period for disease in the study was between birth and 1 mo of age, with approximately two-thirds of all disease events occurring during this time period (Figure 1).

Non-regulated infectious diseases

The landscape of cattle disease control programmes has altered over the past decades. Previously control programmes focussed solely on regulated diseases, for example, bTB (More & Good, 2006), bovine brucellosis (Hayes et al., 2009) and transmissible spongiform encephalopathies (TSEs; Sheridan et al., 2005). The absence of a coordinated approach to nonregulated disease control was highlighted by More (2007, 2008), and a move from government-led disease eradication programmes to a public-private partnership approach was proposed. The European Animal Health policy provided the stimulus for this change; "prevention is better than cure" (European Commission, 2007). The formation of AHI was central to this change. AHI is an industry-led, not-for-profit partnership between all key stakeholders of animal health, including livestock producers, processors, representative farming organisations, service providers and DAFM (More et al., 2011). A Delphi study was conducted to establish the priority order, and three biosecure diseases were highlighted for priority: bovine virus diarrhoea (BVD), IBR and JD (More et al., 2010).

Bovine virus diarrhoea (BVD)

Bovine virus diarrhoea virus (BVDV) is an economically important pathogen and is endemic in many countries worldwide (Ridpath, 2010; Richter *et al.*, 2019) and across Europe (EFSA, 2017). The ability of the non-cytopathic biotypes to establish a lifelong persistent infection of the foetus prior to 120 d of gestation is a key feature in the epidemiology of the disease, with both persistently infected (PI) and transiently infected (TI) animals playing a role in disease propagation (Houe, 1999). In Ireland, BVDV was first reported in ruminants during the 1970s (Hamilton & Timoney, 1973). The work conducted during the 1990s indicated that a high proportion of diagnostic samples from feedlot cattle was positive for BVDV (Healy *et al.*, 1993). National figures generated between 2005 and 2008 by the Central Veterinary Laboratory on diagnostic submissions reported seropositivity between 64% and 69%. Whereas herd-level seroprevalence of 98%–99% was reported in nonvaccinated herds in Ireland (Cowley *et al.*, 2012) and Northern Ireland (Cowley *et al.*, 2014).

Much of Europe has been subject to varying national or regional eradication programmes over the past two decades (Lindberg & Alenis, 1999, 2006; Synge et al., 1999; Houe et al., 2006; Ståhl & Alenis, 2012; Booth et al., 2016; Wernike et al., 2017; Richter et al., 2019), with a number of Scandinavian countries achieving effective eradication (Bitsch et al., 2000; Hult & Lindberg, 2005; Valle et al., 2005; Norström et al., 2014). Earlier programmes were based on an initial herd serological screen followed by investigations to identify PI animals (Lindberg & Alenis, 1999, 2006; Synge et al., 1999; Ståhl & Alenis, 2012). The advent of identification tags that facilitated the collection of a tissue tag sample has paved the way for more recent eradication programmes in Germany (Wernike et al., 2017), Switzerland (Presi et al., 2011), Ireland (Barrett et al., 2011; Graham et al., 2014, 2015) and Northern Ireland (Charoenlarp et al., 2018). Prior to embarking on an eradication programme, it was estimated that BVD was costing €102M annually in Ireland (Stott et al., 2012), with the estimated annualised benefits of eradication far exceeding the cost by multiple factors for all herd types.

The Irish BVD eradication programme

From January 2013, all calves born in Ireland were required to undergo tissue tag testing for the presence of BVD viral antigen (Graham et al., 2014). The science and policy of BVD is guided by AHI's BVD technical working group (BVD TWG), while the BVD implementation group (IG), representing the financial, advisory and farming organisations stakeholders, has steered the programme. Perhaps somewhat ironic, the first step in managing a non-regulated disease is to regulate it, and the BVD Order 2012 (DAFM, 2012) set out the legal requirement to partake in the compulsory programme. The regulations have been revised over the period to reflect the evolving control programme (DAFM, 2014, 2017, 2020b). Herd owners are encouraged to remove positive calves, and supports are available for herds complying with the programme requirements (DAFM, 2021a, 2021b). As with similar BVD control programmes (Wernike et al., 2017), progressive control measures have been implemented overtime to improve compliance with the programme. Herds that fail to partake in testing and herds that disclose positive animals are subject to herd movement restrictions (AHI, 2021a). Since 2016, herds disclosing a BVD virus-positive animal have been required to undergo a mandatory investigation to determine

the likely infection source (Graham *et al.*, 2021). In addition, in 2021, this investigation also extends to a whole herd test for all animals and vaccination of eligible females for a 2-yr period, to reduce the risk this herd poses to itself and others (AHI, 2021a). The prevalence of BVD in the national herd has reduced considerably in Ireland since 2013. Herd prevalence reduced from 11.27% of breeding herds in 2013 to 0.53% in 2020 (AHI, 2021b).

Factors influencing the prevalence of BVD

Herd level and animal factors have been demonstrated to influence the prevalence of BVD within the cattle population. Research conducted early in the eradication phase in Ireland highlighted the importance of prompt removal of positive calves (Graham et al., 2015). Herds that retained positive calves the longest (>170 d) were 4.42 (confidence interval [CI], 3.06-6.35) times greater risk of being classified a positive herd the following year compared with herds that did not disclose a BVD positive the previous year. Dairy herds display a higher odds of BVD infection compared with beef herds (Presi et al., 2011; Barrett et al., 2020; van Roon et al., 2020). Herd size was reported as a significant factor in both Ireland (Graham et al, 2015) and Northern Ireland (Charoenlarp et al., 2018). Data collated in the Irish programme indicated the odds increase by 1.95 for each 2.7-fold increase in herd size (Graham et al., 2015). The movement of animals is an important influence on BVD risk, and in Ireland, there is a large number of farm-tofarm movements annually (McGrath et al., 2018). The risk of BVD infection disclosure was higher in herds that introduced animals (OR, 1.41; CI, 1.18-1.69) or participated in shows or marts (OR, 1.45; CI, 1.10-1.91) compared with those that did not (van Roon et al., 2020). The infection pressure within the neighbourhood has been evaluated and is considered an important risk factor in both Ireland (Graham et al., 2016) and Northern Ireland (Charoenlarp et al., 2018), and the odds ratio associated with any BVD-positive neighbour early in the Irish compulsory programme was 1.92 (CI, 1.37-2.7) compared with herds with no positive neighbouring herd.

Future prospects – the pathway to BVD freedom

In order to progress to a disease-free status enhanced control measures, with immediate movement restrictions, whole herd testing and compulsory vaccination have been introduced in 2021 to ensure Ireland can meet the definition of BVD freedom under the new European Animal Health Law (AHL; AHI, 2021a). The new AHL came into force from April 2021 and makes provision for national eradication programmes to be officially approved and for BVD-free countries to be formally recognised (European Commission, 2016, 2020a). Planning is underway to pursue official programme approval and, in due course, to apply for recognition of freedom under the se regulations by 2023. To achieve BVD freedom under the

AHL, Ireland must achieve 18 mo without a confirmed case of BVD, with 99.8% of bovine holdings, covering 99.9% of the bovine population, categorised as negative herd status, and vaccination against BVD has been prohibited for bovine animals (European Commission, 2019). Once BVD-free status is obtained, the use of vaccination may be authorised in the event of a disease outbreak.

Infectious bovine rhinotracheitis (IBR)

Infection with bovine herpes virus 1 (BoHV-1) is economically important (Sayers, 2017), occurs worldwide (reviewed by Ackermann & Engels, 2006) and is endemic in Ireland (Cowley et al., 2012; Martinez-Ibeas et al., 2015; Sayers et al., 2015; Sayers, 2017). Following primary infection, a lifelong latent infection is established if the animal survives (Ackermann et al., 1982), and reactivation may occur under stress and lead to episodic excretion of virus (reviewed by Muylkens et al., 2007). While the reproductive syndromes were described in the 19th century in Europe (reviewed by Ludwig & Gregersen, 1986), the respiratory form (IBR) was first described in the United States (Schroeder & Moys, 1954) and subsequently in Europe (Gründer et al., 1960). Infection with BoHV1 was first described in Ireland in 1971, with 12 further outbreaks recorded by the Central Veterinary Laboratory until 1992 (Moore et al., 2000). Estimates of prevalence were historically low with a 9% seroprevalence reported in feedlot cattle during the 1980s (Gunn & Wilson, 1991). More recent studies have suggested that prevalence has increased (O'Grady et al., 2008; Cowley et al., 2011), with Sayers et al. (2015) reporting 80% of bulk milk samples test positive for BoHV1. Reproductive syndromes have been detailed by Graham (2013), and reduced milk yields reported by Stratham et al. (2015) and Sayers (2017). Economic modelling indicated that profitability was reduced by €60 per cow annually where the dairy herd was classified as seropositive. At 29 cents per litre, this equated to a 22% reduction in profit (Sayers, 2017).

Since its establishment, AHI has viewed IBR as a priority disease (Graham et al., 2013). An IBR eradication programme will be important to support the health status of live exports within Europe and worldwide. A recent study conducted by Hanrahan et al. (2020) suggests that potential costs of the absence of an IBR eradication or control programme could be in excess of €100 million per annum. The Terrestrial Manual of the OIE (OIE, 2021) outlines the requirements for a country to qualify for disease-free status, while the Commission delegated Regulation (EU) 2020/689 (European Commission, 2020a) prohibits vaccination and sets out the requirement to achieve 99.8% of bovine establishments, representing at least 99.9% of all cattle are free from BoHV-1. Eradication programmes have been successful elsewhere in Europe (reviewed by Ackermann and Engels, 2006). Nonetheless, the challenge to move to

eradicate IBR in Ireland is clear, especially given the high seropositivity in Irish cattle herds. Currently, a national IBR programme is under consideration by the IBR IG, led by AHI, and the IBR TWG is developing and refining a proposed programme. Modelling studies, funded by DAFM, are being conducted to investigate the epidemiology of BoHV-1 infection in Irish herds (Brock *et al.*, 2020). Further research, including abattoir and bulk milk tank surveillance, is being undertaken presently by AHI and DAFM. Ultimately, it will be the stakeholders of the IBR IG who decide as to whether a national eradication programme is undertaken or not.

Johne's disease (JD)

Johne's disease is a chronic infectious disease, caused by infection with "MAP"; it is characterised clinically by chronic continuous or intermittent watery diarrhoea. Clinical disease is the tip of the iceberg (Whitlock & Buergelt, 1996); pre-clinical animals are infectious, and the aim of a control programme is to identify and remove pre-clinical infection from herds and prevent exposure of young calves in particular from infection. Economic losses are associated with its occurrence (Richardson & More, 2009), and McAloon et al. (2016a, 2016b, 2016c) outlined the reduction in milk yield associated with JD positivity. Only limited reports of JD were notified to DAFM up to the year 1992 (92 cases), suggestive that JD was not prevalent before the introduction of the European Single Market when controls on imported bovines were relaxed (Good et al., 2009). A further 232 cases were notified to DAFM between 1995 and 2002 (Good et al., 2009). O'Doherty et al. (2002) highlighted the risk of disclosing JD in imported cattle, as 36% of 36 herds had disclosed at least one enzyme-linked immunoassay (ELISA)-positive imported animal. Based on a serological survey in 2005, the estimated animal-level prevalence was 3% while the herd-level prevalence was 20% (Good et al., 2009). More recently, McAloon et al. (2016a, 2016b, 2016c) reported that the probability of a herd containing at least one truly JD-positive animal in Irish dairy herds was 28% (CI, 23-34%). A comprehensive review conducted in Europe suggested variation in animal-level prevalence, with the true prevalence estimated at 20%, with some countries considerably lower between 3% and 5% (Nielsen & Toft, 2009). Management practices relating to dry cow and calving pen management have been highlighted as important risk factors for JD infection (McAloon et al., 2017), while a survey of management practices on Irish dairy farms highlighted that the presence of risk factors associated with JD transmission is frequently observed on Irish farms (Kennedy et al., 2014).

The Irish Johne's Control Programme (IJCP)

JD control programmes have been initiated worldwide (Sockett, 1996; Geraghty *et al.*, 2014; Whittington *et al.*, 2019), often in response to economic pressures and potential public

health implications. The science of the JD control programme in Ireland has been guided by the JD TWG of AHI and by disease control modelling (Sergeant *et al.*, 2018). The IJCP is a voluntary national programme and is managed by AHI under the guidance of the JD IG (Animal Health Ireland, 2021c). The objectives of the programme are addressed through a combination of risk assessment, voluntary assurance and national surveillance (Jordan *et al.*, 2020). The IJCP enables participating herd owners to have increasing confidence in the absence of infection in their herds and to achieve significant control or elimination, and it underpins the quality of Irish dairy and beef produce in the international marketplace. The programme provides a long-term approach to the control of JD in Ireland (Gavey *et al.*, 2021).

Regulated infectious diseases

The Department of Agriculture, Food and the Marine (DAFM) is the competent authority responsible for the implementation of national and European Union (EU) legislation relating to regulated disease programmes in Ireland. The so-called "regulated" diseases include exotic diseases which are not present in Ireland and for which there is a legislative basis for their exclusion and elimination in the event of an outbreak, such as foot-and-mouth disease. There are also those diseases which, for public health and trade reasons, are also regulated and for which there are national eradication programmes. Bovine Tuberculosis (bTB), brucellosis and bovine spongiform encephalopathy (BSE) have considerable public health and trade implications, and DAFM has made substantial commitments to their eradication over the years. The delivery of these eradication programmes has been underpinned by evidence-based research carried out in Ireland.

Bovine tuberculosis

Bovine TB is a chronic infectious disease caused by *M. bovis* which affects cattle, several domestic and wildlife mammal species as well as humans (O'Reilly & Daborn, 1995). The main concerns regarding bTB relate to its economic losses to the cattle industry and government due to losses in productivity, trade restrictions and control costs (Zinsstag *et al.*, 2016). A voluntary bTB eradication programme commenced in Ireland in 1954, which became compulsory in 1962 (Good, 2006). Considerable progress was made in the early years of the programme, but this progress stalled from the mid-1960s. In late 1980s, DAFM identified a lack of scientific evidence in the development of the policy which underpinned the bTB eradication and so the TB investigation unit was established at University College Dublin in 1988. This later evolved into the Centre for Veterinary Epidemiology and Risk Analysis (CVERA).

Extensive research has been conducted on herd-level risk factors for bTB in Ireland. Over a broad range of studies,

three factors have consistently placed herds at the greatest risk of being diagnosed with bTB, namely herd size, location (including bTB prevalence in the area) and bTB history (More & Good, 2015). Irish research has provided conclusive evidence in support of badgers playing an important epidemiological role in the epidemiology of cattle bTB in Ireland (Martin *et al.*, 1997; Griffin *et al.*, 2005). The transmission of bTB between badgers and cattle is believed to occur through both direct and indirect transmission routes (More & Good, 2006; Ward *et al.*, 2010; Corner *et al.*, 2011). Badgers are considered to be a maintenance host with spillback to cattle – essentially, an upstream driver of infection (More, 2009).

In light of this evidence, Ireland has implemented a national programme of badger culling, specifically to reduce badger density in areas with chronic problems of bTB in cattle herds (Byrne *et al.*, 2013). Culling is initially in the environs of the affected farm, but this may be extended up to 2 km beyond the farm boundary (Byrne *et al.*, 2013). In contrast to UK findings (Pope *et al.*, 2007; Prentice *et al.*, 2019), this culling has not led to badger perturbation and increased TB risk (Olea-Popelka *et al.*, 2009).

There has also been a comprehensive research programme on the development of bTB vaccines for badgers over the years. Initial studies were mainly pen-based experiments to determine if the BCG vaccine had a protective effect against bTB in badgers (Corner *et al.*, 2009). A recent field study concluded that vaccination matched targeted badger culling in four counties in the control of bTB in Ireland (Martin *et al.*, 2020). Such findings have directed the programme away from badger culling to badger vaccination to reduce the risk of bTB from badgers to cattle.

The gamma interferon test, as an ancillary test, has been used in high incidence herds to uncover any residual infection and has laterally been used as a quality control tool to monitor the effectiveness of tuberculin testing at the herd level (Clegg *et al.*, 2016).

The DAFM has outlined the ambition to eradicate bTB by 2030. However, a recent review has concluded that this is not considered likely without additional measures in the areas of addressing the bTB risks from wildlife, implementing additional risk-based cattle controls and enhancing industry engagement (More, 2019).

Bovine brucellosis

Brucellosis in cattle is caused by *Brucella abortus*. Brucellosis is widespread globally and affects the reproductive tract, resulting in abortion in females and infertility in males. It is a zoonosis, and infection occurs in humans through contact with infected animals or their body fluids or via consumption of unpasteurised dairy products. Disease in humans can range from asymptomatic infection to chronic problems including fever, arthritis, endocarditis and bone lesions. A national brucellosis eradication scheme commenced in 1966. A programme using a combination of vaccination, serological testing and anamnestic testing using Br. abortus strain 45/20 vaccine (Cunningham & O'Connor, 1971), and the slaughter of reactors made considerable progress towards eradication. By the mid-1980s, the number of herds being restricted for brucellosis had been reduced to between 300 and 500 annually. However, prior to final eradication being achieved, the programme was relaxed, with the discontinuation of vaccination in 1984, the removal of the annual herd test (1986) and premovement test (1988). A dispute with veterinary practitioners and the expansion of the national suckler herd in the early 1990s were thought to have led to the increased spread of brucellosis (Sheahan *et al.*, 2006).

In 1998, a renewed effort to eradicate brucellosis was commenced. These measures included the introduction of a 30-d compulsory pre-movement test, a full round of annual herd serological testing, rapid depopulation of infected herds, lime treatment of cattle slurry in infected herds to kill any brucella bacteria present, improved diagnostic tests for both milk and serum samples, extended rest periods particularly where contiguous herds were infected and serological testing of cull cows at slaughter (Sheahan et al., 2006). Considerable progress was made in reducing the prevalence of brucellosis over the following 8 yr, until the last recorded case of brucellosis was diagnosed in Ireland in 2006 (Anon., 2021). In the years subsequent to 2006, the intensity of the programme was reduced with the gradual removal of the intensified herd serological screening programme and pre-movement tests. In recent years, passive surveillance provided by the Regional Veterinary Laboratory (RVL) network and the cull cow monitoring programme have evolved as the main elements of the surveillance programme for brucellosis in Ireland. Following the declaration of Brucellosis freedom in 2009, the post eradication surveillance was reviewed and incrementally reduced. However, until 2016 up to 250,000 cows were sampled, which prompted an analysis to devise a more targeted approach having demonstrated the suitability of the Irish cull cow serological sample archive as a basis for establishing countrywide freedom from infection, and, more generally, provided a roadmap for how such surveillance resources could be used in Ireland more efficiently to provide assurance of freedom and to calculate prevalences for a range of endemic diseases (Tratalos et al., 2018).

Bovine spongiform encephalopathy

Bovine spongiform encephalopathy (BSE), a progressive neurodegenerative disorder of adult cattle, was first recognised in the United Kingdom in 1985 (Wells *et al.*, 1987) and the first case was diagnosed in Ireland in 1989 (Bassett & Sheridan, 1989) (Figure 2). The disease is caused by the feed-borne transmission of an infectious prion protein agent (Wilesmith *et al.*, 1988). In 1989. BSE became a compulsory notifiable disease by S.I. No. 61 of 1989 (Diseases of Animals Act (Bovine Spongiform Encephalopathy) Order 1989). Ireland adopted a robust approach to the eradication of BSE from 1990 where a policy of herd depopulation was applied, which was over and above the approach adopted in other European countries, where only the birth cohorts and progeny of confirmed positive cases were culled. The occurrence of BSE was one of the main driving forces behind the European legislation which required the development of national bovine registration and movement databases to facilitate the tracing of progeny and birth cohorts of BSE cases. In 1990, there was an initial ban on the feeding of animal protein to ruminants. In 1996, the occurrence of a new variant CJD in the United Kingdom was linked to BSE (Will et al., 1996) and created considerable anxiety among European consumers. As a result, an enhanced feed ban came into effect in 1996.

In 2001, the EU feed ban came into place, which banned the inclusion of processed animal protein in farmed animal feed. In 2001, all casualty, emergency slaughter and fallen animals over 24 mo of age and all healthy animals slaughtered for human consumption over 30 mo of age were tested for BSE, which was the basis of the active surveillance system for BSE. In 2009, these age limits increased to 48 mo for all categories. The age threshold for testing healthy animals slaughtered for human consumption over 30 mo increased to 72 mo in 2011 and was removed altogether in 2013.

Since 1989, there have been 1,662 confirmed cases of BSE in Ireland (Figure 2), with the greatest number of cases confirmed in 2002 (n = 333), which coincided with the introduction of the active surveillance programme. A spatio-temporal analysis of BSE in Irish herds was carried out from 1996 to 2000. The risk of a herd having a case of BSE increased with increasing herd size and was higher for mixed and dairy herds than for beef-suckler herds. Using the spatial scan statistic, clusters of BSE cases were identified in counties Monaghan, Wexford and Cork, with evidence of spatial association between cases and some large feed suppliers (Sheridan et al., 2005). Although there was a marked decline in the incidence of BSE following the various enhanced controls on animal feed, BSE cases continued to occur in animals born after the various enhancements to the feed ban, the so-called born after the reinforced feed ban or BARB cases. An analysis of such cases concluded that the clustered spatial pattern of Irish BARB cases, and the finding that dairy herd type is a significant risk factor (as was the case for the earlier two phases of the epidemic), is evidence against the hypothesis that BARB cases arise spontaneously and is supportive of the hypothesis of locally distributed feedborne exposure (Ryan et al., 2012).

A wider study carried out by European Food Safety Authority (EFSA) concluded that the BARB cases were related to

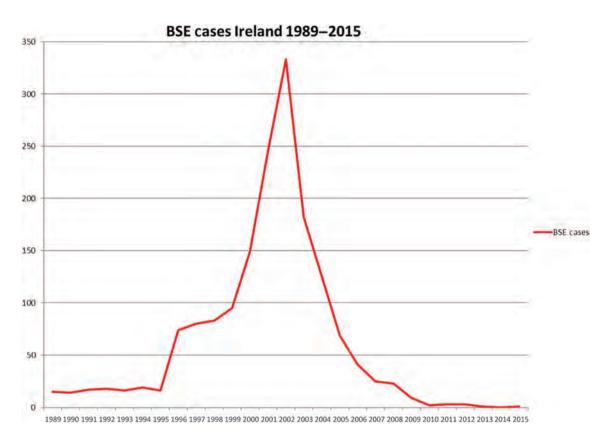


Figure 2. BSE cases in the Republic of Ireland (1989-2015).

historic exposure to contaminated feed, and the data are consistent with exponential decline from epidemic peak to zero (Ricci *et al.*, 2017). In recent years, Ireland has had one case of classical BSE in 2015 in a 2010 born cow and two cases of atypical BSE in 2017 and 2020 in 18-yr-old and 14-yr-old cows, respectively. Atypical BSE is considered a spontaneous pathological change in all cattle populations at a very low rate and has only been identified in older cattle. It occurs spontaneously in cattle, which is in contrast to classical BSE which is associated with the ingestion of prion material. Ireland achieved the OIE BSE negligible risk status in 2021, which was 11 yr after the birth of the last classical case in 2010. Bovine spongiform encephalopathy negligible risk status represents the lowest level of BSE risk status and is of importance in accessing international markets for Irish beef.

Lameness research

Bovine lameness is a major global problem that severely impacts cow welfare (Shearer et al., 2013), longevity (Booth

et al., 2004), fertility (Garbarino et al., 2004) and milk production (Bicalho et al., 2008), causing huge economic loss (\$11B in the US; Kang et al., 2021) and threatening the sustainability of the entire dairy sector. Limited studies on lameness in beef herds report prevalences of below 3%, but this is likely an underestimation (Fjeldaas et al., 2007). This review focuses on lameness in dairy herds only. The worldwide prevalence of dairy cow lameness is approximately 26% (Cook, 2016), but rates as high as 63% have been reported in indoor systems (von Keyserlingk et al., 2012). Lower rates are reported for pasture-based systems; Irish research has documented lameness rates of between 6% and 15% (Somers et al., 2015; O'Connor et al., 2020; Crossley et al., 2021). Herd-level risk factors for lameness in indoor systems include environmental factors related to housing design, cubicle size and comfort, and standing times (Espejo & Endres, 2007; Sarjokari et al., 2013; Solano et al., 2015). Risk factors in outdoor systems differ, with a greater focus on roadway infrastructure and cow handling on roadways (Chesterton et al., 1989, Ranjbar et al., 2016). Individual cow level risk factors are similar for both systems and include parity, genetics and body condition score (Solano *et al.*, 2015).

Until recently, compared with other major health concerns of dairy cows such as fertility and mastitis, lameness has been under-researched (Huxley, 2012), possibly because its prevalence may have been underestimated, and the associated costs are often not well understood (Dolecheck & Bewley, 2018). In recent years, however, a greater appreciation for the multiple and severe impacts of lameness has resulted in greater research focus in this area.

A major advancement in our understanding of lameness concerns its pathogenesis. Previously, the development of claw horn lesions was explained by the "laminitis" theory; high levels of concentrate feeding result in ruminal acidosis and consequent inflammation throughout the body, including in the laminae of the corium which attach the pedal bone to the hoof wall (Maclean, 1965; Vermunt & Greenough, 1994). While it is clear that lameness and ruminal acidosis are linked, research to date does not support a causal relationship (Danscher et al., 2010). It is now understood that the causes of lameness involve a number of factors acting synergistically. Enzymes released at the time of parturition degrade connective tissue in the reproductive tract to allow parturition to occur but also affect the connective tissues that hold the pedal bone within the hoof capsule. Consequently, the connective tissues weaken (Tarlton et al., 2002), allowing the pedal bone to sink within the hoof capsule and damage the layer of hornproducing germinal cells beneath, resulting in the formation of defective horn sole. Additionally, environmental factors that increase the standing time of the cow or the forces acting on the hoof increase pressure in this area (Cook & Nordlund, 2009). Finally, changes to the structure of the hoof, including thinning of the digital cushion in cows with low BCS (Bicalho et al., 2009) and new bone formation on the distal phalanx, as a result of lameness episode (Newsome et al., 2016) result in a hoof that is vulnerable to external pressures. The structural changes that occur in the hoof following a lameness episode explain why the risk of a cow becoming lame is far greater for a cow that has had a previous lameness episode (Randall et al., 2018) and in older cows (Browne et al., 2021) which highlights the critical importance of preventing lameness occurring in the first instance.

A significant body of Irish research has examined the effects of various management strategies on hoof health and cow mobility. Increased comfort in cubicles improved claw health in heifers (Leonard *et al.*, 1994) and overcrowding had a negative impact (Leonard *et al.*, 1996). Cows kept on out-wintering pads during the dry period did not experience worse hoof health or lameness (O'Driscoll *et al.*, 2008), and yearling heifers kept on an out-wintering had reduced limb lesions (Boyle *et al.*, 2008). Hoof health and mobility were improved in cows that were milked once a day (O'Driscoll *et al.*, 2010)

because cows had more opportunity to rest. Nutritional management of grazing cows also impacts mobility; certain aspects of mobility were worse in cows that did not receive an adequate daily herbage allowance, possibly because sub-optimal nutrition resulted in a thin digital cushion (O'Driscoll *et al.*, 2015).

Recent research has demonstrated the huge importance that early detection and treatment of lame cows has in ensuring their recovery. Cows that are detected earlier in the course of the disease are far more likely to make a full recovery (Thomas *et al.*, 2016). This is of particular relevance to Ireland, as a recent study (N. Browne, personal communication) revealed that the vast majority of Irish farmers do not engage proactively in mobility scoring of cows, thus severely limiting their ability to minimise the impacts of lameness on the productivity and welfare of their herds.

Research has shown the benefits that non-steroidal antiinflammatory drugs (NSAID) have in the treatment of lameness, reducing pain (Wagner *et al.*, 2017; Warner *et al.*, 2021) and improving recovery rates (Thomas *et al.*, 2015). However, the use of NSAID in the treatment of lame dairy cows in Ireland is low, with only 3% and 8% of farmers reporting their use in the treatment of mildly and severely lame cows, respectively (N. Browne, personal communication). Using a block on the unaffected claw of lame cows also improves recovery (Thomas *et al.*, 2015), though it is not currently clear how widely blocks are used in the treatment of lame cows in Ireland.

The role of genetics has recently come to the fore also. Previous research has demonstrated that genetics play a significant role in the likelihood of a cow becoming lame (Zwald *et al.*, 2004) and recent Irish research supports this (Ring *et al.*, 2018b; O'Connor *et al.*, 2020; Browne *et al.*, 2021). Therefore, it is likely that an increased emphasis on lameness traits in breeding programmes could significantly reduce herd lameness.

As agriculture becomes increasingly sensor based, so too has the area of lameness detection. A number of methods exist for automated detection of lameness in cows, including accelerometers, pressure-sensing mats and cameras (Kang *et al.*, 2021). Problems remain with these systems, however, including cost and lack of sensitivity and specificity, which thus far have limited their use on farms.

Reducing lameness prevalence is critical to improving cow welfare, the importance of which is highlighted in Ireland's recently published first Animal Welfare Strategy (DAFM, 2021c). Although Ireland's 10% herd-level lameness prevalence (Crossley *et al.*, 2021) is markedly lower than many other countries, it nevertheless indicates that a significant proportion of cows are suffering unnecessarily and failing to realise their full production potential because of pain and reduced mobility. The dairy sector is under increasing

scrutiny from a cow welfare perspective (Wolf *et al.*, 2016) and demonstrating that the Irish dairy production system is sustainable and welfare friendly is vitally important to maintain consumer confidence. It is also key to maximise market returns for increased production in competitive markets worldwide (DAFM, 2015).

The European Green Deal aims to overcome the threat of climate change and environmental degradation by making the economy of the EU sustainable. As part of this, the 2030 Climate Target Plan targets a 55% reduction in greenhouse gas emissions by 2030 (European Commission, 2020b). Given that lameness can significantly increase the environmental impacts of milk production (Chen et al., 2016; Mostert et al., 2018), it is vital that reducing lameness is prioritized as a means by which this target can be reached. The Farm to Fork Strategy targets a 50% reduction in the sales of antimicrobials for farm animals by 2030 (European Commission, 2020c). Lameness is one of the top reasons for antimicrobial use in dairy cows (Obritzhauser et al., 2016; Redding et al., 2019). Currently, antibiotics are the most commonly used medication in the treatment of lame cows on farms in Ireland (N. Browne, personal communication); further research investigating the reasons underlying this is required. Reducing lameness within herds is key to reducing antimicrobial use, but it is also critically important that those involved in the care of lame dairy cows receive correct training and guidance on appropriate treatments such as hoof paring.

Scientific progress over recent years has greatly improved our understanding of how and why lameness develops. Consequently, we are now well equipped to prevent, effectively detect and treat it. While many areas of lameness undoubtedly require further study, we nonetheless have much of the knowledge required to reduce its prevalence in Irish herds; therefore, it is the implementation of lameness prevention and management strategies on farms that is urgently required.

Knowledge gaps remain. The role of NSAIDs in the treatment of lameness in pasture-based herds has not been researched to date, and an understanding of their current low level of use is lacking. Investigation of appropriate management systems to prevent the first time occurrence of lameness, particularly in heifers, is needed. Further research is required to optimise automated lameness detection methods. A barrier to further research is the current lack of consistently recorded highquality claw lesion and lameness data, such as that that exists for the recording of somatic cell count (SCC). Huge scope exists for improvement in this area.

Mastitis research

The purpose of this section is to review the research on mastitis control, selective dry cow therapy, AMU and AMR.

Mastitis is one of the most common diseases of dairy cows and one of the most economically important (Dohoo *et al.*, 2011; Oliveira & Ruegg, 2014).

Mastitis can be caused by bacteria from different sources. Environmental mastitis is caused by bacteria present in the cows' environment (e.g. manure, bedding material) such as *Streptococcus uberis, Escherichia coli, Strep. dysgalactiae,* among others (Cobirka *et al.*, 2020). Contagious mastitis occurs when a healthy teat comes in contact with an infected gland or milk, mainly during milking through the milking cluster or the milker's hands (Neave *et al.*, 1969; Cobirka *et al.*, 2020). The most common contagious pathogens are *Staphylococcus aureus* and *Strep. agalactiae*.

Mastitis control

Dodd *et al.* (1969) and Neave *et al.* (1966, 1969) developed fundamental work on our understanding of mastitis control. Their work revealed that the average proportion of cows infected in a herd could be reduced by 75% when reducing the new infections and the average duration of infections by 50% (Dodd *et al.*, 1969). Therefore, these are the two pillars of mastitis control.

The research by Dodd *et al.* (1969) led to the development of a systematic mastitis control plan referred to as the "five-point" plan (Ruegg, 2017). It consists of effective post-milking teat disinfection, appropriate treatment of clinical cases, antibiotic dry cow therapy, culling chronically infected cows and milking machine maintenance, which will be reviewed in the following paragraphs.

The practice of applying effective disinfectant to the teat and especially the teat end immediately after milking has been shown to be a very effective practice to reduce new infections: close to 50% according to Neave *et al.* (1969) and Pankey *et al.* (1984). The aim of this practice is to remove pathogens on the teats to eliminate most of the bacterial contamination that occurs during milking therefore preventing pathogens from colonizing lesions and teat ducts (Neave *et al.*, 1966; Bramley & Dodd, 1984). However, this practice is not equally effective against coliforms and many streptococcal mastitis (Pankey *et al.*, 1984).

The second practice of the mastitis control plan, appropriate treatment of clinical cases, can help reduce the duration of each infection (Neave *et al.*, 1966). The limitations of this practice for mastitis control are that only a fraction of infections are clinical (Neave *et al.*, 1966) and that treating clinical cases not knowing the aetiology of the disease results in unnecessary antimicrobial treatments due to reduced efficiency of treatments in cases where there is no growth or growth of certain Gram-negative pathogens (Ruegg, 2021). The wide range in bacteriological cure (27%–95%) can vary the success of the strategy depending on the herd management, the cows and the type of bacteria present

(Ruegg, 2021), and therefore treatment effectiveness should be evaluated on each herd.

Work showing that antibiotic therapy for treating staphylococcal infections at the end of the lactation was more effective than in lactation treatment (Dodd et al., 1969) led to the recommendation of application of antibiotic dry cow therapy of all cows. Dry cow therapy also helps prevent many new infections over the dry period, which is a high-risk period for acquiring new infections (Bradley & Green, 2004; Ruegg, 2017). Using antibiotic dry cow therapy can reduce on average 78% of existing infections depending on the pathogen present on the herds (over 90% of streptococcal and 50% of staphylococcal infections) (Neave et al., 1966; Halasa et al., 2009). However, variable cure rates of dry cow therapy (Halasa et al., 2009) can result in PI cows, particularly older cows, which can provide a reservoir of pathogenic bacteria. Therefore, sometimes, culling chronically infected cows from the herd at drying off could have a greater influence than dry cow therapy in reducing the prevalence of infection (the number of infected cows) in many herds (Browning et al., 1994).

The final measure in the mastitis control plan is related to the maintenance of the milking equipment. The milking machine needs to provide adequate vacuum level and vacuum stability and allow a short milking to reduce the risk of mastitis (Thompson *et al.*, 2006). Additionally, the milking machine plays a role in the maintenance of teat condition, which can impact infections (Thompson *et al.*, 2006). Advances in milking machines have greatly improved vacuum stability, duration and teat condition (Mein, 2012; Ruegg, 2017) making milking machine factors less predominant as the main cause of mastitis problems (Mein, 2012).

Additional milking management practices that have been shown to reduce bacterial contamination of teat ends can be important mastitis control measures. Wearing gloves for milking cows is absolutely necessary to avoid the spread of contagious pathogens (Neave et al., 1966). Pre-milking disinfection of teats (not udders) if followed by effective drying can reduce the development of infections caused by Strep. uberis (Galton et al., 1988). Separate milking of cows infected with Staph. aureus has been shown to reduce the prevalence of infection significantly (Wilson et al., 1995). Additionally, regular SCC recording is a key tool in monitoring intramammary infection and allows for improvements in mastitis control (LeBlanc et al., 2006). In Ireland, regular milk recording of approximately 40% of herds is conducted and only on average 4.5 times in the lactation (More et al., 2017). The implementation of the five-point plan has led to a reduction of infections and a change in the aetiology of mastitis in many countries (Bradley & Green, 2004; Zadoks & Fitzpatrick, 2009). In Ireland, most mastitis problems remain associated with contagious mastitis pathogens and especially Staph. aureus. Several studies have shown that Staph. aureus was the most common pathogen found in cows infected at dry off (range 60–90% of infections) (Egan & O'Dowd, 1982; McParland *et al.*, 2019; C. Clabby, personal communication), in sub-clinical mastitis samples (21%; Barret *et al.*, 2005) and in clinical mastitis samples (38%; Keane *et al.*, 2013), followed by *Strep. uberis*.

CellCheck, the national mastitis control programme, coordinated and facilitated by AHI has contributed to reducing SCC in dairy herds on a national basis. However, currently, many farms still have sub-optimal levels of milk quality. Data collected by DAFM showed that in 2018, 38% of herds had an annual bulk tank SCC of >200,000 cells/mL (AHI, 2019). Having information of individual cow SCC combined with the measures in the five-point plan can have a great impact in further improving udder health in national herds.

AMU and selective dry cow therapy

Legislation on AMU on animals (Regulation 2019/6) will come into effect in the EU from 28 January 2022 (European Parliament and the Council of the European Union, 2019) which includes regulation on the preventive use of antimicrobials in groups of animals (e.g. dry cow therapy).

In Canadian dairy farms, Saini et al. (2012) reported AMR to penicillin by Staph. aureus strains in 28% of the herds examined (Saini et al., 2012). Similar results were reported by McDougall et al. (2014) in New Zealand dairy herds. Holko et al. (2019) observed that 62% of isolated mastitis-causing pathogens were resistant to at least one antimicrobial. Strep. agalactiae was resistant to at least one antimicrobial in 100% of isolates, while resistance was found in 86% of Strep. uberis and 79% of E. coli isolates (Holko et al., 2019). Resistance to penicillins by Staph. aureus has been shown to vary greatly between different geographical regions (likely due to treatment decisions and poor stewardship) and temporal trends can be recognised (Aarestrup & Jensen, 1998), which highlights the importance of evaluating resistance profiles for each country. In Ireland, there are limited current data on AMR or mastitiscausing pathogens (Aarestrup & Jensen, 1998). Keane (2016) found that of 53 E. coli isolates from clinical mastitis, 16% were resistant to at least one antimicrobial (most commonly tetracycline), while three isolates were multidrug resistant. Aarestrup & Jensen (1998) reported that 90% of 100 Staph. aureus isolates were resistant to penicillin; however, there was no reference to the resistance profiling methodology applied in that study. There is a need for current data on resistance profiles for the most common pathogens causing clinical and sub-clinical mastitis in Irish dairy herds.

Mastitis accounts for the majority of antimicrobials administered to dairy cows (Pol & Ruegg, 2007; Saini *et al.*, 2012). Stevens *et al.* (2016) reported that approximately 60–70% of all antimicrobials administered on dairy farms are for preventing and treating mastitis. More *et al.* (2017) showed a yearly decrease in intramammary tubes sold for the treatment

of mastitis in lactation since 2003 in Ireland; however, a higher percentage of critically important antimicrobials (i.e. an antimicrobial that is the sole or one of few therapies available for serious human diseases and that is used to treat diseases transmitted to humans from non-human sources or may acquire resistance genes from non-human sources) were being prescribed.

Blanket dry cow therapy (treatment of all quarters of all cows at the end of lactation) was an important measure targeted at curing existing infections and avoiding new infections over the dry period (Dodd et al., 1969). This practice has been widely adopted in Ireland with an estimated adoption of 100% of herds in 2015 (More et al., 2017) which is an increase of the estimated 92.7% coverage in 2010 reported by More et al. (2012). Given the impending legislation to prevent the prophylactic use of antimicrobials, selective dry cow therapy (treatment only of cows that have a proven infection, while the rest receive a teat seal) will become a common practice. International studies have mostly shown that there is no negative impact on SCC by replacing the use of antimicrobials with a teat seal at dry off in uninfected cows (Bradley et al., 2010; Vasquez et al., 2018; Rowe et al., 2020). A study conducted in research herds in Ireland evaluated the effect of treating cows that had no clinical mastitis nor a high SCC recording (>200,000 cells/ mL) with teat seal only compared with antibiotic plus teat seal (McParland et al., 2019). Results showed that cows treated with teat seal only had a significantly higher average SCC in the following lactation compared to cows receiving antibiotic plus teat seal (roughly a 2% higher somatic cell score or 8,200 cells/mL difference when back transformed) (McParland et al., 2019). Reports from a study conducted in five commercial Irish dairy herds found similar results with a large variation between herds, with one herd not showing differences in SCC between the teat seal-only and teat seal plus antibiotic groups (C. Clabby, personal communication). This highlights the importance of mastitis control during the lactation to reduce the risk of implementing a selective dry cow therapy approach because, particularly with Staph. aureus, more new infections are likely to occur in herds with high levels of infected cows (Berry & Hillerton, 2002).

Future research on mastitis control adapted to Irish dairy farms and safe implementation of selective dry cow therapy are warranted with the increased pressure to reduce antimicrobials on dairy farms, which will limit the implementation of blanket dry cow therapy while maintaining the industry goals of udder health and milk quality.

Parasitoses research

Ireland's grass-based production system, coupled with our mild and humid climate, ensures that the challenge of

grazing livestock with a variety of endo- and ectoparasites is a perennial problem. The major endoparasites of concern in ruminant production include protozoa (e.g. Eimeria spp., Neospora caninum. Toxoplasma gondii. Babesia divergens). nematodes (e.g. the lungworm Dictyocaulus viviparus and a variety of gastrointestinal nematode [GIN] species) and trematodes (e.g. the liver fluke Fasciola hepatica) (Murphy et al., 2006). Major ectoparasites of concern include mite infestations, leading to mange or sheep scab, and lice infestations (chewing and sucking lice). Parasitic infections result in significant economic losses, primarily due to reduced production efficiency and treatment costs. The total cost of infections of cattle and sheep in Ireland due to the helminth parasites D. viviparus, F. hepatica and GIN has recently been estimated at almost €240 million per annum (Charlier et al., 2020).

Parasite control

For the past 60 yr, the control of parasites has been heavily dependent on the availability of effective antiparasitic veterinary medicines. Initial compounds, such as phenothiazine, were subsequently replaced by a series of highly effective, safe anti-parasitics that were developed throughout the 1960s-1980s (Gordon, 1961; Turton, 1969; Lucas, 1971; Wolff et al., 1983). The golden era for antiparasitic development arguably culminated with the launch on the market of ivermectin in 1981 (Campbell et al., 1983). This broad-spectrum anthelmintic, which has activity against human as well as veterinary parasites, was developed at Merck Research Laboratories in the United States by a team led by Irishman William Campbell, an achievement for which he was jointly awarded the Nobel Prize in Physiology or Medicine in 2015 for "discoveries concerning a novel therapy against infections caused by roundworm parasites". However, there has been a dearth of new anti-parasitics launched onto the global market in recent years with only two new anthelmintic classes developed: the amino-acetonitrile derivatives and spiroindoles (Kaminsky et al., 2008; Little et al., 2011) with both of these classes licenced for the control of nematodes in sheep only.

Anti-parasitic resistance (APR)

The lack of new effective anti-parasitics coming on-stream is a cause for concern, as the emergence of drug-resistant parasites is now a threat to our pasture-based production system. Anthelmintic resistance is now widespread among GIN of sheep and cattle in Ireland (Keegan *et al.*, 2017; Kelleher *et al.*, 2020). Worryingly, GIN that are simultaneously resistant to all three commonly available anthelmintic classes (benzimidazole, levamisole and macrocyclic lactones) have also been identified (Keegan *et al.*, 2015). Among trematodes, *F. hepatica* resistant to triclabendazole have been confirmed in Ireland (Mooney *et al.*, 2009) and resistance is likely to be widespread (Rose Vineer *et al.*, 2020). As this anthelmintic class is the only flukicide with efficacy against all stages of *F. hepatica*, resistance raises the spectre of uncontrollable liver fluke disease due to early immature stages. Tolerance to the insecticide deltamethrin has also been demonstrated in *Bovicola bovis* (chewing lice) (Mckiernan *et al.*, 2021). While APR has not been documented in Ireland for a number of commercially important parasites such as *Nematodirus* spp. or *D. viviparus*, the lack of regular monitoring or national surveillance programmes for resistance may be responsible for this lack of detection. Ultimately, continued widespread use and misuse of anti-parasitic products will apply an ongoing selection pressure for resistance development and will inevitably culminate in the emergence of further resistance.

A variety of approaches will be required to manage the threat posed by APR. The distribution of parasites in the host is often over-dispersed (Barger, 1985). Hence, the development of novel, cheap, pen-side diagnostics/sensors or infection indicators will facilitate targeted treatment of at-risk individuals or groups of animals at the appropriate time. Irish research has made significant advances in understanding F. hepatica antigenic determinants and the associated immune response (Dalton & Heffernan, 1989; Mulcahy et al., 1998; Mulcahy et al., 1999), which facilitates the design of immunological solutions, such as novel vaccines (Molina-Hernández et al., 2015). By stimulating natural immunity against disease, vaccines are highly effective, easy to administer and have broad consumer acceptance. Increased uptake of existing vaccines (such as lungworm vaccination) should also be encouraged, and research to optimise the use of such vaccines in the context of our pasture-based, spring calving system is required (Downey, 1984). Research on management strategies that slow the further development of APR and approaches to manage parasites in the face of existing and emerging APR are now urgently required. Refugia, the proportion of the parasite population not exposed to resistance selection pressure, is a key determinant for the development and spread of APR (van Wyk, 2001). The concept of refugia management will need to become commonplace on Irish farms and research to optimise refugia within Irish farming systems is required. Breeding animals for resistance to parasitic disease will also improve sustainability and reduce reliance on anti-parasitics. While the heritability of many disease traits is low, heritability of resistance to GIN is moderate in cattle and sheep (*h*² = 0.2–0.3) (Gasbarre *et al.*, 1990; Keane *et al.*, 2018). Breeding values for resistance to liver fluke infection have recently become available in Ireland for AI bulls, and these will be incorporated into breeding indices in time.

Changes in the prevalence of parasite pathogens have also been reported over the last 60 yr, such as the decline in the incidence of bovine babesiosis (Gray & Harte, 1985; Gray *et al.*, 1996; Zintl *et al.*, 2014b). The emergence of new

parasitic diseases is also an area of concern. In recent years. there has been an apparent increase in the prevalence of rumen fluke in Ireland (Murphy et al., 2008; Zintl et al., 2014a). While adult rumen fluke appear to be relatively well tolerated. a large number of larvae in the intestine has been associated with clinical disease (Millar et al., 2012). One hypothesis for the increase in the prevalence of paramphistomosis is the importation (in ruminants) and spread of a new paramphistomum species. Early work identified rumen fluke in the United Kingdom and Ireland as Paramphistomum cervi (Willmott, 1950); however, more recently it has been demonstrated that the major species present is Calicophoron daubneyi (Zintl et al., 2014a; Martinez-Ibeas et al., 2016). Future research may determine whether the recent increase in rumen fluke prevalence is the result of the importation of a new species or a change in local conditions, which favours the transmission of an existing species. The impact of C. daubneyi on ruminant health and production efficiency also remains to be elucidated. While an aquatic snail is the intermediate host for P. cervi, C. daubneyi and F. hepatica share an intermediate host, Galba truncatula, and co-infection of livestock with both species occurs on many farms (Jones et al., 2017). The impact of the increasing prevalence of C. daubneyi on F. hepatica prevalence and the possibility of competition between the two species within the intermediate host warrants further investigation. In addition, only a single product, oxyclozanide, has efficacy against rumen fluke and so there is a need to guard against the development of resistance to this product.

The local environment has a significant effect on the lifecycle and transmission of many parasites (Ollerenshaw, 1966; O'Connor *et al.*, 2006; Morgan & van Dijk, 2012). Climate or land use change may therefore have a major impact on the epidemiology of livestock parasitic diseases by changing the risk period for infection, the window of transmission for specific species or providing habitat for disease vectors (van Dijk *et al.*, 2010). Changed climatic conditions may support the lifecycle and transmission of parasite species, such as *Haemonchus contortus*, not currently commonly found in Ireland. An increase in mean temperatures may also enable the spread of arthropod vectors in Ireland, with a concomitant increase in vector-borne parasitic diseases.

Future research in this field needs to address predicting the influence of climate change on host–parasite dynamics and mitigating the negative consequences of any change in parasite transmission dynamics.

Sheep disease research

This section will give a broad overview of the research into the health status and the most prevalent endemic diseases of sheep in Ireland and internationally over the past 60 yr. In the sheep census, the population of sheep in Ireland was just over 3.7 million with 35,186 flocks. This gives an average of 106 sheep per flock, but the flock size is skewed with many flocks below 100 and few above 300 (Gov.ie Sheep Goat census; http://www.askaboutireland.ie/enfo/sustainable-living/farming-in-ireland-overvi/sheep-farming/#:~:text=In%20 total%2C%20as%20of%20December,%2C%20Mayo%2C% 20Kerry%20and%20Wicklow).

Causes of ovine mortality

A mortality study of Irish flocks (n = 33) was carried out by DAFM laboratories in 2016 (Murray *et al.*, 2019). The median overall submission rate of dead sheep of all ages from sentinel lowland flocks of 13.8% is in line with other international studies. Data for mortality rates in sheep of all ages internationally have not been published for comparison.

Ovine diseases

The health status of a flock has major implications for the welfare, productivity and profitability of sheep farming. (Hosie & Clark, 2007) The health status of the flock also affects the potential for antimicrobial and anthelmintic resistance. Health issues which have a big effect on productivity include lameness, mastitis and teeth problems. The iceberg diseases that are present in Ireland include ovine pulmonary adenocarcinoma (OPA), maedi visna (MV), caseous lymphadenitis (CLA), JD. Iceberg diseases are slow-onset diseases which cause chronic wasting and are referred to as iceberg diseases, as the thin, wasting ewes are the tip of the iceberg, with the vast majority of their negative health issues and productivity losses hidden below the surface (Ogden *et al.*, 2019).

Internal and external parasites are also major issues for sheep health and productivity; they are dealt with in a separate section.

Ovine abortion

The two most important causes of infectious abortion in Ireland are *Chlamydophila abortus* (EAE) and *Toxoplasma gondii* infection. In the 2016 All-Island Surveillance Report (DAFM, 2016), approximately 23.5% of ovine abortions submitted to DAFM Regional Veterinary Laboratories were diagnosed as due to *Toxoplasma gondii* and about 16% due to EAE (N =713). Mearns (2007) found that together these make up over 70% of diagnoses of abortion material at veterinary disease surveillance centres throughout England, Scotland and Wales.

Ovine lameness

Lameness is a major issue for sheep farmers as it impacts welfare, productivity and labour demands. In the work by Bohan *et al.* (2019), the costs/ewe/day associated with lameness in Ireland were $\in 0.25$. Thus, lameness has a huge

impact worldwide on the economics of sheep production. The main causes of lameness in Irish sheep are footrot, "scald" and contagious ovine digital dermatitis (CODD). Footrot is a highly infectious bacterial disease caused by two bacteria – *Fusobacterium necrophorum* and *Dichelobacter nodosus*. Vaccines have been developed over the last 40 yr to try to combat footrot (O'Meara *et al.*, 1993).

Interdigital dermatitis (scald) results in the skin between the claws becoming red and swollen and covered by a thin layer of white discharge. There is no under-running of the hoof wall or sole. It is more common in lambs, especially when underfoot conditions are wet. Contagious ovine digital dermatitis is caused by treponeme bacteria and often occurs in conjunction with footrot. There has been no Irish and only limited international research on lameness in sheep.

Ovine mastitis

Mastitis in sheep is often underappreciated as a productivity and welfare constraint. In the work by Bohan *et al.* (2019), the costs/ewe/day associated with mastitis were $\in 0.24$. In Ireland, McLaren *et al.* (2020) estimated that 19.2% of sheep are culled due to mastitis/udder problems. In the 2016 Irish sheep mortality study, 4.6% of deaths in adult sheep were attributed to mastitis (Murray *et al.*, 2019).

Ovine dental problems

As sheep are ruminants, and in Ireland, the majority of their feed intake is from forage, good dentition is a prerequisite to productivity and longevity in the flock (Nolan & Black, 1970). Incisors are commonly examined by flock owners and sheep are culled on findings; however, overgrown, worn and absent molar teeth and jaw abscesses cause problems with mastication of fibrous feeds and subsequent weight loss. It is estimated in Ireland that 20.9% of sheep are culled for problems with teeth (aged) compared to 38.9% in the United Kingdom (McLaren *et al.*, 2020).

Ovine pulmonary adenocarcinoma

Ovine pulmonary adenocarcinoma (OPA) is caused by the jaagsiekte retrovirus (JSRV). It is characterised by the development of invariably fatal lung tumours primarily in adult sheep. Affected sheep show breathlessness, exercise intolerance and repeated moist coughing. In Irish surveillance work carried out by Lee *et al.* (2017), lungs from 1,911 adult sheep were examined macroscopically in the abattoir and 369 were removed for further testing due to the presence of gross lesions of any kind. All 369 were subject to histopathology and real-time (RT) PCR and 46 to immunohistochemistry (IHC). Thirty-one lungs (31/1,911, 1.6%) showed gross lesions and were positive for JSRV by RT-PCR and/or IHC, but only 10 cases of OPA were confirmed (10/1911, 0.5%). Jaagsiekte retroviruspositive sheep tended to cluster within the same flocks.

Maedi visna

Maedi visna (MV) in sheep is caused by a lentivirus (MVV). The lungs and mammary glands are the main organs affected, with occasionally affected sheep developing nervous signs. In 2020, the first cases of MV in Ireland were diagnosed by Regional Veterinary Laboratory (Kilkenny, Ireland) in two flocks. Surveillance studies carried out by DAFM laboratories on serum collected in 2018 and 2019 suggest, as yet, a very low prevalence (0.25%) in Irish sheep (unpublished). A study by Ritchie *et al.* (2012), using a random sample of UK flocks, found that the prevalence of infected flocks appeared to have doubled between 1995/1996 and 2010 (1.4%–2.8%, P = 0.015).

Pestiviruses

The DAFM has carried out a number of seroprevalence studies in the past number of years (unpublished). In 2019, a seroprevalence study on pestiviruses (border disease and BVD) and Q-fever was carried out in four flocks. The main finding of the study was that there was very low lamb seroprevalence (0.19%) of pestiviruses. Flock seroprevalence was 2% (4/196 flocks positive). There seems to be no significant epidemiological link between the sheep flocks where pestivirus was demonstrated to be circulating and the presence of BVD in cattle on those establishments.

Q-fever

The major finding of the DAFM study (unpublished) on Q-fever is the lower seroprevalence of *Coxiella burnetii* antibodies in sheep flocks. The animal-level seroprevalence of 0.45% is down from the 0.7% found by Ryan in a 2011 prevalence study (Ryan, unpublished) and flock seroprevalence is down to 6.4% from 8.4%. This compares to a serological survey using an indirect ELISA, carried out on 15,186 sheep and goats in The Netherlands in 2008. In total, 2.4% (95% CI, 2.2– 2.7) of the sheep and 7.8% (95% CI, 6.9–8.8) of the goats were seropositive for antibodies against *Coxiella burnetii* (van den Brom *et al.*, 2013).

Future ovine health research

Lameness, mastitis and ovine dental problems are the areas that need more research, as they have a major impact on sheep health and productivity, but there is very little available research. Areas for further research on mastitis are the infectious agents involved and genetic and management factors. Key areas for further research on ovine dental problems are the effects of diet and the extent of problems with molar teeth and jaw abscesses. Further research is also needed into the seroprevalence of JD and CLA in sheep in Ireland. Research into mastitis in milking goats in Ireland is also needed.

Conclusions

The last 60 vr have seen an exponential increase in ruminant health research in Ireland and worldwide associated with technological developments. Some of this has been proactive, but most has been reactive to changing agri-industry (or societal, e.g. AMR) priorities. The advances have been most marked in the economically important infectious diseases, particularly those of regulatory concern. This has sometimes (e.g. BVD. brucellosis), but not always (e.g. bTB), been associated with disease reduction or eradication. Our basic understanding of the causes and effective control measures for ruminant diseases has evolved with each scientific paper, resulting sometimes in re-evaluation of old dogma as the consensual evidence-base strengthened. Improvements in the scientific method (e.g. the use of meta-analyses) have contributed to these incremental gains. The ruminant health research agenda of the future will need to address not just ruminant health but also public perception of the priorities in ruminant health, as has already occurred with animal welfare research.

Acknowledgements

The authors acknowledge the research funding they have received over the years and the invitation to write this paper from the *Irish Journal of Agricultural and Food Research*.

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Irish Journal of Agricultural and Food Research

Animal welfare research – progress to date and future prospects

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Abstract

The welfare status of an animal is dependent on its ability to cope and exist in harmony with its environment, such that good physical and psychological health is maintained. Improving animal welfare is an increasingly important aspect of livestock production systems due, in a large extent, to increased consumer concerns about animal production practices. Animal welfare is an integrated part of quality assurance programmes for sustainable animal production, considering that welfare, health, management, economy, consumer acceptance and environmental impact are interdependent. The major welfare concerns in the livestock industry in recent years relate to the rearing and management of dairy calves, the welfare of the dairy cow, effect of husbandry management procedures on the welfare of beef cattle, rearing of sows in gestation and farrowing crates, and the broiler (meat) chicken sector. The paper will focus on scientific research underpinning these welfare concerns, with a particular focus on research conducted on the island of Ireland.

Keywords

Animal welfare • beef • dairy • pig • poultry • welfare assessment

Introduction

In Ireland, the proportion of respondents to an European Union (EU) survey who believe the welfare of farmed animals should be better protected than it is now increased by 22% from 2006 to 80% in 2016 (European Commission, 2016a, 2016b, 2016c, 2016d). Indeed, it is now widely accepted that as sentient beings with a capacity to feel pain and experience emotions, our farmed animals deserve to experience a life that is worth living (Mellor, 2016). During the last century, dairy production systems expanded and intensified giving rise to growing public concerns surrounding the welfare of dairy animals (Barkema et al., 2015; Wolf et al., 2016; Mee & Boyle, 2020). There is growing evidence that such expansion is associated with challenges to the welfare of dairy animals on farm (Osawe et al., 2021). Thus, the issue of dairy calf and cow welfare is becoming increasingly present in research agendas in Ireland, and internationally. Beef cattle production within the EU, and in Ireland in particular, is less intensive than areas of animal agriculture associated with the greatest welfare concerns such as pig and poultry production. Nonetheless, there are aspects of beef cattle production such as the castration, weaning, transport and housing of beef cattle which have the potential to cause stress, pain and injury if not managed correctly. In Ireland, commercial pig farming is a small, intensive industry, with nearly all pigs bred and reared indoors on slatted or semi-slatted systems. According to the 2020 pig census, 284 pig farms contain 96% of the 1.7 million pigs in the country (DAFM, 2020). Indeed the average size of commercial herds is among the largest in Europe. Volatility and high prices of cereals and compound feeds, a relatively low pig price and a high level of farm credit mean that Irish pig farmers are particularly vulnerable to economic pressures. This contributed to the need to achieve economies of scale in Ireland and internationally, and management of pig farms in a way that is as resource and labour efficient as the law allows. The broiler (meat) chicken sector is undergoing a period of welfare-driven transformation. Over 100 million broiler chickens are produced per year in Ireland¹, and this sector is

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¹https://www.teagasc.ie/rural-economy/rural-development/diversification/broiler-production/.

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of major importance globally with over 100 million tonnes of chicken meat produced annually. In fact, the Organisation for Economic Co-operation and Development (OECD) figures for 2020 indicate average global consumption levels (kg/capita) of 14.9 for poultry meat, 10.7 for pork, 6.4 for beef and veal and 1.8 for sheep meat. More broiler chickens are farmed than any other type of animal (FAO, 2019), which suggests that more individuals are impacted by changes to on-farm welfare standards than with any other livestock enterprise.

Animal welfare assessment

Over the last decades, the welfare of farm animals has become increasingly important, both for the general public and for the scientific community. National (e.g. Department of Agriculture, Food and the Marine (DAFM), Animal Health and Welfare Act 2013) and EU regulations (Simonin & Gavinelli, 2019) or international codes of welfare (World Organisation for Animal Health [OIE]) increasingly include provisions that address the welfare management of livestock. Animal welfare is not a new concept and was defined by Brambell since 1965. The original Brambell Five Freedoms were simply expressed around concepts "stand up, lie down, turn around, stretch, flap wings". Subsequently, the five freedoms were developed into a useful framework to identify welfare components and problems (Botreau et al., 2007, 2009; Velarde & Dalmau, 2012). However, due to the general nature of these ideal states, there were limitations to the use of the five freedoms to describe animal welfare (Botreau et al., 2007).

The Welfare Quality project was the largest European project concerning animal welfare (Blokhuis *et al.*, 2010). It was designed to develop European standards for welfare assessment on farms (Blokhuis *et al.*, 2010). The Welfare Quality project re-examined the original concepts of the "Five Freedoms" and developed and extended them into Welfare Quality Assessment Protocols (Botreau *et al.*, 2007; Blokhuis *et al.*, 2010).

The emotions that animals experience are a key component of animal welfare and the focus on emotions as an element of positive animal welfare is well recognised (Lawrence *et al.*, 2019). Animal-based indicators provide the best means of assessing welfare, as they directly reflect the experience of the animal within its environment (Whay *et al.*, 2003). It is now acknowledged that welfare assessment protocols should also include measurements of the affective state of the animal (i.e. how it feels) and assess its ability to have positive experiences, as it is now accepted that good welfare does not simply mean the avoidance of negative experiences, but must also include positive ones (Yeates & Main, 2008). The five domains model (Beausoleil & Mellor, 2015; Mellor & Beausoleil, 2015; Mellor, 2016) assess animal welfare under the following five criteria: nutrition, environment, health, behaviour and mental state. The three orientations approach (Fraser *et al.*, 1997; Webster *et al.*, 2015; Mellor, 2016) assess animal welfare under three criteria: biological functioning, affective state (feelings and emotions) and natural living. Affective states are one of the three commonly discussed components of animal welfare (Mendl *et al.*, 2009, 2010; Mendl & Paul, 2020), the remaining two being natural living and physical health (Fraser *et al.*, 1997).

Dairy calf welfare

Young calves are particularly vulnerable to poor health and static morbidity and mortality rates across the dairy industry worldwide suggest this is an area where animal welfare must be improved (Mee, 2020). In Ireland, dairy bull calves or beef breed heifers are most typically sold from the farm preweaning and they most commonly leave the dairy farm within the first 2–4 wk of life (>75%; Barry *et al.*, 2020). Dairy breed heifer calves stay on the farm and are reared as replacements for the dairy herd. The optimal rearing of female replacement calves is a fundamental component of the future success of dairy herds (Roche *et al.*, 2015). For example, if replacement heifers are reared with technically proficient practices, which implement high standards of animal welfare, there is lower morbidity and mortality.

Technical proficiency in calf rearing involves a number of areas, pre-weaning nutrition of calves (e.g. colostrum, transition milk and milk [whole milk and milk replacer] feeding as well as concentrate feeding) and management practices (e.g. environmental conditions, weaning procedures) as these can have a pronounced effect on physiological health, welfare, behaviour and mortality of the calves (Miller-Cushon *et al.*, 2013; Webb *et al.*, 2013; Leruste *et al.*, 2014; Sutherland *et al.*, 2014) and can influence their future performance (Soberon *et al.*, 2012; Gelsinger *et al.*, 2016).

To provide protection from infectious diseases in early life, neonatal calves are dependent on the passive transfer of antibodies from colostrum (Godden, 2008). Recent research focused on establishing the quality of colostrum in the Irish national dairy herd (Conneely et al., 2013; Barry et al., 2019). Good-quality colostrum is defined as that which has an immunoglobulin G (IgG) content >50 mg/mL; in general, colostrum from Irish dairy cows is of high quality (>85 mg/mL IgG; Conneely et al., 2013; Barry et al., 2019). However, there is considerable variation both within and between herds indicating the requirement to test colostrum quality before feeding, a practice currently rarely undertaken (Barry et al., 2019). Some of the factors found to affect the quality of colostrum of Irish dairy herds include parity, month of calving, time between calving and colostrum collection and weight of colostrum (kg) (Conneely et al., 2013).

Due to the compactness of the calving season, over 90% of farmers report storing colostrum for use at a later time; almost one-quarter of farmers are storing it at room temperature (Barry *et al.*, 2019), a practice which leads to exponential growth of bacteria which can inhibit IgG absorption by the calf (Cummins *et al.*, 2017). This can have negative consequences on calf health.

As there is considerable variation in cow type within the Irish dairy herd (Coffey *et al.*, 2016; O'Sullivan *et al.*, 2020) and a resultant difference in calf birth weight, it necessitated the examination of colostrum feeding strategies based on calf birth weight. The results showed that passive transfer was maximised when calves were fed 8.5% of their birth bodyweight in high-quality (>50 mg/mL IgG) colostrum, when compared to either 7% or 10% of their birth bodyweight (Conneely *et al.*, 2014a, 2014b). This research also showed the benefits of improved calf health when transition milk is fed for at least four feeds after the initial colostrum feed (Conneely *et al.*, 2014a).

Following colostrum and transition milk feeding and in order for calves to grow at an appropriate rate, they need adequate nutrition (milk feeding volumes); traditionally, Irish dairy farmers offered 4 L of milk to each calf daily. This volume is insufficient, particularly in early life when the calf's rumen is not fully developed and cannot adequately utilise nutrients from concentrate (Lorenz, 2021). Feeding calves 15% of their birth bodyweight in high-quality milk increases weight gain during the pre-weaning period and ensures that the nutritional requirements of the calf are satisfied (Conneely *et al.*, 2014b), while also ensuring they express normal behaviour (Sinnott *et al.*, 2021).

Clearly optimal practices for colostrum feeding and artificial rearing are required for all calves in the dairy herd. However, there is ample research to indicate deficiencies in the nutritional and housing management of male dairy calves worldwide (Boyle & Mee, 2021). This is because of their lower economic value (Marquou et al., 2019), exacerbated in recent years by breeding practices (Kelly et al., 2020). Herd expansion is also associated with an increased likelihood of shipping calves surplus to the needs of the dairy herd (mostly males) abroad and of early slaughter (Osawe et al., 2021) which are contentious practices (Haskell, 2020). Recent research outlines ways to protect the welfare of such animals including incorporation of animal-based outcomes relevant to health and welfare at calf slaughter, greater use of sexed semen and more focused breeding plans as well as expanding calf housing facilities (Balzani et al., 2021; Mee & Boyle, 2021; Osawe et al., 2021). However, future research is essential to investigate the calf transport conditions. This includes the appropriate movement age to ensure their health is not compromised, feeding strategies immediately prior to

transport, mixing of herds both during and after transport, and management systems at the destination farm.

Any calf management system, regardless of whether for replacement heifer rearing, beef production or a combination of both, should ensure calf health and welfare are not compromised. Welfare assessment protocols can be a key tool in protecting the welfare of calves on dairy farms. To this end, a reliable, feasible and time-efficient welfare assessment protocol, for male and female dairy calves, during milk feeding and weaning was developed (Barry et al., 2019). Although there are a number of welfare assessment protocols available (e.g. the Welfare Quality® project), one did not exist which combined the three factors of animalbased data (e.g. physiological health parameters, general appearance assessment and behavioural measurements), routinely collected data and resource-based indicators (management and environment). Specifically, there were no available welfare assessment protocols for dairy heifer and bull calves, to give an overview of all calves but also to allow for differentiation of the sexes. Figure 1 details the three main areas of the welfare assessment protocol which involved (i) management practices, ascertained via one-to-one survey with calf manager, (ii) independent animal assessment, and (iii) evaluation of environmental conditions (Barry et al., 2019).

Early dairy cow–calf separation

The importance placed on the ability of dairy cows to express their natural behaviour is also evidenced in the growing body of research accumulating in the area of cow–calf contact rearing systems. The dairy industry and the public are increasingly interested in management systems that allow cow–calf contact (Sirovnik *et al.*, 2020). The cow is highly motivated to visit her calf (Johnsen *et al.*, 2021), indeed will push up to 90 kg to access it (Wenker *et al.*, 2020). There is currently no evidence to indicate early separation is beneficial to cow health (Beaver *et al.*, 2019). In fact, systems which allow contact between the dam and the calf reduce the risk of mastitis in dairy cows (Beaver *et al.*, 2019).

Newborn dairy calves are usually permanently separated from their dams within a few hours after birth. This is a typical practice in dairy farming and applies to conventional production systems (Kennedy *et al.*, 2014). Heretofore, best practice was to remove the calf from the cow immediately postcalving for biosecurity reasons (Lorenz *et al.*, 2011) and to promote greater health (e.g. minimise risk of Johne's disease; Kennedy *et al.*, 2014). However, consumers are currently questioning this practice of immediate removal in terms of the welfare implications for both the cow and calf. While a number of studies are being undertaken internationally examining the effect of retaining the calf with its mother post-calving (Beaver *et al.*, 2019), pasture-based systems of dairy production, such as those that predominate in Ireland and New Zealand, pose a

Management practises

Interview with calf manager on 6 different areas

1. General information

- 2. Calving & colostrum feeding
 - 3. Post-colostrum feeding
 - 4. Health & treatments
 - 5. Hygiene practises
 - 6. Weaning & calf sales

ASSESSING CALF WELFARE

Animal assessment

Clinical health (visual) Serum IgG concentrations Enteropathogen infection rates Heart girth measurements Colostrum quality Behaviour observations

Environmental conditions

Space allowance Ammonia concentrations Bedding conditions Feed/water availability Temperature/wind speed Feeding equipment hygiene

Figure 1. An overview of the components involved in assessing calf welfare. Management and environmental factors affect the animals. Animal welfare can be best assessed by using animal-based measures, while measures on management and environment can help to find factors affecting animal welfare. IgG, immunoglobulin G.

unique problem. These systems are characterised by compact seasonal calving patterns and by their reliance on pasture in the diet which necessitates the early turnout of dairy cows to pasture (Kennedy *et al.*, 2005). Future work will ascertain the effects of retaining the calf with its mother until weaning on animal welfare, productivity and on the implications for workload on the farmer in a pasture-based scenario (One Welfare; García Pinillos *et al.*, 2016). Recommendations for future calf management will be dependent on these results.

Dairy cow welfare

Much research on dairy cow welfare in Ireland focused on the issue of pasture access for dairy cows. Pasture-based systems are viewed as superior to housed systems for cows, as they allow cows to perform their natural grazing behaviour, which is a high-priority activity for them (Krohn, 1994). Pasture access also promotes more synchronous herd lying behaviour, as well as increasing cow comfort which facilitates longer lying bouts and overnight lying durations (Crump et al., 2019). However, lying duration at pasture is dependent on grass allowance; cows on a low feed allowance spend less time lying (O'Driscoll et al., 2019). Furthermore, access to pasture may lead to more positive state of mind in dairy cows (Crump et al., 2021). Grazing also benefits health, sometimes reducing lameness (Olmos et al., 2009a) and mastitis (Fontaneli et al., 2005) and improving reproductive health (Olmos et al., 2009b). However, cows at pasture may be more likely to suffer metabolic/nutritional stress (Olmos et al., 2009b), and may be at increased risk of parasitism and other health problems including grass tetany, ketosis and subacute ruminal acidosis (EFSA, 2009). Recent Irish research demonstrated that cows had greater skin damage to the head and neck during the housed period (Crossley et al., 2021) but more nasal discharge during the grazing season. Therefore, it should not be assumed that welfare is automatically better when cows are outdoors. The ideal

situation would allow the cow to choose, as environmental conditions may alter her preference (Legrand *et al.*, 2009), although, in general, cows show an overall preference for pasture (Arnott *et al.*, 2017). Management of the system (in terms of animal husbandry) may be as important as the type of production system (confinement, pasture-based or hybrid) in ensuring good dairy cow welfare (Mee & Boyle, 2020).

Irish research shows that increased comfort levels in cubicles during the winter housing period were associated with improved claw health in heifers, mediated through an increase in lying time (Leonard et al., 1994). Overcrowding reduced lying time, with negative consequences on claw health (Leonard et al., 1996a, 1996b). Cows prefer to stand on softer surfaces; when the passageway and feed face were covered in rubber flooring, cows spent more time standing at the feed face, whereas cows on a concrete floor spent more time in the cubicles (Boyle et al., 2007). In Ireland, cows must be managed off pasture during the winter months due to low grass growth and the risk of damage to the ground conditions. This period of confinement can last anywhere between 3 and 6 mo, and traditionally cows were kept in cubicle houses. However, these are expensive to build, so alternatives to indoor housing of cows were also examined. Keeping cows on out-wintering pads during the dry period did not negatively impact lameness and hoof health (O'Driscoll et al., 2008a; 2008b), or mastitis incidence (O'Driscoll et al., 2008b), and in fact, conferred welfare benefits by allowing more synchronised lying behaviours (O'Driscoll et al., 2008c). As cows are herd animals, synchrony of lying behaviour is an internally motivated natural behavioural characteristic and is considered reflective of natural behaviour patterns and, as such, good welfare (Crump et al., 2019). Out-wintering pads also provided welfare benefits to yearling heifers, reducing limb lesions and increasing comfort, social and play behaviours (Boyle et al., 2008). Research investigating the effect of milking frequency on dairy cow welfare concluded that in general once-a-day milking resulted in improved hoof health and mobility, by allowing increased time for cows to lie (O'Driscoll et al., 2010, 2015), and did not negatively impact cow comfort (O'Driscoll et al., 2011). However, once-a-day milking reduces phagocytic activity of polymorphonuclear neutrophils (PMNs) and monocytes, and would be detrimental for the immune system in high-yielding dairy cows during early lactation (Llamas Moya et al., 2008a).

It is increasingly recognised that the human–animal relationship is a key factor influencing the welfare of dairy cows (Hemsworth & Coleman, 2011). Negative tactile interactions such as slapping cause cows to become fearful, which results in avoidance of humans, and may reduce milk yield (Breuer *et al.*, 2000). Conversely, an improved farmer–cow relationship can reduce stress indicators (Ebinghaus *et al.*, 2020) and fear, and improve yield (Hemsworth *et al.*,

2002). Fearful responses increased with time spent at grass and decreased with time spent indoors (Crossley *et al.*, 2021), suggesting that as cows are less exposed to humans they become less comfortable around them. The impact on their well-being is unclear, however.

Affective state is defined as an umbrella term that encompasses both emotions and mood (Kremer *et al.*, 2020), and in dairy cows, it may be assessed by measuring spontaneous physiological responses (including cortisol, heart rate variability, eye/nose temperature and eye white) and spontaneous behavioural responses (escape and wound directed behaviours, vocalisations and facial expressions). Affective state can also be evaluated using preference tests, approach/avoidance tests and motivation tests (Ede *et al.*, 2019). Potential indicators of positive welfare include comfort index, duration of lying bout time and duration, exploration/ chewing of branches, licking while standing on three legs, rumination, synchronisation of behaviours, allo-grooming and avoidance of distance (Mattielo *et al.*, 2019).

Pain, because it is one of the most unpleasant negative affective states, is of particular importance, it causes the most public concern (Weary *et al.*, 2006) and is widely recognised as an important issue for dairy cow welfare. Pain can result from many issues, including lameness, mastitis, dystocia and tail docking and disbudding. Tail docking is not legal in Ireland, yet Crossley *et al.* (2021) demonstrated that cows with docked tails were present on almost 65% of farms visited, indicating that this is nonetheless a significant issue. Research to identify (Gleerup *et al.*, 2015) and manage pain in dairy cows (Stillwell *et al.*, 2014, 2019) is ongoing.

Future challenges

In response to policy changes which focus on driving milk production in the absence of quota constraints, herd sizes are increasing (Kelly *et al.*, 2020) and grazing practices are becoming more intensive (Roche *et al.*, 2017), which has potential impacts for the behaviour and welfare of cows (Boyle *et al.*, 2015). Significant scientific advancements greatly increased our understanding of what constitutes good welfare for dairy cows and how best to assess it. As a result, we are better equipped to improve the welfare of the dairy cows in our care, which is vital if the Irish dairy sector is to respond to future challenges.

The European Green deal, which aims to overcome the threat of climate change and environmental degradation by making the economy of the EU sustainable, targets a 55% reduction in greenhouse gas emissions by 2030 (European Commission, 2020a), and a 50% reduction in the sales of antimicrobials for farm animals (European Commission, 2020b). Improving the welfare of dairy cows can contribute to these goals. Cows experiencing good welfare are likely to be less stressed and consequently less susceptible to disease (Chrousos, 2009; von Keyserlingk *et al.*, 2009), and require less antimicrobial treatment as a result. Healthy animals are also likely to remain in the herd for longer (De Vries & Marcondes, 2020). Extending the dairy cattle productive lifespan could decrease the environmental footprint of milk production because fewer heifers need to be raised (De Vries & Marcondes, 2020). Therefore, improving dairy cow welfare is of key importance to reducing the environmental impacts of dairy farming.

Consumer food preferences are evolving. The number of people adopting a vegan diet is increasing (Alcorta et al., 2021) and those that continue to consume animal products seek confirmation that food is produced in an ethical, animalfriendly manner (Cembalo et al., 2016). However, while recent work confirmed Ireland is performing well in certain areas of cow welfare, there remains considerable scope to improve (Crossley et al., 2021). Indeed, Ireland's recent Animal Welfare Strategy highlights the importance of doing so (DAFM, 2021). Demonstration of high cow welfare standards is also crucial to maintain Ireland's image as a sustainable producer of dairy products in order to maximise market returns for increased dairy production in competitive markets worldwide (DAFM, 2015). As such, dairy cow welfare must be a priority. In this regard, there is a requirement within the Irish dairy sector for schemes to monitor, benchmark and incentivise improvements to cow and young stock welfare on farms.

Beef cattle welfare

At present, there is no specific EU legislation addressing the welfare of cattle kept for beef production (European Commission, 2001). Welfare concerns with veal production led to the implementation first in 1991, and later in 2008, of legislation laying down minimum standards for their protection (Council Directive 2008/119/EC, 2008).

Castration

The castration of male calves intended for beef production is probably the most significant acute tissue- and structurealtering procedure that beef cattle commonly undergo, apart from the act of slaughter itself. Thus, castration has the capacity to represent a major source of acute stress and trauma, and also one which may reasonably be used to investigate links between acute stress and alterations in immune system function in cattle. There are also concerns regarding the ethical and social acceptability of castration procedures.

Calves are castrated because it reduces management problems associated with aggressive and sexual behaviour. However, from an animal welfare perspective, the inflammation and pain due to handling and tissue trauma are potent activators of the hypothalamic–pituitary–adrenal (HPA) axis (Earley & Crowe, 2002) and cause distress. The three main castration methods are: a rubber ring or latex bands to restrict the flow of blood to the scrotum, bloodless castration by crushing the spermatic cords with the Burdizzo and surgical castration. There is a general perception that delaying castration could extend the production advantages of keeping animals as bulls until weaning or beyond puberty. Keane (1999) showed no advantage in delaying castration of bulls from birth up to 17 mo of age in terms of live weight, growth rate or carcass weight at slaughter.

The issue of pain relief during castration of bulls is increasingly important in the scrutiny of the ethical treatment of farmed animals. Systemic analgesia with a non-steroidal antiinflammatory drug (NSAID), ketoprofen, was more effective than local or epidural anaesthesia in modulating cortisol and inflammatory responses, and in the suppression of immune function (Earley & Crowe, 2002). The NSAID, ketoprofen, effectively suppressed the surgical castration-induced peak cortisol response, and the 12-h integrated cortisol response by 56% relative to surgery alone and by 40% relative to surgery with local anaesthesia in 5.5-mo-old Friesian calves. Furthermore, a combined administration of ketoprofen and local anaesthesia delayed the peak cortisol response by 4 h relative to surgery alone (Earley & Crowe, 2002). Calves at 47 d of age have lower plasma cortisol responses to castration compared to older castrated calves (76-165 d of age), and the use of an NSAID is a better alternative to local anaesthesia for the alleviation of inflammatory and painassociated behavioural responses to castration (Ting et al., 2005). The findings showed that calves at 47 d of age exhibited lower stress responses (plasma cortisol and inflammatory responses) to Burdizzo castration compared with older calves (76-165 d of age). Issues of pain relief during routine husbandry procedures are likely to become increasingly important as societal scrutiny into the ethical treatment of farmed animals converges with the scientific evidence on the acute and chronic painfulness of routine husbandry practices.

Weaning

In Ireland, spring-born suckler beef calves are typically weaned at the end of the grazing season in autumn, between 6 and 9 mo of age, at which time they are also housed (Drennan & McGee, 2009). Weaning of the beef calf under modern cattle production systems constitutes a multi-factorial stressor as it incorporates nutritional, physical and psychological elements (Hickey *et al.*, 2003b). The weaning process involves separating the calf from its mother, resulting in numerous stressful events including dietary change, housing and social reorganisation. Indeed weaning of beef calves is one of the most stressful events in the calf's lifetime (Hickey *et al.*, 2003b; Blanco *et al.*, 2009; Lynch *et al.*, 2010a, 2010b, 2011; O'Loughlin *et al.*, 2011, 2012, 2014). Lynch *et al.* (2010a) identified that beef calves that were abruptly weaned and returned to familiar pasture had a less marked stress response than calves that were abruptly weaned and introduced to a new environment of a slatted floor shed and were offered a new diet of grass silage *ab libitum* plus supplementary concentrates simultaneously. The more marked stress response was attributed to decreased number of lymphocytes, the attenuated production of interferon- γ (IFN- γ) and greater concentrations of the acute phase protein, fibrinogen, post-weaning in abruptly weaned and housed calves compared with those that were abruptly weaned and returned to pasture.

Additionally, Lynch et al. (2010a, 2010b) demonstrated that movement from a pasture environment to a housing environment in a slatted floor shed is capable of inducing a transient stress response in beef calves and cows. Collectively, these studies identified a profile in which neutrophilia and concurrent lymphopenia are evident for a brief period following relocation. Due to the pronounced neutrophilia and lymphopenia observed by Lynch et al. (2010a, 2010b), a more in-depth examination of the effects of abrupt weaning on neutrophil function and lymphocyte immunophenotypes was undertaken by Lynch et al. (2012). Transient neutrophilia was evident post-weaning, and this population of circulating neutrophils was less active in terms of phagocytosis than the neutrophil population in circulation prior to weaning (Lynch et al., 2012). Utilising the profile of changes observed in neutrophil number and function and lymphocyte subsets identified by Lynch et al. (2012) as sensitive biomarkers of weaning stress in beef calves, the provision of concentrate supplementation pre-weaning was examined to determine if this practice could ameliorate the stress response post-weaning. Calves that were offered concentrate supplementation pre-weaning had a lesser degree of neutrophilia compared with calves that were not supplemented pre- and post-weaning (Lynch et al., 2012). Other weaning management practices include the use of antisuckling devices (nose clips) for a period prior to weaning (Haley et al., 2005), fence-line contact between calf and dam post-weaning (Stookey et al., 1997) and a combination of both practices before complete separation (Newberry & Swanson, 2008).

There are limited studies on the effects of weaning on beef cows. In line with the findings of Lynch *et al.* (2010b) and other studies examining the effects of weaning stress in beef calves (Hickey *et al.*, 2003b; Blanco *et al.*, 2009), weaning resulted in neutrophilia and concurrent lymphopenia which was coupled with decreased *in vitro* production of IFN- γ and increased acute phase response in beef cows. Thus, it is apparent that the beef cow is stressed by separation from her calf. However, when the magnitude and duration of these perturbations in the cow are compared with those in the calf, it appears that stress response is activated to a lesser degree and for a shorter

period (Lynch *et al.*, 2010b). Early weaning is not practiced in Ireland due to favourable climatic conditions for grass growth. Beef cows express distinct distress behaviours, such as increased vocalisations and locomotor activity following abrupt separation from their calves (Price *et al.*, 2003). Therefore, it is reasonable to assume that physiological and immunological alterations in abruptly weaned beef calves would also be seen in beef cows following abrupt separation from their offspring.

Transport

The infrastructure of the beef cattle industry is associated with a need for the transportation of cattle, by road and sea, including within the EU, and internationally. The buying and selling of cattle from one producer to another, the finishing of weanling calves at large feedlots and the endpoint of slaughter all necessitate transportation. Transportation can combine physical and psychological stressors, and weaning, method of and the handling during (un)loading, commingling of unfamiliar animals, loud noises, overcrowding, food and water deprivation, extreme temperature and the novelty of the truck or new feedlot facility can be individually stressful, let alone in combination with each other. Kenny & Tarrant (1987) observed that confinement on a moving vehicle is the most stressful component of transportation. The transport of livestock can have major implications for their welfare, and there is strong public interest and scientific endeavour aimed at ensuring that the welfare of transported animals is optimal (Earley & O'Riordan, 2006; Earley et al., 2010, 2011, 2012, 2013). Physical factors such as noise or vibrations, psychological/ emotional factors, such as unfamiliar environment or social regrouping, and climatic factors, such as temperature and humidity, are also involved in the transport process. Increased neutrophil and decreased lymphocyte numbers following transportation are documented (Earley & O'Riordan, 2006; Earley et al., 2010, 2011, 2012, 2013).

Transport journeys from Ireland to France (23 h) and Italy were investigated both with bulls and heifers, in which the cattle remained in their vehicle transporters (Earley & Murray, 2010; Earley et al., 2012). The percentage of time that bulls spent lying was 63.5% for the sea journey and 35.4% for the journey from the French lairage to the Italian feedlot. While transient changes in physiological, haematological and immunological variables were found in the transported and control animals relative to baseline levels, the values were within the normal physiological range for the age and weight of animals involved. Physiological measurements made after the road and sea journeys indicated that the 24-h rest in the lairage, with hay and water freely available, was adequate to maintain homeostasis. Within the conditions of the studies (Earley & Murray, 2010; Earley et al., 2010, 2011, 2012, 2013), there was no evidence to suggest that the health, welfare or performance of animals was adversely impaired

as a consequence of the transport journeys. Earley et al. (2011) investigated the effect of transport by sea, from Ireland to Lebanon, on performance, physiological, immunological and behavioural responses of bulls and found no evidence to suggest that their welfare was impaired by the journey. Nevertheless, under normal commercial shipping conditions, adverse weather or disease outbreaks (in humans or animals) can prolong the journey or delay the unloading process and thereby pose potential threats to animal welfare. Hence, animal transportation is a very relevant issue for animal welfare and therefore is subject to specific legal requirements such as European Convention for the protection of animals during international transport (1968) and European Council regulation 1/2005 (EU, 2005) on the protection of animals during transport and related operations. Teagasc research on animal transport has informed the latter regulation.

Housing

The main critical issues for beef cattle welfare during housing were identified by EFSA (2006a, 2006b, 2012), the European Commission (2001) and the EU Welfare Quality® project (2009); these include: housing conditions, areas for feeding, walking and resting, space allowance and flooring, social and maternal behaviour, dominance, grouping and regrouping of animals. Most recently, concern for the welfare of finishing cattle, particularly in relation to housing conditions (space allocation and floor type), was expressed at national, EU and OIE levels. There is the view that conventional slatted floors without access to lying areas should be replaced by more animal-friendly systems. Outdoor wintering of beef animals is not an option on many Irish farms due to poaching of ground conditions. Winter housing is therefore a necessary alternative and is dominated by concrete slatted floored sheds. The main floor types used for accommodating beef cattle in Ireland are concrete slatted floors (CSFs), CSF overlaid with rubber mat (RM) and loose bedded systems, mainly containing straw (Mazurek et al., 2010). Many farms have a combination of both these floor types.

As well as facilitating winter feeding and management, accommodating cattle indoors provides additional benefits such as preventing land poaching and protecting animals from inclement weather conditions. Since the 1960s, the number of beef cattle on CSF increased (Wechsler, 2005). Although they cost more to construct initially, CSFs are popular due to the lower labour input required for the removal of slurry than would be required with solid floor systems (Lowe *et al.*, 2001a).

The duration of the indoor housing period varies from 3 to 6 mo depending on climate, soil type and management system. In some systems, particularly with spring-born beef bulls, the housing period is not limited to the winter months as bulls may be housed after their first summer and finished intensively indoors over a period of 9 or 10 mo (Keane & Allen, 1998; Keane, 2003; Drennan & McGee, 2009). While steers tend to have shorter housing periods than bulls, the amount of time they spend indoors is greater as they are usually slaughtered at 24 mo or above (Keane & Allen, 1998; Keane, 2003; Keane, 2010), thus spending two winter periods housed indoors.

There are suggestions to increase the space allowances per animal on CSF to 3.0 m² for a 500-kg animal ± 0.5 m² per 100 kg above or below this (Scientific Committee on Animal Health and Animal Welfare [SCAHAW], 2001). The majority of studies carried out on the effect of space allowance on the performance and welfare of finishing beef cattle on CSF investigated space allowances below 3.0 m². Fisher et al. (1997a, 1997b) reported that housing finishing heifers, weighing 560 kg, at space allowances below 2.0 m², instead of at 2.5 and 3.0 m² per animal, impaired performance and lying time. Furthermore, Hickey et al. (2003a) reported a reduction in carcass weight and a decrease in the production of IFN- γ to the mitogen Concanavalin-A, a marker of cell-mediated immunity, in steers, weighing 610 kg, housed at 1.5 m² per head compared to 3.0 m². Similarly, Gupta et al. (2007) found that housing bulls at 1.2 m² compared to 2.7 m² reduced performance and raised plasma cortisol concentrations suggesting that the performance and stress response of animals at the lower space allowance was inhibited. Keane et al. (2017) investigated the effect of space allowance and floor type on performance and welfare of finishing beef heifers at either (i) 3.0 m², (ii) 4.5 m² or (iii) 6.0 m² space allowance per animal on a CSF and (iv) 6.0 m² space allowance per animal on a straw-bedded floor, for 105 d. The number of heifers lying at any one time was greater on straw than on CSF. Space allowance and floor type had no effect on the number of hoof lesions gained or on any of the haematological or metabolic variables measured. Hence, increasing space allowance has no negative impact on performance but did improve cleanliness.

The increased popularity of CSF led to an increased interest in floor types that combine the labour-saving efficiency of CSF with a softer floor surface (Benz *et al.*, 2002). Rubber mats were developed for this purpose, as they can be overlaid on CSF with relative ease. There are numerous different types of RMs available. The structure of individual varieties can vary greatly in terms of hardness, friction, compression and abrasiveness; therefore, their effects on animal performance and welfare vary greatly between studies. Lowe *et al.* (2001a) compared CSF with CSF overlaid with RM and found no difference in average daily gain (ADG) or carcass weight of cattle. In contrast, Keane *et al.* (2015) reported a greater ADG for cattle on CSF overlaid with the Durapak RM than on CSF, but found no difference in carcass weight.

Wechsler (2011) recommended that CSF should not be used for housing beef cattle and instead must be replaced with alternative floor types such as RM or straw. Previous research showed that cattle on RM can develop more leg swellings (Graunke et al., 2011) and hoof lesions (Earley et al., 2015, 2017; Keane et al., 2015) compared to those on CSF. Others have concluded that the RM may not be the ideal replacement for CSFs however, as they do not provide sufficient claw wear thereby causing overgrown claws (Bergsten, 2010). This can lead to further problems such as heel erosion caused by a displacement of the main load-bearing points (Dembele et al., 2006). The results of Keane et al. (2015) indicate that housing bulls on an RM improved daily live weight: however. this result was not reflected in slaughter or carcass weight. While there was no evidence of lameness in bulls on RM in that study, the increased number of hoof lesions suggests that hoof health may be compromised. In a recent study, Earley et al. (2017) reported similar findings in finishing beef steers using three different RMs. Prior to the adoption of concrete slatted housing, the most common floor type for cattle housed indoors was straw bedding (Maton et al., 2012). From an animal welfare perspective, straw bedding is preferable (Burgess & Hutchinson, 2005) as cattle display a strong preference for straw bedding and would rarely choose to lie on a slatted floor if there was any other floor type available (Lowe et al., 2001b). However, straw bedding has its limitations in relation to labour efficiency, space requirements, straw availability and cost (Tuyttens, 2005). For example, in Ireland, if all beef producers replaced CSF with straw-bedded systems, the national supply of straw would run out within 1 mo (Wilkinson, 1998).

Additional topics at present that feature most prominently are (i) antimicrobial use and resistance, and (ii) calf health, with particular reference to factors affecting morbidity and early mortality. The two topics are interdependent and are addressed in more detail in Mee *et al.* (2022).

Pig welfare

Pigs are protected by a specific EU directive (Council Directive 2008/120/EC) which lays down minimum standards for their protection (e.g. standards relating to flooring, living space, access to materials for rooting). Most Irish pigs are managed in high-density, low-complexity environments, which are sub-optimal with regard to the animals' biological needs. Unfortunately, the consequence is a high prevalence of health and welfare problems for pigs across all production stages (piglets: Quinn *et al.*, 2015; sows: Boyle *et al.*, 1998, 1999; Quinn, 2014; weaner, grower and finisher pigs: Quinn, 2014; van Staaveren *et al.*, 2017, 2018; da Costa *et al.*, 2020).

Sows and gilts

Tethering of pregnant sows (permanently tied by a collar around the neck or chest for the duration of pregnancy) was

common in the EU for several decades, until it was banned from 2006 under the 1991 Pigs Directive. In the lead up, a longitudinal assessment of skin lesions in stall-housed sows throughout the production cycle and a cross-sectional study of the same lesions in tethered and stall-housed pregnant sows were conducted on 25 commercial pig farms (Boyle *et al.*, 1999). In general, there was a high prevalence of lesions to the hind limbs, reflecting the difficulty for sows of manoeuvring in close confinement and the unforgiving nature of the flooring used. Boyle *et al.* (1998) also determined that high culling rates in the early parities for reproductive failure, locomotor problems, disease and injury reflected major challenges to gilts' ability to adapt to close confinement on entering the breeding herd.

Given these issues it was not surprising that in 2008 the EU imposed a partial ban on sow stalls (Council Directive 2008/120/EC), which came into force on 1 January 2013. This required sows to be group housed from 4 wk after service. However, aggression between sows at mixing, during competition for access to resources and due to hunger, is a major cause of stress and injury, and can have a negative impact on sow reproductive performance (Read et al., 2020; Lagoda et al., 2021). Research on group housing was already underway in Ireland prior to the EU ban (e.g. Boyle et al., 2002a; O'Connell et al., 2003, 2004; O'Connell, 2007) prompted by the demand from the UK which banned gestation stalls in 1998. Subsequent investigation of high-fibre diets and foraging substrates, both requirements of EU legislation (Stewart et al., 2008, 2010, 2011), aided identification of strategies to improve welfare. Research comparing group and stall housing systems for pregnant sows confirmed the major problem of lameness in the former (Calderon Diaz et al., 2014), and epidemiological research on lameness in all classes of pigs confirmed that the ubiquity of fully slatted concrete flooring on Irish pig farms was a major contributory factor (Quinn, 2014). On-farm research then found that rubber flooring had considerable benefits to sow welfare, locomotory ability, reproductive performance, etc. during pregnancy (Calderon Diaz et al., 2013, 2014; Calderón-Díaz & Boyle, 2014a, 2014b; Lagoda et al., 2021) although these did not carry over to during the farrowing/lactation period (Calderon Diaz & Boyle, 2014a).

On most Irish farms, gilts destined to enter the breeding herd are treated in the same way as finisher pigs, and fed diets designed for fast growth rates and lean meat deposition. However, Quinn (2014) confirmed hypothesised benefits of preferentially treating young replacement gilts in terms of diet and housing on farm. Furthermore, terminal line gilts fed a restricted diet formulated for fat rather than lean deposition and supplemented with minerals for optimal bone and joint development had improved locomotion scores likely associated with slower weight gain (Quinn *et al.*, 2015). More recent work by Hartnett *et al.* (2019, 2020a) confirmed that integrating supplementary minerals into maternal line gilt diets improved joint health (i.e. less cartilage damage), reduced claw lesion severity and improved production performance throughout life (Hartnett *et al.*, 2020b).

Hartnett *et al.* (2020a) showed that keeping replacement gilts in all-female groups from weaning was likely responsible for the benefits described above, as gilts were exposed to less sexual and aggressive behaviour performed by the males. Ireland is one of few European countries that raises male pigs as entire boars. This offers welfare advantages to piglets as they are spared surgical castration in the first week of life (Llamas Moya *et al.*, 2006a, 2006b, 2008b, 2008c). However, pigs in entire male pig production systems suffer challenges to welfare later in life arising from intense aggressive and sexual behaviour during the finisher (Bjorklund & Boyle, 2006; Teixeira & Boyle, 2014) and pre-slaughter (van Staaveren *et al.*, 2015) stages.

Farrowing facilities

Sows are usually confined in crates for the farrowing and lactation period to protect piglets from crushing, and enable quick, safe and easy checking of the animals by the stockperson. Protection from crushing is ever-more important with the increases in litter size that occurred due to selection for higher sow productivity (Boyle et al., 2022). Larger litters are also associated with increased competition between piglets for access to a teat and considerable fighting between piglets when trying to establish the "teat order" (Fraser & Thompson, 1991). Associated injuries to the sows' teats and piglets' faces are reduced by clipping the needle teeth; pilot work at Teagasc demonstrated that leaving these teeth intact results in facial lesions and reduced growth rate for piglets during the first three critical days of life (O'Driscoll & Schmitt, 2016). However, even when carried out for welfare reasons, teeth clipping can still cause immediate and long-term pain (Sinclair et al., 2018), and as such is regulated under Council Directive 2008/120/ EC. An alternative is grinding, which has benefits for sows and piglets (Lewis et al., 2005a, 2005b, 2005c; Llamas Moya et al., 2006a, 2006b). Providing piglets with shredded paper and ropes in the farrowing crate redirects their behaviour away from the sow and may also help to reduce lesions (Lewis et al., 2006).

Even older research on farrowing facilities extends back to the mid-1990s when the injurious nature of floor types used in farrowing crates for piglet skin and feet as well as negative impacts on piglet behaviour were documented (Leonard *et al.*, 1996a, 1996b; O'Connell *et al.*, 1996). Early research also documented the injurious nature of confinement in farrowing crates for sows (Boyle *et al.*, 1999, 2000a, 2002a, 2002b). One of the first attempts to reduce injury and improve sow comfort was through the use of RMs in the farrowing crate (Boyle *et al.*, 2000b).

The introduction of group housing during gestation posed yet another new challenge for gilts and sows: freedom during pregnancy (or most of their life to that point), followed by sudden confinement prior to farrowing, can act as a stressor (Boyle et al., 2000a, 2002a; Baxter et al., 2011). However, a strategy whereby sows are confined only from the initiation of milk let-down until 4 d post-farrowing (i.e. free lactation) could somewhat address this issue. Indeed sows in free lactation pens have improved locomotory ability at weaning relative to sows in crates, use all orientations in the pen and have less tear staining under the left eye (indicative of mental stress; DeBoer et al., 2015) at weaning (Kinane, 2020). Most importantly, mortality was not higher than in standard crates; there was slightly more crushing in the free lactation pens after the crates were opened, but this was offset by fewer deaths from hunger and failure to thrive (Kinane et al., 2021). Piglets from the free lactation pens also tended to perform less damaging behaviour, weighed more at weaning, were significantly heavier at slaughter and took fewer days to reach the target weight of 105 kg.

Tail biting

Irish producers recognise tail biting (a behavioural disorder which occurs when pigs experience a level of stress which is beyond their coping abilities) as a serious issue (Haigh & O'Driscoll, 2019), although over 99% of Irish pigs' tails are docked to prevent biting, and about two-thirds of tails exhibit some evidence of damage (Harley et al., 2012, 2014). Inability to perform natural behaviours and inadequate housing and management are the primary triggers (D'Eath et al., 2014; Valros, 2018). Improving compliance with the ban on routine tail docking is currently one of the European Commission's priorities in the area of animal welfare (Nalon & De Briyne, 2019). However, a significant challenge in Ireland is the physical structure of most pig facilities (e.g. fully slatted systems) which means that the recommended gold standard enrichment material, straw bedding on the floor of the pen (D'Eath et al., 2014), cannot be provided.

Initial Irish research focused on a dietary solution. However, neither Mg supplementation nor a higher fibre level in the diet (both of which were hypothesised to have a calming effect) reduced biting or damage to tails (O'Driscoll *et al.*, 2013a, 2013b; Chou *et al.*, 2020a). Work conducted on commercial farms attempted to identify enrichment materials which could be attached to the walls; soft wood, such as spruce, was identified as being more favourable to pigs than harder wood (beech, larch and Scots pine; Chou *et al.*, 2018), or than compressed straw blocks (Haigh *et al.*, 2019). Indeed, soft wood and rubber are used more often by pigs than harder items (Chou *et al.*, 2020b). However, these materials were

insufficient alone to prevent biting outbreaks in undocked pigs (Chou *et al.*, 2020a). As such, Teagasc research moved on to investigating greater enrichment allowances, including racks of loose material (Chou *et al.*, 2019, 2020c; D'Alessio *et al.*, 2021; Misra *et al.*, 2021); grass was favoured by pigs over straw, paper and miscanthus (Chou *et al.*, 2019). Future work will aim to identify materials which are easily available, affordable, have a low biosecurity risk and can be stored without risk of degradation.

Link between pig welfare and pig health

On-farm research by Teagasc documented poor welfare arising from sub-optimal management and housing practices (Diana *et al.*, 2019a; da Costa *et al.*, 2021) and associated deficiencies in performance and health and increased mortality (Calderon Diaz *et al.*, 2017a, 2017b, 2018). Antibiotics are viewed by farmers as the most cost-effective way to address health and performance challenges, and thereby protect pig welfare (Diana *et al.*, 2021), but from January 2022 any prophylactic use is banned. However, Teagasc research found that by removing in-feed medication in current systems, and by employing good management and housing practices, there are no adverse effects on pig health, welfare or productivity (Diana *et al.*, 2017, 2019b).

Poultry welfare

Most European citizens consider it is important to protect the welfare of farm animals (European Commission, 2016d), and there appears to be particular concern about the welfare of poultry (Clark et al., 2016). The use of cages for laying hens is particularly contentious. While conventional or "battery" cages were prohibited under EU legislation from 2012, there is now increased momentum to move to cagefree systems entirely. This would invariably provide birds with more behavioural freedom, but is associated with increased mortality (Weeks et al., 2016). In free-range systems, this mortality may result from a variety of causes including disease, smothering and predation (Elson, 2015; Rayner et al., 2016; Bestman & Bikker-Ouwejan, 2020). Some of the welfare issues associated with cage-free production contributed to increased interest in the use of more "robust" breeds of hens that are better able to cope with these environments (e.g. Fernyhough et al., 2019).

Concern over the use of cages means much of the public conversation about poultry welfare focused on the laying hen sector in recent years. This section will therefore focus on the broiler chicken sector, the scale and importance of which was outlined in the Introduction. There are different aspects of broiler production that could be discussed, including welfare during handling, transport and slaughter, and specifically of broiler breeders. Our focus, however, will be on environmental enrichment strategies for broiler chickens in order to reflect a key research theme on the island of Ireland. The majority of broiler chickens are reared indoors over a 5-6-wk period in groups of more than 20,000 birds. The fact that they can reach slaughter weight in such a short time reflects, to a large extent, targeted genetic selection for production traits such as growth rate. This rapid growth is associated with health and welfare problems, including leg health issues and cardiovascular disease (see EFSA, 2010; Hartcher & Lum, 2019), and genetic selection strategies are associated with reduced activity levels (McLean et al., 2002). Levels of activity often decline with age (Weeks et al., 2000), and this inactivity can further add to health problems. While there is much focus on bird genetics, low levels of behavioural activity may also reflect lack of appropriate stimulation within housed systems. This is supported by the fact that increased activity is shown by fast-growing broilers in response to certain environmental enrichment (Riber et al., 2018).

In order to address welfare concerns while also meeting global demand for chicken meat, there is increased interest in developing enhanced housing systems and using slowergrowing breeds. This is evident in the commitments being made by many leading companies in the food supply chain (European Chicken Commitment, 2018). It is also evident in the enhanced housing systems already emerging from within the industry. Research into the use of slower-growing breed types gathered pace in recent years, and studies show benefits including improved health and reduced mortality (Rayner et al., 2020) and improved gait (Dixon, 2020). Continued evaluation of the welfare outcomes of different slower-growing breed types reared under commercial conditions would be beneficial. Enhanced housing systems typically involve provision of environmental enrichment items, natural light and additional space. These systems emerged as part of voluntary initiatives or quality assurance schemes, and there is significant progress in recent years in capturing actual welfare outcomes of these strategies on commercial farms. This is essential to ensuring that these policies have a tangible effect on broiler welfare, and progress in relation to this area will be discussed in more detail below.

Environmental enrichment items

Environmental enrichment items in commercial broiler houses provide birds with an opportunity to engage in highly motivated behaviours, and may also stimulate general activity levels and consequently improve leg health. While there is a wealth of research into appropriate environmental enrichment for pigs, the same does not appear to apply with broiler chickens. This is perhaps reflected in the fact that provision of enrichment items to broiler chickens is not required under EU legislation. As mentioned, however, these items are often required as part of quality assurance schemes or by others in the sector such as retailers. While this is a very positive step, it is important to ensure that what is provided meets the needs of the birds. The enrichment items typically provided on commercial farms include straw bales, pecking objects and perches, and research shows that these items are used by broilers. For example, research conducted in Northern Ireland by Baxter et al. (2018b) showed that an average of 30 birds clustered around straw bales on commercial farms, suggesting that they provide perceived protection. The birds also dismantle the bales over time on commercial farms, which helps to maintain litter quality, and also sometimes use them as perches. Research by this group also showed that pecking objects such as string and chains are used quite frequently by broiler chickens (Bailie & O'Connell, 2015; Baxter & O'Connell, 2019). For this type of enrichment item, more research is needed on optimum level of provision. Providing pecking objects such as string at minimum levels stipulated in some high welfare quality assurance schemes (e.g. 1 per 1,000 birds) does not appear to lead to sustained beneficial effects on general activity levels or leg health in commercial broilers (Bailie & O'Connell, 2015; Bailie et al., 2018b). Similarly, research in commercial windowed houses showed limited benefits of providing 1.3 straw bales per 1,000 birds on general activity levels and leg health (Bailie et al., 2013), and no additional benefits of increasing levels to 2 bales per 1,000 birds (Bailie & O'Connell, 2014).

Perching is a highly motivated behaviour in chickens, but the type of perch provided on commercial farms is likely to have a significant impact on beneficial effects. Bailie & O'Connell (2015) did not find any significant benefits of providing standard bar perches in commercial broiler houses on activity levels and leg health. Subsequent research by Bailie et al. (2018a) demonstrated a preference among fast-growing birds for platform rather than bar perches, which corresponds with findings by Norring et al. (2016). This preference may be linked to the conformation of the bird, and further research will be needed to determine optimum perch type for slowergrowing breed types. As with other types of enrichment items, more evidence is needed on optimum level of provision of perches. Recently, Baxter et al. (2020) investigated four different levels of platform perch provision (0, 0.5, 0.6 and 0.7 m²/1,000 birds) in commercial houses. They found evidence of reduced fearfulness among birds when platform perches were provided, and high levels of perch occupancy in all treatments (on average 11.5 birds/m²), but no significant differences between treatments in terms of average gait score or activity level.

It may also be important to design environmental enrichment strategies that facilitate other important behaviours in broiler chickens. These birds are motivated to perform dustbathing but litter in commercial houses may not always be suitable for this type of behaviour. Research by Baxter et al. (2018a) investigated the preferences of broiler chickens for different dustbathing material (including peat, oat hulls, straw pellets, clean wood shavings and standard litter), and found more dustbathing behaviour in peat and oat hulls than in the other materials provided. Follow-on research investigated the effect of providing discrete dustbaths filled with oat hulls in commercial broiler houses and showed that they promoted more foraging behaviour than straw bales (Baxter et al., 2018b). Importantly, the provision of dustbaths also led to a significant improvement in gait score at the end of the production cycle. This whole-house effect on this leg health measure demonstrates the potential benefits achievable with appropriate environmental enrichment. The engagement that the broilers showed with dustbaths led to further research to investigate if use of other types of enrichment such as pecking objects may be increased by placing them within "activity clusters" containing both dustbaths and straw bales (Baxter & O'Connell, 2019). There were no obvious beneficial effects on use of the enrichment items when they were clustered together rather than distributed separately throughout the house; however, further research on optimum placement of enrichment items within the house would be beneficial. This will be aided by developments in tracking technology (e.g. Baxter & O'Connell, 2020) which will enable long-term monitoring of the use of different parts of the house by broiler chickens.

Light and space

Under current EU legislation, broilers must be provided with at least 6 h of darkness in each 24-h period during much of the production cycle. Research by Schwean-Lardner et al. (2012, 2013) indicated that longer dark periods were beneficial for bird welfare. This might be particularly important at the start and the end of the production cycle when longer light periods are permitted. The quality of light provided also appears to have a significant impact on broiler welfare. Bailie et al. (2013) investigated the effects of providing commercially housed broilers in Northern Ireland with access to natural light through windows and found significant benefits in terms of activity levels and leg health. This and more recent research by De Jong & Gunnink (2019) appear to validate a requirement to provide natural light within enhanced housing. These effects may reflect the increased intensity of light and also the presence of ultraviolet (UV) wavelengths in windowed housing (Bailie et al., 2013). Research evidence from commercial systems also supports the provision of additional space. In a study involving almost 2 million birds, Bailie et al. (2018b) showed increased severity of dermatitis lesions when stocking density increased from 30 to 34 or 36 kg/m². Dawkins et al. (2004) also showed evidence of poorer gait at higher stocking densities in a large on-farm trial that

evaluated space allowances of 30, 34, 38, 42 and 46 kg/m². Importantly, however, they also indicate that conditions on the farm (likely linked to litter and air quality) had a more important impact on broiler welfare than the space allowance provided.

Conclusions

The science of animal welfare has evolved considerably over the last 60 yr and with it the recognition that animals are sentient beings. This is partly due to changing attitudes towards animals and also to the increased intensification of animal production in western countries. Although this intensification greatly increased efficiency and levels of production from animal agriculture, it also brought new problems to be addressed by animal and veterinary scientists, as well as a questioning of many farming practices by the consuming public. The OECD (2020) acknowledged that animal welfare is an emerging trade issue, and the international conventions already in place and ongoing work with the OIE confirms this. Throughout this review, emphasis was placed on the scientific evidence informing three main aspects of livestock animal welfare: (i) physical health and well-being; (ii) naturalness, meaning that animals can express normal behaviour; and (iii) subjective states, in that animals experience positive states and that negative states (e.g. pain) are minimised.

Acknowledgements

The authors acknowledge the research funding they have received over the years and the invitation to write this paper from the *Irish Journal of Agriculture and Food Research*. The broiler chicken element of the paper includes material summarised from a chapter prepared by N. O'Connell for a publication funded by Eurogroup for Animals (Eurogroup for Animals, 2020).

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Perspectives Paper • DOI: 10.15212/ijafr-2020-0153 IJAFR • 61(1) • 2022 • 109-125



Irish Journal of Agricultural and Food Research

An overview of Irish pig production, research and knowledge transfer since 1960

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Abstract

Pig production in Ireland has gone through enormous changes during the past 60 yr, from pigs being primarily produced as a sideline on dairy farms, to an industry with one of the highest average herd sizes in Europe. This happened in part due to external pressure on the industry, whereby economies of scale were needed to compete with pigs produced in other countries, but largely due to the instigation of national programmes to support the pig industry through research, education and knowledge transfer. These efforts helped producers to take advantage of genetic improvements and monitor their own performance over time, as well as allowing for benchmarking of the national herd against other countries. The research programme initiated in the 1960s continues to grow and expand, providing the pig industry with internationally renowned data and knowledge in the areas of nutrition, animal welfare, the environment and energy use. Recent initiatives such as the establishment of the Teagasc and Irish Farmers Association Pig Joint Programme, and a Pig Health Check section in Animal Health Ireland, will help to promote further cross-collaboration between stakeholders in the pig industry, and enable it to rise to the challenges of the years ahead.

Keywords

Environment • health • legislation • management • nutrition • performance

Introduction

Pig production is a major sector of the agricultural economy of Ireland. It ranks third in gross agricultural output (8%) after milk and beef, and the value of pig meat exports in 2020 was almost \in 1 billion. Traditionally, pigs were produced alongside the dairy sector, as historical by-products of dairy production (whey and skim milk) provided an excellent and cheap source of feed for pigs. However, the structure of the pig sector in Ireland transformed during the past 60 yr. In 1960, there were 111,000 pig famers with an average herd size of eight pigs, and a national output of \leq 1 million pigs. Today Ireland has 280 commercial pig farms comprising ~200 sow breeding/ integrated farms with an average herd size of ~700 sows and ~80 specialised finishing farms, and a national output of 3.8 million pigs (Teagasc, 2021 personal communication).

Up to the 1960s, most farms comprised of small breeders with a few sows producing pigs for finishing on their own farms, or for sale to specialised finisher farms. An initiative undertaken in the 1960s by the Department of Agriculture (Department of Agriculture, Food and the Marine [DAFM] today) was the development of pig cooperatives where small breeders could sell their weaned pigs at 25–30 kg live weight for finishing in a central farm. This allowed small breeders a share in the profit from finishing pigs to slaughter. However, it soon emerged that mixing of pigs from several farms resulted in disease incidence, which led to this system ceasing. Thus, over time, the production model in Ireland evolved from small breeding and specialised finisher farms, to the "integrated pig farm" which breeds, rears and finishes pigs all produced on the same farm.

The Teagasc Pig Development Department

One of the most significant developments for the Irish pig sector occurred in 1959, when Dr Jim O'Grady was appointed to the Moorepark Research Centre (part of the new agricultural research institute to become known as An Foras Talúntais,

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AFT). Because of the close linkages between pigs and milk production at farm level at the time, it was decided that pig research should be located at the same campus as the dairy research centre. Jim was tasked with developing the facilities and programme that would provide the vital technology for what was to become an internationally competitive pig production sector. His initial team included technicians Tom Gardiner and Sean Scanlon, who oversaw the construction of an 80-sow farm with farrowing pens and dry sow accommodation on straw, with individual feeders. Indeed, in 1968 Moorepark was one of the first farms in Ireland to fit individual stalls for pregnant sows to allow tailored feeding for individual animals. A strategic programme was developed aimed at providing the technologies for housing, feeding and fertility that would revolutionise the Irish pig industry over the following decades.

Early experiments focused on feeding sows during pregnancy and lactation. Subsequently, the first major experiment compared the Jordan (an uninsulated concrete structure originally used in Northern Ireland, later to become known as the "sweat box"), the Solari (a hayshed-type structure with kennels, under which the pigs slept with straw stored on top) and the Danish house (the most expensive of the three, it had a single feeding passage through the centre and small pens on each side, with a feed trough parallel to the passage).

In the late 1960s, the research team was further strengthened with the recruitment of two new scientists, Tom Hanrahan and Brendan Lynch. This led to a massive expansion in the research programme, especially in the area of feeding and nutrition, and subsequent dramatic improvements in the efficiency of pig production at farm level. The late 1960s saw the development of the "Moorepark Diet", a barley-soya bean meal diet, which became the standard diet for finisher pigs and, with subsequent improvements over the years, it remains the benchmark diet to date in Ireland. Moorepark also developed blueprints on housing and hygiene, which enabled the further development of large farms.

Knowledge transfer

Dissemination of research from Moorepark and further afield came about via nationally funded advisory services, operated over the years by the Department of Agriculture, the County Committees of Agriculture, the national advisory and training body (ACOT) and currently, by Teagasc. In 1970, two young agricultural graduates, Pat Tuite and Michael Martin, were appointed Specialist Pig Advisors by the Department of Agriculture. As the pig sector developed, it became clear that specialisation was needed and Pat and Michael put together a national team of eight Specialist Pig Advisors in the early 1980s. In the mid-1990s, the pig research and advisory departments were amalgamated into the Pig Development Department (PDD).

Education

Skilled staff, motivated to deliver a high level of technical performance, are essential in pig production. Education and training for staff to supply the pig sector was initially provided at Mellows College, Athenry where the Certificate in Pig Husbandry trained managers and skilled stock persons for the industry from 1969 to 2003. Numbers in the first year of the course peaked at 32. However, a greater range of training options outside agriculture and the fall from favour of narrow agriculture-only courses in general contributed to the demise of the course. The final intake of six was in 2000 and of these, four graduated in 2003. This created a dearth of skilled labour, which in the short term was part-filled by foreign-born labour, particularly from Eastern Europe. However, in 2009 the PDD initiated a level-5 certificate in Agriculture (Pig Production; National Framework of Qualifications Level 5) which has since trained 140 students. A level 6, advanced certificate in agriculture (Pig Management), followed in 2018.

The joint programme

The PDD has always worked closely with pig farmers, and in 2012 Teagasc and the Irish Farmers Association agreed on a "Pig Joint Programme", which facilitated the recruitment of additional researchers, advisors and technical support for the research and advisory programme. This led to a significant increase in the capability of the PDD. On the research side, the PDD currently hosts ~12 postgraduate students and 4 postdoctoral researchers at any one time, compared to ~4 and 2, respectively, prior to the joint programme's establishment. Along with this, in 2016 a newly built Teagasc Pig Research Facility, which could accommodate 200 sows and their offspring, opened in Moorepark. This facility contains stateof-the-art feeding systems (both wet and dry), a "baby-feed" system for pre-weaned and immediately weaned pigs, as well as specialised facilities and equipment to measure individual pig intake, detailed animal behaviour testing and measures of physical condition (e.g. blood sampling, hoof scoring, etc.). With regard to knowledge transfer activities, this greater critical mass allowed the PDD to establish multiple outreach activities which were previously not possible, through a dedicated communication officer. These activities include a monthly newsletter, a bi-monthly podcast "The Pig Edge", a dedicated Twitter account, an annual research dissemination day, facilitated pig farmer discussion groups across all regions of the country, a regularly updated suite of infographics and posters for use on pig farms, and a YouTube "skills series". In addition, the Pig Research Facility releases a video diary every month, so that stakeholders can stay up to date with research and performance indicators. The success of the joint programme is evidenced in the results of an external peer review across all the livestock sectors in Teagasc, carried out in 2017. Not only did the PDD rank highest within Teagasc,

but the Peer Assessment Panel described the PDD as "one of the largest and arguably best applied pig research/extension programmes operating globally today".

Improvements in performance

Key performance indicators (KPIs) are important in the management of any business, as they enable business owners to make decisions using data, and monitor those decisions. Teagasc Pig Advisors have worked with pig producers over the years to develop a number of industry-relevant KPIs. These were initially collated from the mid-1990s using the Teagasc PigSys recording system, and in 2014 the system was switched to the Teagasc eProfit Monitor (ePM) recording system. Participating pig farmers submit their data to their Teagasc Advisor on a quarterly basis, and the data from all participating farms are compiled and published by Teagasc as the "National Pig Herd Performance Report" each year. Although not available since 1960 (when the average litter size was 11.4 piglets, sows produced 15 pigs/yr and feed conversion efficiency from weaning to sale was 4.0), annual data are compiled since 2000.

Data were collected from 141 farms in 2000 (average of 400 sows/herd), 98 farms in 2010 (average of 654 sows/herd) and 88 farms in 2020 (average of 799 sows/herd). The database currently represents over 55% of the Irish sow herd.

KPIs over the years

Table 1 provides an overview of the main KPIs used in the Irish pig industry and provides values for 2000, 2010 and 2020. Numbers born alive (BA) per litter have risen steadily with a 30% increase between 2000 and 2020. Although the number of litters per sow per year is stable, this meant an increase of 28% in pigs produced (sold) per sow per year in 2020 relative to 2000. Between 2000 and 2020, there was an increase in live sale weight of 25.2 kg, and an increase in deadweight (carcass weight) of 20.1 kg. Indeed, average daily gain (ADG) from weaning to sale has improved by 150 g per day over the same period. The increase in pigs produced/sow per year and carcass weight of each pig has contributed to more pig meat sold/sow per year (an increase of 66% between 2000 and 2020). The amount of feed required to produce each kilogram of carcass is also decreasing over time, and can be seen in the drop from 3.66 to 3.50 kg of feed to produce a kilogram of pig meat.

The market for pig meat

In 1960, Ireland recorded an annual pig throughput of just under 1 million pigs (3.8 m today) equating to 71,586 t of pig meat valued at almost IR£160 m. Slaughter pigs were
 Table 1: Key performance indicator values from the Irish pig industry in 2000, 2010 and 2020

| | 2000 | 2010 | 2020 |
|--|-------|-------|-------|
| Measures of sow performance | | | |
| Litters/sow per year | 2.29 | 2.32 | 2.31 |
| Born alive/litter | 10.85 | 12.01 | 14.26 |
| Piglet mortality % | 9.0 | 9.9 | 11.1 |
| Weaner mortality % | 2.6 | 2.4 | 2.8 |
| Finisher mortality % | 2.3 | 2.5 | 2.7 |
| Pigs produced/sow per year | 21.5 | 23.9 | 27.5 |
| Performance weaning to sale | | | |
| Liveweight at sale (kg) | 90.1 | 103.6 | 115.3 |
| Deadweight at sale (kg) | 68.1 | 78.9 | 88.2 |
| ADG (g) | 585 | 668 | 735 |
| Feed conversion efficiency | 2.34 | 2.47 | 2.40 |
| Pigmeat produced | | | |
| Carcass weight sold/sow per year (kg)* | 1471 | 1886 | 2426 |
| Total feed/sow (kg) | 5385 | 6966 | 8488 |
| kg feed/kg of carcass | 3.66 | 3.69 | 3.50 |

(Source: Teagasc PigSys herd recording system, 2000, 2010, replaced by Teagasc eProfit Monitor, 2020).

*This is the pigs produced/sow/year multiplied by the average deadweight at sale.

ADG = average daily gain.

processed in 38 factories or "curers" operating at the time at various locations throughout the country. The organisation of the pig meat market throughout the 1960s remained under the control of the Pigs and Bacon Act (PBA) first introduced in 1935. The PBA and subsequent amendments were a set of national measures aimed at stabilising the market, which was subject to large fluctuations, to ensure orderly and reasonably profitable pig production on the island. Established in 1939 under the PBA, the Pigs and Bacon Commission regulated the production and marketing of pig meat and was responsible for managing Irish pig meat exports via a quota arrangement with individual curers.

The shift to modern pig management systems from the mid-1980s brought about major rationalisation and investment in the sector, which helped Ireland to develop an internationally competitive export-orientated pig meat industry (see Table 2). The impact of EU membership, government policy, technological developments and market forces influenced the type of pig products exported in the intervening years. Ireland is over 200% self-sufficient in pig meat and in recent years has shown exceptional growth in exports. In 2020, the Irish product was exported to over 50 different countries throughout

| | Gross output | | Expo | orts |
|------|---------------------|---------------------|---------------------|--------------------|
| | Output ¹ | Volume ² | Volume ² | Value ³ |
| 1970 | 1.93 | 128.7 | 45 | 68 |
| 1980 | 2.38 | 154.3 | 54 | 87 |
| 1990 | 2.37 | 156.9 | 54 | n/a |
| 2000 | 3.15 | 230.4 | 121 | 270 |
| 2010 | 2.66 | 214.3 | 134 | 317 |
| 2020 | 3.54 | 320.0 | 317 | 586 |

 Table 2: Details of the pig meat sector at 10-year intervals from

 1970 to 2020

Source: the Central Statistics Office.

¹Million head

²Thousand tonnes.

³Million €.

Willion C.

the world. The UK has remained a principal market for Irish pig meat exports dominating supplies since the 1960s. The outbreak of African swine fever (ASF) in 2018, particularly in China, dramatically reshaped the global meat market and its trade patterns. Shipments of Irish pig meat to the Asian market now account for 47% of the total volume and 41% of the total value of exports, with China being the leading destination for Irish product in 2020. Asian markets have now overtaken the UK market in terms of both volume and value for Irish pig meat exports. The UK market as our closest neighbours, however, will still remain a key market in the future for Irish pig meat accounting for 30% of the total value and 23% of the total volume of exports in 2020 (Bord Bia, 2021).

Genetics and breeding

One of the major reasons for the improvements in the aforementioned KPIs is a change in pig genetics. In the early 1960s in Ireland, the pig industry was composed of many small individual pig breeders, each specialising in one or two pig breeds. These breeders competed in national shows (e.g. the Irish Spring Show), for the prize of National Champion Boar for each individual breed. Indeed this national competition lasted until the mid-1980s. However, by that stage there was a significantly reduced number of Irish pig breeders, and along with an increased awareness of disease transmission/biosecurity and consequently a reluctance to risk bringing pigs to public shows/events, the competitions were no longer sustainable.

The development of larger pig farms from the 1960s, and the shift into modern pig production, coincided with the introduction of the Landrace and Large White breeds and their establishment as the predominant breeds. A government breeding programme in the mid-1960s, supported by the importation of high-quality breeding stock, brought about initial rapid improvements in carcass leanness. In more recent years, the pig breeding industry developed independently from government programmes, and since the 1990s a new model emerged. The number of Irish pig breeders declined until only Hermitage Pigs remained as the last of the original pedigree pig breeders in the Irish Pig Herd Book, and currently only four genetic sources supply the Irish market. This followed an international pattern, whereby since the 1990s the global pig genetic companies amalgamated. The large-scale uptake of artificial insemination (AI) in the commercial pig production sector means that today pig breeding is almost 100% by AI. The dominant breeds remain the Landrace and Large Whites, with the Duroc breed also gaining in popularity in recent years.

Rate of genetic change

Adoption of AI in Ireland during the late 1980s means that at each service a high genetic merit boar can now inseminate 20 sows instead of one. National, and eventually international, AI delivery increased access to high genetic merit boars, contributing to the emergence of global pig genetic companies. These larger companies, along with the greater use of BLUP (Best Linear Unbiased Prediction) computing and genomic selection, allowed for increased accuracy and acceleration in genetic improvement for key performance/economic traits during the last 20 yr. Indeed, pigs were initially considered "dual purpose" (i.e. equally suited for breeding and finishing) but since the 1980s are separated into separate breeding goals for sire and dam lines.

The focus on dam-line fertility largely concentrated on 1) reduction of the weaning-to-service interval (WSI) and 2) increasing the number of piglets BA. Advances in fertility were initially made by individual breeders with small "nucleus" herds, and therefore genetic progression was slow, but this increased rapidly after the consolidation of the industry. This is evidenced by the increases in BA in Ireland (Table 1). Unfortunately, the strive for higher BA over this period was negatively correlated with birth weight, and positively correlated with within-litter variation in birth weight and increased pre-weaning mortality. Wientjes et al. (2012) estimated that the average birth weight fell by 40 g for every extra piglet born; therefore, over the last 20 yr an increased BA of 4 pigs/litter equates to an estimated average reduction in birth weight of 160 g/piglet. As such, in recent years the industry introduced a "survivability by day 3/5" into their damline selection traits.

The split into separate breeding goals for sire-line and damline allowed for a significant increase in sire-line growth rates and feed efficiency (FE), and by extension, reduced back-fat and increased lean meat percentage. Indeed, these traits improved even though sale weight has increased steadily over the last 21 yr (Table 1); the average growth rate from weaning to sale increased by 150 g/day (585 g to 735 g) even though birth weight decreased by ~160 g/pig over the same period.

The challenge of rearing large litters

As a result of recent increases in litter size, sows are often not capable of rearing all of their own piglets to weaning, because the number of piglets increasingly exceeds the number of teats. Additionally, larger litters are associated with a decrease and variation in piglet birth weight, meaning piglets are increasingly susceptible to injury and death (Calderón Díaz *et al.*, 2017). Thus, the genetic changes listed earlier have resulted in concurrent changes to sow and piglet management.

Cross-fostering (CF) is the practice whereby piglets are moved between sows to match piglet and teat numbers, and to even up piglet sizes within litters, when sows are all within the same farrowing batch. It often occurs throughout lactation, although usually during the first week. Results from a recent survey conducted on 79 Irish pig farms show that in 51.9% of farms CF takes place 4 d after farrowing and in 46% of farms, only late CF is practiced (unpublished data). However, movement is stressful for piglets (they need to repeatedly attempt to establish their own teat on the udder), and ultimately results in lighter carcass weights, greater risk of mortality and greater risk of pericarditis and heart condemnations (Calderón Díaz et al., 2017, 2018). Average daily gain was reduced by 21 g/d for CF piglets, resulting in them being ~550 g lighter than nonfostered piglets at weaning. Moreover, the heavier the piglet was at birth, the more detrimental the effect of CF (i.e. greater the differences in weaning weight between piglets that were or were not CF; O'Driscoll et al., manuscript in preparation). A piglet may end up being moved several times if care is not taken to monitor piglet movement, and as such Teagasc recommend tagging all CF piglets.

Nurse sow strategies are an alternative, highly structured, version of CF, used when multiple sows in a batch have more piglets born than teats available. The nurse sow is a sow later into lactation. If her piglets are at least 21 d old, they are weaned, and if not, they are moved to another sow, who has had her own piglets moved off of her (again, weaned or moved to another sow). Newly born piglets from multiple large litters are then moved to the nurse sow at between 12 and 24 h after birth, once they consume colostrum from the mother. Thus a new litter of very young piglets is formed, rather than piglets entering an already established one.

Teagasc research found that when nurse sows were left without piglets for 3 h, all accepted their new litter (Schmitt *et al.*, 2019a). There was intense fighting between piglets at nursing during the first few days, which was associated with piglets completely missing nursing bouts, until the teat order was formed about 1 wk later (Schmitt *et al.*, 2019b). Interestingly, this research also found that when piglets were moved as a litter to a new sow, there was an increase

in piglets switching teats during nursing. This suggests that the teat order was disturbed just by the transfer onto a new sow, and highlights again that movement of piglets should be minimised (Schmitt *et al.*, 2019b). In this research, the heavier piglets were moved from their mothers to form the nurse sow litters, which had the consequence of all litters being a similar weight at weaning; this has benefits for pig management later on in the production cycle. In addition, there was no evidence of compromised welfare associated with nurse sow strategies (Schmitt *et al.*, 2019a).

Other options for management of large litters is provision of supplementary milk in the pen, or indeed a complete artificial rearing strategy. Pilot work in the Moorepark unit, which is being expanded upon in the coming years due to installation of a milk-feeding system in the farrowing and weaner rooms, indicates that a supplementary energy supply has benefits for weaning weight (O'Driscoll & Schmitt, 2016). However, removing 7-day-old piglets from their mother, and artificially rearing them in a plastic enclosure with a milk-feeding system (Rescue Deck®) until 28 d of age, was not beneficial for growth. These piglets also had more harmful behaviours and were dirtier than sow-reared piglets (Schmitt *et al.*, 2019c). Thus, artificial rearing is not a suitable strategy to rear piglets.

Pig nutrition

As feed costs account for ~70% of pig production costs, improving FE is possibly the principal determinant of profitability in pig production. Since its inception, Teagasc conducted nutritional research on all phases of pig production, aiming to determine the most efficient feeding strategies, while optimising animal health and welfare.

The sow

Inadequate nutrition of the gestating sow can negatively influence both the sow and her offspring, immediately, and in the longer term, and thus have a significant effect on farm profitability. Teagasc has performed both gilt and sow nutrition research, as they may respond differently to dietary adjustments. For instance, in the early 2010s, Teagasc research determined that back-fat for gilts should be targeted at ~19 mm by the time of first insemination. A daily feed allowance of ~2.5 kg of gestation diet (6.2 g/kg total lysine, 13.0 MJ digestible energy [DE]/kg) should be provided to gilts between day 25 and 90 of gestation, to maximise growth to slaughter in offspring (Amdi *et al.*, 2013, 2014).

A high proportion of Irish sows are liquid-fed. Frequently, producers inadvertently restrict the intake of liquid-fed sows during lactation by using feed curves (computerised plan of daily allocation of feed which increases during lactation) that do not provide sufficient feed to match the intake capacity of sows. This results in excessive lactation weight loss, increased days to oestrus, reduced farrowing rate and reduced litter size at the subsequent farrowing. Indeed, increasing commonly used feed curves by 30% reduced the number of days between weaning and oestrus, reduced excessive sow weight loss and potentially increased litter size by two piglets. Thus, increasing lactation feeding levels holds promise to increase subsequent litter size and reduce the number of empty days (days not pregnant or suckling their litter) per sow (Lawlor *et al.*, 2007a; Ryan *et al.*, 2009).

Large litters mean that there is increased pressure on the sow to produce healthy, efficient piglets. L-carnitine is a watersoluble quaternary amine, and plays a role in the transport of fatty acids across the mitochondrial membrane. Thus, it is hypothesised to improve energy generation through fatty acid oxidation. Supplementation to hyper-prolific gestating gilts (~15 piglets born) not only increased the number of pigs weaned and litter weight at weaning, but also increased the carcass weight of offspring at slaughter (Rooney *et al.*, 2019, 2020b). Moreover, supplemented sows gave birth to heavier piglets, particularly for sows with >14 piglets born. Carnitine also improved piglet vitality at birth (Reid *et al.*, 2016). Thus, carnitine holds promise as an option to increase piglet survivability and growth where litters are large.

Energy intake depends both on the quantity of the diet consumed and on its energy density. Sufficient lactation energy intake is critical to maximise milk yield, minimise mobilisation of body reserves and maximise subsequent reproductive performance. Increasing the energy density of the lactating sow diet in increments from 13.8 to 15.9 MJ DE/kg did not depress sow-voluntary feed intake, and feeding a high-energy dense diet (>14.5 MJ DE/kg) improved only some indicators of piglet vitality. As no other measures were affected, the study concluded that energy intake of hyper-prolific sows is used with greater efficiency for piglet growth when sows are fed a low- versus a high-energy density lactation diet (Rooney *et al.*, 2020a).

The effect of supplementing sow diets with enzymes between day 109 of gestation and the following service was investigated as an alternative method to improve energy intake. Indeed, supplementation with a non-starch polysaccharide-hydrolysing enzyme increased energy intake during lactation for both gilts and sows. For gilts, the loss of body reserves (back-fat) at weaning was reduced (Walsh *et al.*, 2012a), and in multiparous sows, the extra energy was reallocated to increasing litter weight gain, resulting in an increase in piglet weight at weaning (Cozannet *et al.*, 2018). Finally, one of the practical limitations to applying accurate nutritional recommendations for sows on commercial farms is that accurate sow weights are not always available. A simple equation using easily obtained morphometric measurements to estimate sow weight was developed; sow girth was the

single most accurate estimator of body weight ($R^2 = 0.81$), and, including back-fat thickness, parity number and day of gestation in the model improved the estimate further ($R^2 = 0.89$; O'Connell *et al.*, 2007).

The newly weaned pig

When planning routine management and nutrition programmes for weaned pigs, the influence of weaning age on post-weaning intake and growth is critical. A 1-kg increase in weaning weight results in a 1.7-kg increase in weight at 28 d post weaning, and increasing weaning age by 1 d is associated with a 500-g increase in weight at that time (Lawlor et al., 2003a). In addition, each weekly increase in weaning age between 3 and 5 wk increased feed intake (week 3 to 4: 13%, week 4 to 5: 69%) and ADG of pigs between weaning and 10 wk of age (week 3 to 4: 11%, week 4 to 5: 67%; Leliveld et al., 2013). Thus, Teagasc recommends that pigs are weaned at a minimum of 4 wk of age. From this age, pigs can better digest and absorb dietary nutrients. Therefore, they have increased growth and less post-weaning diarrhoea, both of which are increasingly important in light of the impending ban on pharmacological levels of zinc oxide in post-weaning diets, which, to date, has been used as prophylaxis against post-weaning diarrhoea.

Pigs that are heavier at birth outperform their lighter littermates post weaning, and reach slaughter weight sooner (Lawlor et al., 2002a, 2005a). However, Teagasc studies found no clear relationship between increasing global nutrition of the sow (increased feed intake rather than an increase in specific nutrients) or energy supply at critical nutritional windows on piglet birth weight (Lawlor et al., 2007b; Markham et al., 2009; McNamara et al., 2011). Although weaning weight is increased by supplementing piglets with creep feed in the farrowing pen, this advantage can be lost by 14 d post weaning (Lawlor et al., 2002a), most likely dependent on the proportion of pigs within the post-weaning group that have consumed creep feed and so classified as "eaters". Thus, to minimise the weaning "growth lag", in late 2020 Teagasc commenced a 4-yr research programme aimed at increasing energy and nutrient intake, and stimulating earlier enzyme secretory capacity, in suckling piglets from large litters, by feeding liquid milk replacer and starter diets prior to weaning.

The post-weaning growth lag, normally experienced by pigs, is due not only to the change in feed consistency and reduced feed intake, but also to a limited digestive and absorptive capacity, resulting from insufficient production of gastric hydrochloric acid and pancreatic enzymes. Feeding organic acids or reducing the acid-binding capacity of post-weaning diets helped increase intake and growth with the benefit being greatest when diets contained low levels of milk products. These strategies are beneficial because they supplement the newly weaned pig's limited capacity to produce gastric hydrochloric acid (Lawlor *et al.*, 2005a, 2005b, 2006). These strategies are now widely used in the commercial production of post-weaning pig diets, and the work is receiving renewed attention due to the previously mentioned changes to the regulations with regard to veterinary medicinal products.

Ingredients and feed delivery

Although post-weaning growth rate is increased by feeding high levels of milk powder in diets immediately after weaning, and time taken to reach slaughter weight is reduced, feeding excessive levels of these expensive diets post weaning was not cost-effective (Lawlor et al., 2002a, 2003b, 2005a). Thus, Teagasc recommend that a target of 2 kg/pig of starter diet and 5 kg/pig of link diet (a diet intermediate in composition between that of a starter and a weaner diet) should be fed post weaning. Alternatively, a starter diet should be fed for 7-10 d post weaning followed by a link diet for another 12–14 d. Heat-treated (steam-flaked, micronised, expanded, extruded, etc.) cereals were also once common in post-weaning diets, but are expensive, and Teagasc research demonstrated that although starch was effectively gelatinised by the process, the heat processing did not significantly improve animal growth or FE (Lawlor et al., 2003a, 2003b). Therefore, it is no longer recommended to include heat-processed maize and wheat in post-weaning pig diets.

In the early 2000s, it was thought that liquid feeding could be a panacea for successful feeding of newly weaned pigs, so a series of trials in which pigs were liquid-fed (fresh, fermented and acidified) for 28 d post weaning were performed in Teagasc. Contrary to popular opinion at the time, the practice was found to be quite wasteful of feed depending on the design of the feeding trough; in one trial, liquid feeding actually caused a reduction in growth rate (Lawlor *et al.*, 2002b). As a result, very few liquid feed systems for weaned pigs were installed on Irish pig units, resulting in savings related to FE through reduced feed waste.

Growing pigs

Feed enzymes

There is now a move towards the use of novel ingredients and co-products in the pig industry in order to reduce feed costs. Although pig diets are primarily composed of ingredients of vegetable origin, pigs lack the enzymes needed to break down fibre and therefore cannot efficiently digest fibrous ingredients. However, supplementing the diet with enzymes could potentially improve nutrient availability and FE.

Two meta-analyses of data from the literature confirmed that dietary supplementation of multi-enzyme complexes appears to be the most consistent strategy to improve FE in both weaner and finisher pigs (Torres-Pitarch *et al.*, 2017, 2019). Results were most consistent when maize-based diets were

supplemented with mannanase, barley-based diets with protease and when the diets were low in nutrient and energy density. Experimental work confirmed that supplementing carbohydrases and phytase as a multi-enzyme complex to low-nutrient-density diets returned the growth and FE of the pigs, as well as metacarpal and foot areal bone mineral density, to the levels reached by pigs fed diets meeting nutrient recommendations (Lawlor *et al.*, 2019).

Nevertheless, the results from other Teagasc studies were less consistent. Growth and FE of grower-finisher pigs fed a wheat-dried distillers grain with solubles and rape seed meal-based diet did not improve when supplemented with an enzyme complex containing phytase, carbohydrases and protease (Torres-Pitarch *et al.*, 2018). Supplementation of xylanase and beta-glucanase to liquid diets increased nutrient digestibility in two liquid-feeding studies but improved FE in only one (Torres-Pitarch *et al.*, 2020a, 2020b). Interestingly, when FE was improved due to enzyme supplementation, bacterial taxa in the gastrointestinal tract (GIT) that were correlated with increased pig growth increased in abundance, whereas in the experiment where FE was not improved, they did not. This may help to explain the inconsistency often observed between enzyme supplementation studies.

Liquid feeding – growing finishing pigs

Computerised liquid-feeding systems reduce on-farm labour because they can mix feed ingredients and automatically deliver complete diets to troughs. These systems feed more than 70% of Irish pigs, and were often installed when significant volumes of liquid co-products (e.g. liquid whey and skim milk) were readily available in Ireland. However, these co-products are no longer easily and cheaply sourced, and the systems require a high degree of skill to operate optimally. Indeed, there is clear evidence of uncontrolled spontaneous fermentation of liquid feed leading to amino acid degradation and a reduction in energy, on Irish pig farms (O'Meara et al., 2021). O'Meara et al. (2020a) found that wet/dry feeding a pelleted diet was the optimum method (out of six options) of feeding grow-finisher pigs as it maximised carcass growth and optimised FE; liquid feeding also maximised growth rate, but resulted in poorer FE. The question then was how to improve FE when liquid feeding. O'Meara et al. (2020b) found that a water-to-feed ratio of less than 3.5:1 on a DM basis optimised FE, and could be lowered to 2.4:1 to reduce the manure volume. Benzoic acid in liquid feed did not improve growth or FE (O'Meara et al., 2020c), but an acid blend containing formic acid (SALMO-NIL® Dry LC; Nutri-Ad International NV, Turnhout, Belgium) did. Controlled cereal or whole diet fermentation did not improve FE (O'Meara et al., 2020d). Work on optimising feeding management and hygiene routines with liquid-feeding systems is continuing with the objective of improving FE.

Phase feeding

The nutrient requirements of pigs change from birth to slaughter. Adjusting the nutritional composition of diets to these requirements (phase feeding) is important to minimise costs and reduce environmental impact. Feeding programmes for growing finishing pigs should include at least two to three diets, with a progressive reduction in nutrients, mainly protein. However, many Irish farms work with only one diet from 30–40 kg to slaughter (Teagasc eProfit Monitor, 2020), as they often only have one feeding line. However, moving to diets with lower protein levels, especially around 80 kg to slaughter, results in important financial savings and reduces N excretion significantly (Goodband *et al.*, 2017). This will be more important in the coming years as DAFM target an average crude protein level in pig diets of <16%.

Gut microbiome and feed efficiency

The bacteria present in the GIT play a role in nutrient digestion and metabolism, as well as development and regulation of the host immune response. Teagasc studies were among the first to show that this gut microbiome is associated with FE in pigs (McCormack et al., 2017, 2019a). However, many FEassociated bacterial taxa are present at low relative abundance, and few consistent reliable FE-associated bacteria were identified across different rearing environments (McCormack et al., 2019a). Furthermore, faecal microbiota transplantation of inocula derived from highly feed efficient pigs, to pregnant sows, and/or their offspring, was not effective in improving FE or slaughter weight of their offspring (McCormack et al., 2018), even if offspring were supplemented with the prebiotic inulin at weaning (McCormack et al., 2019b). Nevertheless, the existence of a number of growth- and FE-associated bacterial taxa within the gut microbiome of pigs means that microbiota-targeted strategies offer real potential to improve productivity in pigs (Gardiner et al., 2020). However, it is likely that the most appropriate strategy for the future is to select for production traits based on core functionality of the microbiome and to modulate overall functionality of the microbiome, rather than focusing on individual taxa per se.

Carcass lesions

Meat inspection (MI) determines the health of animals both prior to death (ante-mortem) and after death (post-mortem) to ensure meat quality and safety. MI findings are currently underutilised (EFSA, 2011), and relaying this information back to pig farmers could contribute to reducing carcass losses and improving pig welfare on farm (Harley *et al.*, 2012a). In Ireland, carcass condemnation is a major source of financial loss in the pig industry (Harley *et al.*, 2014), with abscessation caused by tail biting being one of the main reasons (Harley *et al.*, 2012b). Furthermore, given the scale of the problem of tail biting for pig welfare (Boyle *et al.*, 2021a), tail injuries are likely one of the most important carcass lesions to be recorded at MI (Harley *et al.*, 2012b).

Tail lesions (TL) are strongly associated with farm productivity parameters, and are less common on farms that avail of record keeping through the Teagasc advisory service (van Staaveren et al., 2017a). They are also associated with lung pathologies at slaughter (Boyle et al., 2021a); thus they appear to be negatively associated with better management in general (Teixeira et al., 2016; van Staaveren et al., 2016). Apart from severe TL in the finisher stage, carcass TL can also identify farms with problems with poor body condition in the first weaner stage, and bursitis in the second weaner stage (van Staaveren et al., 2017b), and TL acquired both early and late in the production cycle are visible on the carcass (Carroll et al., 2018). Indeed, TL are best detected after scalding and dehairing rather than at ante-mortem inspection (Carroll et al., 2015). As mixing, transport, slaughter and carcass processing do not disrupt the visibility or presence of TL on the carcass (van Staaveren et al., 2015), there is a strong case for including measures of the severity of carcass TL in the MI process.

However, consultations with stakeholders revealed a preference to focus on lesions related to health (such as lung lesions) in the MI process as a first priority (van Staaveren et al., 2019). Thus, a programme of research to validate lung pathologies at MI against coughing on farm (Pessoa et al., 2020) and to standardise methods of scoring was undertaken. Stakeholders also expressed positive attitudes towards the use of MI data to inform pig health and welfare if both standardisation of recording and feedback were improved, and if the MI system could provide real-time benchmarking possibilities (van Staaveren et al., 2019). In 2021, DAFM rolled out a computerised antemortem recording system in Irish meat-processing plants, with a post-mortem system to follow in 2022. This will greatly improve feedback of information to producers, and will facilitate improvements to husbandry practices which are associated with lesions detectable on the carcass.

Salmonella

Salmonella carriage in pigs is a significant food safety concern (EFSA, 2008). A number of Teagasc studies investigated the epidemiology of Salmonella on Irish pig farms. On high seroprevalence farms, second-stage weaners had the highest rate of Salmonella shedding, closely followed by finishers and gilts, with monophasic variants of Salmonella Typhimurium predominating (Burns, 2015). However, sows do not appear to pose a major risk in the maintenance and transmission of Salmonella to their progeny, but instead the contaminated pen environment is more significant in on-farm perpetuation (Lynch *et al.*, 2018). Although feed was found to play a role in the transmission of *Salmonella* to pigs, *Salmonella* prevalence in pig feed and feed ingredients is low (Burns, 2015; Burns *et al.*, 2015). Interestingly, surveillance data highlighted feed form, biosecurity and disease control as significant factors associated with *Salmonella* infection on farrow-to-finish pig farms (Arguello *et al.*, 2018).

Much Teagasc research investigated low-cost practical solutions to control Salmonella in pig production. In finisher pigs, supplementation with fumaric acid or a seaweed extract reduced intestinal counts of bacterial species indicative of pathogens such as Salmonella (Campbell et al., 2006; Gardiner et al., 2008). Supplementation with coated sodium butyrate or a blend of formic and citric acids and essential oils was effective in reducing Salmonella shedding and seroprevalence, but only in the absence of secondary infections (Walia et al., 2016, 2017a). In grower pigs, supplementation with these latter products also reduced Salmonella shedding and improved ADG (Lynch et al., 2017a, 2017b). In weaned pigs, a novel combination of five probiotic strains selected for their anti-Salmonella activity (Gardiner et al., 2004; Walsh et al., 2008) reduced Salmonella shedding (Casey et al., 2007). In addition, Arguello et al. (2019) revealed that gut microbiota composition and maturation (transition from a suckling to a post-weaning microbiota) appear to influence resistance to Salmonella infection in weaned pigs; thus, gut microbiota manipulation has potential to protect against infection.

Finally, *Salmonella* control strategies can also be effective when applied at the abattoir. Drying of lairage pens after cleaning with detergent and a chlorocresol-based disinfectant was the most effective hygiene routine to eliminate *Salmonella* contamination (Walia *et al.*, 2017b). Topical misting of pigs in the lairage with a peroxygen disinfectant was also beneficial as a *Salmonella* decontaminant prior to slaughter (Walia *et al.*, 2017c). These strategies should be adopted by the processing sector in an effort to reduce carcass contamination with *Salmonella* at the abattoir. The sanitisation strategies also have relevance in guiding on-farm hygiene routines.

In 2021, Animal Health Ireland (AHI) and Teagasc carried out a case-control study in Irish farms to identify management practices associated with a *Salmonella*-free status, which could be effective in reducing prevalence nationally. The outcome of this work will help further to implement the national *Salmonella* control programme.

Feed safety

Genetically modified (GM) feed

The Irish feed industry is highly reliant on imported GM protein sources, particularly soya and maize co-products. Teagasc research showed that both short- or long-term feeding of GM Bt-maize, which expresses the truncated Cry1Ab toxin from *Bacillus thuringiensis* which confers resistance to certain insect pests of maize, to pigs is as safe as its conventional counterpart with respect to pig health and growth (Buzoianu *et al.*, 2012a, 2012b, 2012c; Walsh *et al.*, 2011, 2012b, 2012c). Neither was there any cause for concern regarding the safety of peas expressing α -amylase inhibitor to provide protection against the pea weevil (Walsh *et al.*, in press). This work offers assurance to regulators, farmers and consumers alike as to the safety of GM feed ingredients in pigs of different ages, even when fed for extended periods or transgenerationally (Buzoianu *et al.*, 2012d, 2013a, 2013b; Walsh *et al.*, 2013). Given that pigs are an excellent model for humans (Bergen, 2022), this work also provides reassurance to consumers as to the safety of directly consuming these GM ingredients.

Mycotoxins

Mycotoxins are secondary metabolites produced by fungi, mainly the moulds Aspergillus, Penicillium and Fusarium. They affect ~25% of the world's food crops, causing significant economic losses, as well as being a health concern in humans. A review conducted by Teagasc advised that if mycotoxin contamination is identified, the contaminated grain should be disposed of or, if safe to do so, diluted with clean grain and fed, along with a binder, to the least susceptible species and type of animal (Lawlor & Lynch, 2001a). Following removal of contaminated feed, the storage area should then be thoroughly cleaned and disinfected to prevent cross-contamination. A follow-on review highlighted that the clinical response in pigs to mycotoxins can vary; vomitoxin causes pigs to refuse feed, zearalenone affects the reproductive organs, ochratoxin causes kidney damage and aflatoxins increase susceptibility to disease through their action as immunosuppressants and can also cause haemorrhages and digestive disorders (Lawlor & Lynch, 2001b).

Pig production and the environment

Although the overall density of pig production expressed as agricultural area used per sow in Ireland (26 ha/sow) is relatively low (e.g. Netherlands, 1.9 ha/sow; Denmark, 2.0 ha/sow), the pig industry generates large volumes of animal manure on a small area of land. This must be managed in order to comply with national and EU environmental legislation. Since September 1996, pig farms above a certain size were incorporated under the Environmental Protection Agency (EPA) Act (1992) as "intensive agriculture" and require an Industrial Emissions Licence. This licensing regime was introduced on a phased basis; currently, if a facility exceeds 750 sows and/or 2000 production pigs (pigs >30 kgLW), they must have an Industrial Emissions Licence, and 118 licences have been issued to date.

Management of pig manure

Over the past 15–20 yr, provision of low protein diets and phytase enzyme has greatly reduced the levels of N and P excreted, respectively. This was driven by research work showing that performance on farms was not negatively impacted by these strategies (Campbell & Bedford, 1992; Hayes *et al.*, 2004; Humer *et al.*, 2015). The issue of managing slurry to ensure minimal impact on water resources was managed by a code of practice until 2005/2006 when the EU Good Agricultural Practice for Protection of Waters Regulations (the "nitrates" regulations) came into force. This requires all pig farms to have capacity for a 26-wk slurry storage. The regulations also encouraged better farmyard management by minimising the volumes of soiled water generated on farms.

There are a number of available technologies for using and treating pig manure (reviewed by Dennehy *et al.*, 2017a). Those investigated by Teagasc include anaerobic digestion (Xie *et al.*, 2011a, 2011b, 2012a, 2012b, 2017), composting (Nolan *et al.*, 2011; Troy *et al.*, 2012, 2013b) and pyrolysis (Troy *et al.*, 2013a, 2013b, 2014). Treatment of the liquid fraction of pig manure through integrated constructed wetlands (ICW; Harrington *et al.*, 2012), woodchip biofilters (Carney *et al.*, 2013, 2016) and intermittently aerated sequencing batch reactors (Zhang *et al.*, 2011, 2012) was also assessed. However, none of these technologies are currently cost-effective in Ireland, other than in limited scenarios (e.g. anaerobic digestion on integrated pig units with >2000 sows; Nolan *et al.*, 2012). Thus, land spreading remains the most cost-effective use for pig manure in Ireland.

Pathogen removal was also investigated to assess potential biosafety risks, as antibiotic-resistant Salmonella, for example, is common in pig manure (McCarthy et al., 2013). Manure separation generated a solid fraction with lower faecal indicator counts than the manure (McCarthy et al., 2013), and storage for 84-112 d reduced/eliminated Salmonella, including antibiotic-resistant strains, in manure and its solid and liquid fractions (McCarthy et al., 2015b). Composting manure solids also reduced faecal indicators so that the compost complied with animal by-products regulations (McCarthy et al., 2011a). Treatment of the liquid fraction of anaerobically digested (AD) pig manure in meso-scale (midway between bench and pilot-scale) ICWs reduced indicator bacteria (McCarthy et al., 2011b). Furthermore, in on-farm ICWs treating agricultural wastewater, including the liquid fraction of AD pig manure, and woodchip biofilters treating the liquid fraction of manure, Salmonella, including antibiotic-resistant strains, was undetectable in the effluent (McCarthy et al., 2011b, 2015a). Thus, management strategies can be successful in reducing pathogens, including antibiotic-resistant strains, in pig manure and its separated solid and liquid fractions.

A large body of Teagasc research was also performed on co-digestion of pig manure and food waste (FW). At batch-scale, co-digestion had synergistic effects on specific methane yields and digestion kinetics (Dennehy et al., 2016). However, varying the digester feedstock composition did not affect digestate biosafety or dewaterability (Dennehy et al., 2018). Decreasing hydraulic retention time (HRT) from 41 to 21 d did not increase the counts of pathogenic indicator microorganisms (Dennehy et al., 2018), but reducing HRT below 21 d had a negative effect on indicator reduction rates (Dennehy et al., 2017a). Dennehy et al. (2018) also concluded that hydrogenotrophic methanogenesis may be a key methanogenic pathway at low HRTs (Dennehy et al., 2018). Further research into dry co-digestion of pig manure and FW focused on methane production kinetics, inactivation of Salmonella and enteric indicator bacteria, system stability and the roles of, and interaction amongst, microbes (Jiang et al., 2018a, 2018b, 2018c, 2019). Together with a review of the literature (Jiang et al., 2020), the conclusion was that for successful anaerobic co-digestion of pig manure and bio waste, operating conditions need to be optimised in order to mutually benefit energy recovery, pathogen inactivation, economic feasibility and bio waste stabilisation.

The final part of this research involved development of an economic model to assess the financial viability of on-farm biogas plants in Ireland (Dennehy *et al.*, 2017b). Despite lower operational and capital expenditure than co-digestion, mono-digestion of pig manure was not financially viable. In terms of co-digestion, Monte Carlo simulation revealed that net revenues from a small farm were least sensitive to any future changes in FW availability, gate fees (fees charged by the anaerobic digester operator for disposal of the FW), digestate disposal costs and renewable energy feed-in tariff. Due to its potential to treat greater amounts of FW than a small farm, whilst requiring a lower amount of FW to remain profitable relative to a large farm, medium-sized farms had the highest revenue-generating potential under optimal market conditions (Dennehy *et al.*, 2017b).

What does the future hold for the Irish pig sector?

The European pig sector currently faces challenges that could have significant long-term implications for the industry. These include ASF, volatility of feed prices and EU regulations in the areas of health (e.g. Regulation [EU] 2019/6 on veterinary medicines), welfare (e.g. Council Directive 2008/120/EC on minimum standards for the protection of pigs) and the environment. The Irish pig sector has an added challenge with Brexit due to the UK, along with China, taking a significant proportion of Irish pork exports. To face these challenges, it is essential that the industry as a whole improve standards of production. This includes not only investigating the potential to produce value-added products, but also optimising efficiency

and innovation to ensure maintenance of existing presence in the domestic, European and international markets.

Market opportunities

In the short term, Irish pig exports will face a significant challenge when the Chinese pig herd recovers from the impact of ASF. The increased volume of global pig meat production will likely exceed demand, resulting in downward pressure on pig meat prices and margins. In the medium term, economic and population growth in developing countries will be the main drivers of meat consumption globally, which may provide new markets for Irish pig meat. Nonetheless, producers and processors face continuous challenges when competing in the international marketplace, ranging from high feed and energy costs to market access disruption, supply surges, currency fluctuations, etc.

Ireland currently has only a very small number of pig producers producing low volumes of potentially high-value products such as outdoor pigs and organic product. The vast majority (99%) of our pig meat output is not a high-margin product (Teagasc, 2019). One way that the Irish pig meat industry could differentiate itself on the international markets is to develop a "bespoke" high value-added pig meat product. To this end, Teagasc researchers recently commenced market research into consumer demand for high-welfare pork, which will include interviews with major buyers (e.g. supermarkets, etc.) and economic analysis to determine the return needed to remain profitable, upon conversion to a higher-welfare system.

Health and welfare

A significant challenge for the pig industry across the EU is the growing emphasis on enforcement of Council Directive 2008/120/EC, which mandates that pigs should not be routinely tail docked to prevent tail biting, and provided with environmental enrichment that satisfies their behavioural needs. Moreover, the outcome of the recent European Citizen's Initiative to "End the Cage Age" and the EU's Farm to Fork Strategy will both see the enactment of additional pig welfare legislation in the coming decade. In addition, all EU countries must implement the Regulation (EU) 2019/6 on Veterinary Medicinal Products in 2022, effectively banning the routine use of in-feed antibiotics and zinc oxide. Such legislation will require significant changes in the way pigs are housed and managed. However, the risk factors for tail biting and poor health (and thus the need to use antibiotics/zinc) are similar (Boyle et al., 2021b), and as such, efforts to comply with both sets of legislation will be complementary.

Another change to pig farming in Ireland is likely to be a shift towards increasing the time that the sow has freedom of movement. Several producers already manage free lactation systems, and Teagasc research demonstrated that pigs from these systems perform better than those from standard crates (Kinane *et al.*, 2021). Thus, "free" systems are likely to grow in popularity, and there is potential for entirely free farrowing systems to be adopted; plans are in place for conversion of half of the farrowing rooms in the Moorepark research unit to free farrowing pens. Adoption of such systems could form part of a marketing plan to enhance the image of Irish pig production both at home and internationally.

Finally, in 2021 DAFM committed to fund the largest pig welfare project to date on the island of Ireland, drawing together a collaboration between Teagasc, University College Dublin, Queens University Belfast and the Agri-Food and Biosciences Institute in Northern Ireland. Apart from investigating commercially feasible alternatives to current systems (provision of outdoor access to growing pigs, and investigation of a range of alternative enrichment materials), the work will explore the feasibility of outdoor and agroforestry pig production. This will include a social, economic and environmental lifecycle assessment, as well as an analysis of the economy of changing land use to alternative systems of pig production.

Optimising system efficiency

The Irish pig sector has fewer but bigger farms than many other countries, the management of which could benefit from specialisation and the establishment of superstructures for coordination and decision-making. In the long term, this could involve a shift from individual farms, the current norm, to vertical integration at a range of levels. However, in the immediate term, and on the basis of a 2-yr recently completed pilot study, Teagasc are co-ordinating a new project to bring LEAN methodologies (management practices to improve efficiencies by eliminating waste) to pig farms. The first aspect of the project will involve two pilot farms which will have their management and health systems evaluated, with the aim of shifting towards ceasing docking of pigs' tails. Another project that is currently underway is a feasibility study investigating whether the Moorepark Pig Production Model (Calderón Díaz et al., 2019) could be commercialised as a spin-out company. The aim would be that the model could be used as a consultancy tool to assist producers in improving biological and financial efficiency.

Increased collaboration across industry stakeholders

During the past 4 yr, Teagasc, DAFM and AHI worked to establish schemes to collect data on different areas of pig production such as biosecurity, welfare, slaughterhouse findings, antimicrobial use and *Salmonella* status (AHI, 2021). The launch of the AHI Pig HealthCheck programme, and the hiring of a programme manager to co-ordinate activities in 2019, streamlined this process. Activities included upskilling private veterinary practitioners in the pig sector in how to audit farms with regard to biosecurity and animal welfare, establishment of a database for recording the output of such, and co-ordinating, running and management of both a pig technical working group and a pig industry implementation group. Both of these groups include stakeholders from across the industry. These activities will enable robust benchmarking of current standards and help to improve efficiency of production and the quality of the pork produced in Ireland.

Conclusion

The pig industry worldwide faces an enormous challenge in terms of meeting demands for protein from a growing world population, while simultaneously improving pig health and welfare, minimising damage to the environment and remaining economically sustainable. The Teagasc vision is to increase profitability in the pig sector by producing environmentally sustainable and welfare-friendly pig meat to the highest safety and quality standards. Teagasc has an integrated approach to pig production research, advisory and education supported by a vast network of international collaborators and close contact with all of the major industry stakeholders. This, and the legacy of its success in the past 60 yr, means that the Teagasc PDD is in a strong position to assist the Irish pig industry in adapting to become a more resilient and sustainable industry for the future.

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Irish Journal of Agricultural and Food Research

Irish research response to dairy quality in an era of change

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Abstract

The Irish dairy sector is recognised for its very significant contribution to the national economic status; it is now worth -€5 billion annually and represents the largest food and drink export category, which, in turn, represents one of the four largest manufacturing industries in the country. Given anticipated further growth in global demand for dairy products and the positive attributes and capabilities that Ireland has to meet that demand, in terms of pasture-based production and cost competitiveness, it is incumbent for the sector to attain the highest quality milk and dairy products. The combined collaborative approach between research and industry has ensured significant progress and enabled Ireland to remain at the forefront globally in terms of production of quality milk and dairy products. This paper highlights some specific scientific platforms and technologies currently shaping the industry in this regard and discusses current research activity as well as anticipating key requirements for future progress. While research, and farm and processing plant management have accomplished very significant advances in milk and dairy product quality, some overarching emerging challenges include product substitution and sustainability. Some key pillars for the future have been identified on which a strong, efficient dairy sector can be maintained and progressed. Specifically, the use of evidence-based information and real-time measures in prediction and decision-making will be a crucial pillar for the dairy sector of the future. This can promote an approach of proactive maintenance and optimisation of production through improved predictability and control of manufacturing processes.

Keywords

Grass-fed milk • Irish dairy sector • milk processing • milk quality • seasonality

Introduction

Positive changes in the quality of milk have had a profound impact on the development of the Irish dairy industry over past years. The description and interpretation of milk quality in the early 1960s was very different to today's standards; at that time, only 7% of milk passed a 3-h methylene blue test, regarded as the minimum quality standard for manufacturing milk. However, from this point onwards, a strategy was initiated to improve milk quality encompassing advice at farm and creamery level and payment incentives based on quality. Further significant milestones on the journey to enhanced quality included the introduction of on-farm refrigeration, which was a key development at that time, but it was accompanied by challenges such as a requirement for consistent and adequate electrical power, which was not widespread in rural areas then. This was followed by the development of a vacuum system to transfer milk from the farm tanks to the tanker lorries of the milk purchaser; this, in turn, allowed the milk to be collected by the purchaser and transported direct to central creameries. Likewise, following the development of milking machines, which in the early years often caused mastitis spread in the herd (Walshe, 1968), a greater understanding of milking technology, development and testing of equipment specifications and design of milking parlours all had a positive impact on milk quality. From this point, increasing emphasis was also placed on breeding cows for enhanced milk production in terms of volume and fat content. While butter continued to be a key product, cheese production and milk drying capacity expanded significantly. These changes, along with an ever-growing emphasis on production of consumer products for international markets,

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resulted in the adoption of new and ever-increasing quality standards.

In more recent times, the concept and progression of milk quality has been defined and influenced by a wide range of parameters and standards that need to be achieved; these are dictated by the dairy products being produced, efficiencies of production and processing, consumer requirements and perceptions, international market requirements and regulatory agencies. While these parameters and standards are critical for the quality of the manufactured dairy product, they also have significant implications at the farm production and plant processing levels. Milk quality at farm level is mainly defined in terms of composition (fat, protein, lactose), somatic cell count (SCC), bacterial load including total bacteria count (TBC), thermoduric bacteria count and presence/ absence of chemical residues. While monetary incentives for optimum standards of these parameters benefit the farmer, most notably the A + B - C system of milk payment (where A is the price paid per kg of protein, B is the price paid per kg of fat and C is a processing cost deduction), which more accurately reflects the true value of milk protein and fat (Dillon et al., 2008), improved milk composition also has positive implications for the processing plant. This has become even more critical following the changed structure of the industry following the abolition of milk quotas, which has seen a 54% increase in milk production in 2018 versus the 2007-2009 base, and a 21% increase in milk solids per cow, from 334 kg to 405 kg (Kelly et al., 2020).

So, the sector must remain vigilant; there is an anticipated growth in global demand for dairy products, but this is likely to be accompanied by ever-increasing consumer interest in animal welfare and environmental perspectives. A pre-requisite for the manufacture of quality dairy products is to start with milk of the highest quality. The definition of optimum quality milk will evolve over time, but it is a measure of success for an industry sector to be able to retain flexibility and meet changing demands and trends. This paper will highlight some scientific advances and examine some current research aspects and knowledge of milk quality that can contribute to meeting future targets in support of the Irish dairy industry.

Key scientific advancements

Animal genetics and practical implications for milk quality Ireland has been at the forefront in both research and the application of animal genetics. Genetic selection is known to contribute substantially to gains in performance traits, including milk yield and quality in dairy cows (Berry, 2018). In Ireland, prior to 2000, the Irish dairy cow breeding index was based on milk, fat and protein yield and protein concentration. This index was revised in 2001 to include calving interval (i.e.

a measure of fertility) and survival, while protein concentration was removed from the index, then termed the Economic Breeding Index (EBI). The EBI is routinely revised both in the number of traits considered and the weighting on each trait. The current EBI comprises 18 traits divided into 7 subindexes (Berry et al., 2022), offering breeders the choice to select sires on the basis of genetic merit for overall improved profitability, genetic merit for a particular aspect such as overall milk production or selection for a particular trait. Over the past two decades, the overall emphasis on milk production in the EBI has reduced from 72% in 2001 to 34% in 2020, yet genetic potential and on-the-ground phenotypic performance continues to improve (Figure 1). While the concentration of fat and protein in milk is not explicitly included in the EBI, the negative weighting on milk yield, coupled with the positive weighting towards greater fat and protein yield, contributes to greater concentration of these components. The predicted transmitting ability (PTA) for milk fat and protein yield by year of first calving between the years 2010 and 2020 is shown in Figure 1. This increased genetic potential contributed to a 0.029 (s.e. = 0.002) and 0.019 (s.e. = 0.002) increase in phenotypic milk fat and protein percent, respectively, of first parity cows across the same time period (Figure 1). This validates results of Ring et al. (2021), who demonstrated a change in phenotypic milk yield and solids per unit change in respective estimated breeding value close to the expectation of 1, based on a cross-sectional analysis of 526,923 Irish dairy cows born between 2012 and 2015.

Milk recording, a paid service accessed by dairy farmers representing 53% of Irish dairy cows (www.icbf.com), involves harnessing Fourier transform infrared (FTIR) spectrometry to quantify the macro milk constituents of total fat, protein and lactose of individual cows at points throughout lactation. Over the past decade, the potential of FTIR to describe more about the milk sample and about the cow that produced the milk has been reported (DeMarchi *et al.*, 2014; McParland & Berry, 2016). The attraction of FTIR in predicting otherwise

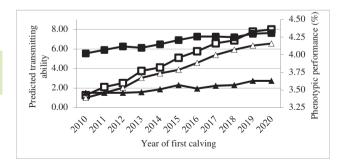


Figure 1. Genetic (white markers) and phenotypic (black markers; secondary axis) trend in milk fat (squares) and protein (triangles) yield (PTA) and composition (phenotypic) from 2010 to 2020 for first parity Irish dairy cows.

difficult-to-measure traits arises from the routine application of FTIR to milk samples of individual cows during milk recording and to bulk tank samples at milk collection. Therefore, the pipelines already exist to capture and analyse the data, and new traits predicted from this technology can be recorded and reported at little or no additional expense or effort either to dairy farmers or to milk processors. Accuracy of the predicted traits is variable; nonetheless, some traits, including individual milk fatty acids (FAs), are predicted with very high accuracy (Soyeurt *et al.*, 2009). Milk technological traits, including coagulation properties, heat stability, pH and colour, are moderately predicted, with a correlation between true and predicted values of these traits ranging from 0.30 (for milk greenness [a*]; Table 1; McDermott *et al.*, 2016) to 0.81 (for pH; Table 1; Frizzarin *et al.*, 2021).

Genetic gain per generation is a function of the intensity of selection, the accuracy of selection and the genetic variability. Genetic variability is one of the key determinants of genetic gain; while variability is often depicted based on the extent of the standard deviation, a more useful statistic to compare across traits is the coefficient of genetic variation, which is unit-less, thereby enabling comparison of the extent of variability across traits. Table 1 demonstrates that the coefficient of genetic variability for some FTIR-predicted milk quality traits ranges from 0.3 to 10.9, which is within the range of genetic variation for milk yield, fat percent and protein percent estimated using the same dataset (Visentin *et al.*, 2017). Hence, lack of genetic variation in milk quality is not a concern. The accuracy of selection is a function of the heritability of the trait and the

information available from which to make selection decisions; while information used in dairy cow breeding traditionally meant phenotypic records, this is now being complemented by genomic information. The lower the heritability, the greater the number of records required to achieve a high accuracy of selection. Table 1 also summarises the heritability of a number of milk quality traits; these generally range from 0.16 to 0.46, with the exception of milk greenness (a*) at 0.10. These estimates are similar to those for milk yield and composition; hence, should these quality traits be predictable from milk samples, then a sufficiently high accuracy of selection for milk quality would be possible, equivalent to that achieved for milk yield.

As datasets increase in size and expertise in handling complex data structures improves, research continues to identify the optimal method to handle spectral data to maximise the relationship between the FTIR spectrum and novel phenotypes (Frizzarin *et al.*, 2021). Genetic improvement of milk quality is currently a hot topic and, through the use of FTIR, access to thousands of cow lactations with regularly predicted milk quality parameters is possible. This information will assist in improving understanding of how milk quality changes across lactation, as well as quantifying relationships between milk quality and other traits of importance to the breeding goal.

Molecular and bioinformatic techniques for tracking the dairy supply chain microbiome

Central to the improvement in milk quality is the ability to rapidly identify microbes at species level across the dairy

| Trait | Prediction accuracy ¹ | | FTIR-predicted trait parameters ² | | |
|----------------------|----------------------------------|------|--|--------------|-------|
| | RMSE | r | Mean (s.d.) | h² (s.e.) | CVg |
| Milk yield (kg/day) | — | _ | 20.87 (6.35) | 0.18 (-0.02) | 10.79 |
| Protein (%) | _ | _ | 3.71 (0.39) | 0.46 (-0.02) | 4.58 |
| Fat (%) | — | _ | 4.6 (1.07) | 0.29 (-0.01) | 7.83 |
| RCT (min) | 6.40 | 0.71 | 20.37 (6.22) | 0.28 (-0.01) | 8.10 |
| Heat stability (min) | 5.46 | 0.67 | 6.79 (4.4) | 0.16 (-0.01) | 10.90 |
| pH (units) | 0.06 | 0.81 | 6.69 (0.08) | 0.27 (-0.01) | 0.30 |
| Lightness (L*) | 1.57 | 0.55 | 81.63 (NA ³) | 0.29 (0.02) | 0.37 |
| Greenness (a*) | 0.52 | 0.30 | -4.05 (NA) | 0.10 (0.01) | 1.73 |
| Yellowness (b*) | 2.03 | 0.72 | 8.23 (NA) | 0.35 (0.01) | 1.46 |

Table 1: Accuracy of prediction of milk quality traits, including the RMSE and the correlation between true and predicted values (r) in a validation dataset and the mean, heritability (h²) and coefficient of genetic variation (CVg) of FTIR-predicted traits in Irish dairy cows

RCT = rennet coagulation time; RMSE = root mean square error.

¹Prediction accuracy of RCT, heat stability and pH obtained from Frizzarin *et al.* (2021). Prediction accuracy of lightness, greenness and yellowness obtained from McDermott *et al.* (2016).

²Population parameters for milk yield, protein %, fat %, RCT, heat stability and pH obtained from Visentin *et al.* (2017). Population parameters for lightness, greenness and yellowness obtained from Scarso *et al.* (2017).

³Not available.

supply chain, from farm to finished product. Conceptualising ways of combining tracking, identification and enumeration of microbes and microbial populations (microbiota) into one methodology is now possible due to advances in molecular and digital technologies. Targeted molecular approaches, such as polymerase chain reaction (PCR) and, especially quantitative (qPCR) methods of analysis are generally more sensitive, user-friendly, easier to automate and time-efficient for analysis of specific pathogens and spoilage microorganisms. Highthroughput DNA sequencing has become critically important for deeper analysis of specific strains or broader analyses of the microbiota of the dairy supply chain. Ireland is at the forefront in this research, as evidenced by the establishment of the Irish Next Generation Sequencing (NGS) Centre at the Teagasc Food Research Centre, Moorepark in 2009. This facility is the largest of its kind in Ireland and currently contains a range of DNA sequencing platforms including Ion PGM, Ion Proton, Illumina MiSeq, Illumina NextSeq and the Oxford Nanopore MinIon and GridION platforms. This allows the provision of complete genomic (i.e. specific strains) and metagenomic (i.e. the genomes from the multitude of microorganisms present among a specific microbiota) analysis relevant to food manufacturing and human/animal health.

These sequencing platforms have been used in a variety of ways to study the microbiome of the dairy supply chain. One early study examined the bacterial populations in Irish artisanal cheese and revealed the presence of a number of bacteria that had not previously been associated with cheese including Faecalibacterium, Prevotella, Helcococcus, Arthrobacter and Brachybacterium (Quigley et al., 2012). This study also confirmed a number of previously observed patterns, including the dominance of typical starter and non-starter lactic acid bacteria (NSLAB) in the cheese, the increasing dominance of NSLAB as the cheese ripens and significant differences in the microbial populations of raw and pasteurised milk cheeses, all of which increased confidence that this technology could be used to study microbial populations in cheese and dairy systems. Similarly, this technology has been applied to monitor the microbiome of raw and pasteurised milk (Quigley et al., 2013) and to assist in the confirmation of Thermus thermophilus as the causative agent of the "pinking" colour defect in cheeses (Quigley et al., 2016). A recent example relates to the use of molecular and bioinformatic techniques in the dairy sector as reported by McHugh et al. (2020). The study used both 16S rRNA gene amplicon sequencing (an approach that provides information about the proportions of different bacteria present in a sample) and shotgun metagenomic sequencing (which provides information about all types of microorganisms in a population and the genes that they encode) to track changes in the microbiota of fresh, mid- or late-lactation milks from on-farm bulk tanks, collection tankers, milk silos, skim/cream silos and finished

skim milk powder (SMP) samples. This high-throughput DNA sequencing analysis was complemented by bioinformatics infrastructure and expertise to allow interpretation of the data. The data obtained confirmed the complexity of the microbiota in raw milks from farm bulk tanks and collection tankers and highlighted the presence of species of *Pseudomonas* and *Acinetobacter*, potential spoilage bacteria that grow at the low storage temperatures used for milk on-farm and during transport. During storage of the milk in silos prior to processing, *Pseudomonas fluorescens* and *Acinetobacter baumannii* grew to become the dominant population. Upon processing to SMP, the population continued to reflect that of the raw milk for latelactation milks, while *Thermus* and *Geobacillus* dominated in powders made from mid-lactation milk.

The studies demonstrate the potential for integration of this technology across the dairy supply chain and the implication for quality and safety is immense. Expectations are high, as development of DNA sequencing platforms has rapidly evolved over recent years, driven by advances in molecular biochemistry, leading to, for example, handheld sequencing devices. These advances, combined with automated DNA extraction approaches and high-end computing, have revolutionised this science, providing several opportunities to place Ireland's dairy sector at the forefront of advanced analytics with a possible market advantage. When coupled with bioinformatics, these new technologies have the potential to deliver traceability, safety and provenance within today's complex dairy supply chain. It is expected that this will provide the dairy sector with powerful datasets from on-farm and factory microbiota, and information on environmental factors that influence the microbiome of dairy products. International standards are currently based on traditional microbiological agar-plate methods and there is a need to validate the use of new techniques in dairy product manufacturing processes in situ. Traceability, for instance, is key in the case of sensitive consumer markets such as in the infant formula sector, which is a prominent utiliser of Ireland's dairy ingredients. Teagasc researchers are currently working on establishing methodologies that are sufficiently robust to work in dairy ingredient processing environments, where, for example, sequential heating steps are used that will significantly impact the microbiome. However, limitations of molecular methods include the ability to enumerate viable bacterial cells, after such heating regimes. Teagasc has an active programme of work with the objective of determining viable cell recovery throughout different dairy processes. The research has the potential to provide a foundation for development of new quality control protocols and release criteria for the dairy sector to protect existing, and develop new, markets for the future. In addition, these molecular techniques can provide additional safety information for products (including raw milk products) and for countries with developing infrastructures and/or climates not conducive to effective control of microbial growth.

Characteristics and challenges of the Irish dairy sector and research activities to address them

Seasonality of milk production in Ireland

A seasonal milk supply is a fundamental characteristic of milk production in Ireland, with implications for milk quality, processing characteristics and price. Primary milk production in Ireland is driven by the use of pasture as a natural lowcost feed source, which has led to the widespread adoption of a seasonal calving pattern, synchronised to maximise pasture utilisation, with the majority of cows calving in early spring and a dry period of 8-10 wk during winter. This grassbased production system maximises cost efficiency and sustainability; however, the seasonal milk supply creates a volume and guality/functionality constraint for milk processors, particularly during the early- and late-lactation periods. Seasonality of milk is defined as changes in milk composition and functionality linked to the stage of lactation, that is, time post-partum, coupled with dietary changes throughout the season, which affects the suitability of milk for production of dairy products.

Fat, protein and lactose are the major macro components of milk, which are subject to variation in quantity and, in some respects, quality over the season. A study by O'Callaghan et al. (2016a) determined a significant increase in milk fat and protein contents and a significant decrease in milk lactose content in late-lactation milk derived from a grass-based, spring-calving herd. A recent study by Parmar et al. (2020) examined the effect of seasonal variation on milk composition and density in spring-calving Jersey and Holstein/Friesian cows, highlighting the importance of milk density in milk volume-weight calculations throughout the season. Milk fat content was significantly lower during summer (4.71%), in comparison to spring (5.00%) and autumn (5.13%), while milk lactose content was significantly higher in autumn (4.68%) than in spring (4.59%) and summer (4.62%). Milk density also varied significantly throughout the year, with the lowest average value observed during the spring months (1.0304 g/cm³), which was significantly lower than in autumn (1.0309 g/cm³), which was, in turn, significantly lower than in summer (1.0314 g/cm³), primarily due to the substantially lower milk fat content during the summer months. This is critical for milk processors, as milk volume at collection is converted to mass using a density conversion factor, which, in industrial practice, currently remains constant throughout the season. Thus, the compositional variation that occurs throughout the season is not accurately reflected in estimates of milk volume-mass ratios using the standard density value,

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which could instead be adjusted periodically to improve accuracy.

Many studies have reported poor processing characteristics of late-lactation milk and associated quality parameters of products manufactured from that milk (Auldist et al., 1996; O'Brien et al., 2006; Downey & Doyle, 2007). Late-lactation milk has shown poor rennet coagulability, impaired curd syneresis, high moisture content in Cheddar cheese and lower recovery of total milk fat in the cheese (Auldist et al., 1996). Maintenance of good nutritional status in spring-calved herds as they transition into late lactation (278 days in lactation) has been found to maintain better milk processing quality (heat stability, free FA levels, alcohol stability and rennet coagulation properties), as lactose, protein and casein contents were maintained at >4.3% (w/w), 3.6% (w/w) and 2.8% (w/w), respectively (Guinee et al., 2007; Guinee & O'Brien, 2010). O'Connell et al. (2016) investigated the effects of storage temperature and duration on microbial guality of bulk tank milk in mid and late lactation, and showed that proteolytic bacterial count was greater in milk in the latter stages of lactation.

A recent study by Lin et al. (2017) examined seasonal changes in the compositional, physicochemical and processing characteristics of skim milk from a mixed herd with varying proportions of milk from spring- and autumn-calving cows. These authors reported that season significantly affected concentrations of total phosphorus (P) and serum P, levels of α_{a1} - and β -caseins (as proportions of total casein), casein micelle size, zeta potential and ethanol stability at different pH values. While season did not influence the rennet gelation or heat stability characteristics of the milk, ethanol stability of autumn/winter milk was lower than that of spring/summer milk. The absence of significant seasonal effects on many of the compositional parameters, rennet gelation and heat stability characteristics suggests that milk from a mixed herd of spring- and autumn-calving cows is more suitable (than that from spring-calving cows only) for the manufacture of cheese and milk powder on a year-round basis. Thus, where milk is predominantly derived from a pasture-based, spring-calving system, as in Ireland, the use of autumn-calving herds at critical times of the year could help to reduce the processing problems frequently encountered at the extremes of lactation. While Ireland's seasonal milk production profile facilitates cost advantages in milk production at farm level, it can involve extra costs in the processing sector, such as elevated plant capacity during the peak supply period, with under-utilisation of plant capacity in early/late lactation. This is often coupled with a seasonal labour requirement and higher fixed costs. From a national perspective, the seasonality trade-offs can be complex and evolving strategies are very much influenced by international dairy markets. A seasonal milk supply will always have a focus on bulk commodities during peak supply; however, the Irish dairy sector has engaged in innovative investments and has the capability of delivering a range of value-added ingredients while seasonality remains the dominant feature of Irish milk production. The driver of seasonality, that is, a grass-based/grass-fed milk production system, also creates a unique selling point for sustainable Irish dairy produce in international markets and has the potential to generate a financial return for all stakeholders within the sector.

Grass-fed milk

In recent years, there has been an increased prevalence of grass-fed dairy products on the market, driven by consumer demand associated with a perception of a more natural, environmentally sustainable production system providing improved animal welfare and better nutritional attributes. This has resulted in grass-fed dairy products achieving a premium price over more conventional non-grass-fed dairy products in some geographical markets, and has also resulted in Irish milk producers achieving a greater price in some countries. Significant research has been undertaken to examine, identify and characterise the unique compositional and sensory attributes of grass-fed dairy products, highlighting the fact that such consumer perceptions appear to have some basis in fact.

Grass-fed dairy systems are best suited to regions with a temperate climate, plentiful rainfall and fertile soils that can enable cows to be maintained outdoors grazing pasture for the majority of their lactation, whereby calving periods are synchronised for milk production to coincide with the grass growing periods of the year, that is, spring-calving dairy herds. However, this seasonal approach to milk production poses challenges to dairy manufacturers, due to synchronised changes in milk composition and quality as the herd transitions through early, mid and late stages of lactation (see review by Timlin et al., 2021). The definition of grass-fed, as such, can vary from region to region, often differing in the levels of fresh pasture in the diet, the type of grass or portion of required access to outdoor paddocks per day or per lactation. In that regard, not all grass-fed dairy products are the same, and for that reason, it is vital for regions to have clear, defined and accredited grass-fed standards (Moscovici Joubran et al., 2021).

Pasture feeding has a significant effect on the composition and quality of milk and dairy products (Alothman *et al.*, 2019; Magan *et al.*, 2021), with one of the greatest impacts affecting the fat fraction of the milk. A positive correlation between the proportion of fresh grass in the cow diet and levels of conjugated linoleic acid (CLA) and omega 3 FAs in the milk is well established (Kelly *et al.*, 1998; Couvreur *et al.*, 2006; O'Callaghan *et al.*, 2016a). O'Callaghan *et al.* (2016b) found that non-grass diets (total mixed ration) produced milk with high solid content and yields and also higher levels of palmitic acid and omega 6 FAs. Grass-fed diets enhance levels of carotenoids such as β -carotene and lutein, which are natural antioxidants and precursors for vitamin A synthesis, in milk (Kalač, 2011).

The sensory characteristics of milk have also shown to be influenced by diet (Faulkner et al., 2018; Clarke et al., 2019). β-Carotene content has been shown to significantly influence the colour of dairy products and can also influence consumer perception (Faulkner et al., 2018). Multiple studies have identified differences in volatile compounds due to cows' diet and some of these have the potential to influence sensory characteristics, while others may be used to authenticate grass-fed milk and dairy products in the future (Kilcawley et al., 2018). The volatile compound p-cresol, which is particularly odour-active and has a barnyard-like aroma, is more prevalent in grass-fed dairy products, as it is a product of rumen metabolism of β -carotene and isoflavones in clover (Faulkner et al., 2018; Kilcawley et al., 2018; Clarke et al., 2019). This barnyard-like aroma appears to be more easily percieved by US (compared to Irish) consumers, persumbly due to lack of US familarity with grass-fed milk and dairy products (Kilcawley et al., 2018).

Changes in milk composition due to cow diet were shown to impact products derived from that milk. Grass-fed butter has a characteristic golden or yellow colour due to significantly higher levels of β -carotene naturally present in fresh grass (O'Callaghan et al., 2016a). Alterations to the FA profiles were shown to significantly affect the texture of butter (Couvreur et al., 2006; O'Callaghan et al., 2016b) with softer butter being produced from grass-fed than nongrass-fed milk. The impact of feed systems on the sensory perception of butter was studied by Garvey et al. (2020), who found that there was no significant difference in overall preference between grass-fed and non-grass-fed butters among US, German and Irish consumers, but cross-cultural preferences were evident and likely influenced by familiarity with grass-fed or non-grass-fed butters. The impact of pasture feeding on water-soluble vitamins (Magan et al., 2020) and metabolites (Magan et al., 2019) in SMP indicated that vitamin B3 and B3-amide concentrations were higher in total mixed ration derived samples, while vitamin B1, B2 and B7 concentrations were significantly higher in grass-fed derived samples. Cheng et al. (2020) found that cow diet impacted the sensory perception of SMP and that perception differed between Chinese, Irish and US consumers. The impact of diet on the sensory characteristics of cheese is less clear, mainly due to the fact that significant biochemical changes occur during cheese production and ripening that likely supersede pre-existing dietary-derived differences in the milk (O'Callaghan et al., 2017; Panthi et al., 2019). The impact of terpenes present in wild mountain pasture may, however, impact the sensory character of some regional cheeses (Kilcawley et al., 2018).

There is a need for legislation to distinguish and protect grassfed milk products, but in order to achieve this, methods are required to authenticate grass-fed milk and dairy products. These methods are likely to be based on the unique characteristics associated with grass-fed milk, such as FA profiling, quantification of specific carotenoids, volatiles or vitamins; however, rapid spectral approaches would be of most benefit due to their low cost, robust and practical nature (Capuano *et al.*, 2014a, 2014b; O'Callaghan *et al.*, 2018; Gómez-Mascaraque *et al.*, 2020; Magan *et al.*, 2021).

Somatic cell count

In dairy cows, the initial stage of mastitis infection is subclinical, with inflammation so slight that it is not detectable by visual examination. However, at this stage of the infection, somatic cells transfer from the blood to the milk in an effort to prevent or reduce the inflammation/infection. There can be a rapid increase in milk SCC during this time, with udder quarters potentially having an SCC of 200–5,000 × 10³ cells/mL. In the absence of detection, this milk becomes part of the bulk manufacturing milk, and the high SCC can negatively impact the quality and suitability of the milk for processing.

Much research has been undertaken on farm management factors influencing bulk herd milk SCC, both in Ireland and internationally. A study conducted by Kelly *et al.* (2009) on Irish dairy herds showed that management practices associated with maintaining low SCC included the use of dry cow therapy, participation in a milk recording scheme and the use of teat disinfection post-milking. An association between low SCC and an increased level of hygiene and frequency of cleaning of the holding yard, passageways and cubicles was also observed. In Ireland, as per European Union (EU) regulations, the SCC threshold for milk purchasers is 400 × 10³ cells/mL. However, much research has indicated negative impacts of SCC below this threshold on milk processing quality, and therefore, it is clear that for production of quality dairy products, more stringent SCC levels need to be achieved.

The influence of SCC on the composition of milk and its processability into dairy products, particularly cheese, has been studied extensively; increasing SCC in milk is associated with marked changes in the concentrations of milk constituents, the state (degree of hydrolysis) of the milk components and cheesemaking properties (Politis & Ng-Kwai-Hang, 1988a, 1988b, 1988c). An increase in SCC in the range of 100×10^3 to 1000×10^3 cells/mL has generally been found to reduce lactose, fat and casein contents in milk, casein as a percentage of true protein, gel firmness, recoveries of protein from milk to cheese and cheese yield, and to increase cheese moisture and rates of primary and secondary proteolysis during maturation. Authors generally agree that high milk SCC is accompanied by a detrimental effect on the organoleptic properties of cheese (Barbano *et al.*, 1991). More recent work

by Geary *et al.* (2013a) also showed a significant negative relationship between SCC and recoveries of protein and fat; as SCC increased, cheese protein content declined and cheese moisture content increased. The impact of these compositional changes as a result of elevated SCC potentially could have significant impact on product sales, processing costs and milk returns across the dairy industry.

Mastitis is a costly disease within the dairy industry, which manifests itself at both farm and processor levels and has been identified as one of the most economically relevant diseases of dairy cattle in Ireland (More et al., 2010). Geary et al. (2012) found that Irish farms sustained large losses in profit when bulk milk SCC increased above 100 × 10³ cells/mL. Furthermore, a study by Geary et al. (2013b), in which the farm and processor costs were combined, showed that, if the cell count was reduced by 10% on a national basis, this would be worth €37.6 million for the Irish dairy industry, at that time. Consequently, a concerted effort has been undertaken to reduce SCC which included the introduction of payment structures to incentivise for lower SCC milk. Payment systems, either in the form of a penalty or bonus or both, are effective tools to encourage reductions in milk SCC (Berry et al., 2006). This strategy was introduced in Ireland with the principle being that maintaining the farm bulk milk SCC below 400 × 10³ cells/mL was not sufficient, while highlighting that a bulk milk SCC < 100 × 10³ cells/mL was optimal.

The other significant approach used to reduce national milk SCC was the development of the CellCheck programme in 2010. CellCheck is the national mastitis control programme in Ireland which is coordinated and facilitated by Animal Health Ireland (https://animalhealthireland.ie/). This programme provides the knowledge to reduce SCC on farm, while also raising awareness of the costs of mastitis at farm level. Tools have been developed internationally to assist the farmer awareness/education process, for example, the Dutch cost of mastitis tool (Huijps et al., 2008). A similar decision support tool was developed for Ireland (CostCheck) using the analysis carried out by Geary et al. (2012). CellCheck has played a critical role in facilitating the collaboration of farmers, processors, service providers and government, and partnerships at farm level, co-operative and farm advisors, milking machine technicians and vets, all with the goal of improving mastitis control and milk quality on a national basis. A study by O'Connell et al. (2015) initiated the collection of bulk tank SCC data directly from each of the milk processors. These data are now collated by the Department of Agriculture, Food and Marine (DAFM) and are analysed by Animal Health Ireland every 4 mo. This dataset accounts for over 95% of the milk supplied in Ireland and is invaluable in monitoring the udder health of the national herd. Figure 2 outlines the annual average SCC from 2007 to 2020. It is clear that significant reduction in SCC was achieved over the period 2007-2017



Figure 2. Annual average SCC (2007-2020).

and reduced levels were maintained thereafter, at annual SCC <185,000 cells/mL.

Continued SCC data collection and analysis is essential for measuring industry progress and change. This is an important learning for the industry, particularly as it enters a period of significant change in relation to antimicrobial use (further discussed in the paper of Mee *et al.* (2022) in this journal edition).

Milk enzymology

Milk has long been known to contain a diverse and complex set of indigenous enzymes from sources such as mammary epithelial cells, lysosomes of somatic cells, blood and the milk fat globule membrane. These enzymes are of significance for milk and dairy product quality from a number of perspectives, such as influence on quality (plasmin, lipoprotein lipase), use as indicators of severity of processing (alkaline phosphatase) and antimicrobial function (lactoperoxidase). For many enzymes, milk contains a complex mixture of zymogens, activators, inhibitors and substrates, some of which appear to be inactive in milk and are of unknown function (for overviews, see Fox & Kelly, 2006a, 2006b; Fox et al., 2006; Kelly & Larsen, 2021). Levels of enzyme activity in milk are variable and affected by factors such as stage of lactation and mastitis; for this reason, some enzymes have been proposed as potential diagnostic indicators of diseases, such as β-Nacetyl-glucosaminidase (NAGase).

In addition to indigenous enzymes originating from the cow, raw milk is increasingly recognised (as a consequence of high-throughput sequencing tools) as containing a wide range of psychrotrophic bacterial species, especially of the genus *Pseudomonas* (Machado *et al.*, 2017; Zhang *et al.*, 2019). Many strains of such bacteria, if they grow to significant numbers, secrete extremely thermostable proteases and lipases. These are sufficiently thermally stable to withstand ultra-high temperature (UHT) processing (at 138–142°C for 2–4 s), and can result in physical instability during long-term storage; this is assisted by their ability to coagulate casein very slowly by a chymosin-like action, due to a relatively

similar specificity against κ -casein, leading to a gel forming in the package (Zhang *et al.*, 2018).

While there have been many studies on the impact of such bacterial enzymes on UHT milk quality, there have been far fewer on other dairy products, such as cheese. Recent studies between Teagasc, Moorepark and University College Cork (UCC) attempted to bridge this gap and evaluated the impact of an extracellular protease of P. fluorescens on rennet coagulation properties of milk and guality of Cheddar cheese. Interestingly, it was found that the protease could actually enhance rennet coagulation properties, presumably due to a synergistic action with chymosin, but that more extensive proteolytic action resulted in formation of weak gels; the impact on Cheddar cheese during ripening was relatively minor, perhaps again due to a similar action to that of chymosin (Paludetti, 2020a, 2020b). Overall, there are significant knowledge gaps that remain about the microbiology of Irish manufacturing milk in specific relation to the production of such enzymes and their persistence and role in product quality.

Another aspect of milk enzymology that has been of recent focus concerns the partitioning of enzymes during production of next-generation milk protein ingredients. For example, the indigenous milk protease plasmin is found in milk as part of a complex system that includes the inactive zymogen plasminogen, plasminogen activators (PA) and inhibitors of both plasmin and PA. Heat treatment can inactivate the inhibitors, effectively upregulating plasmin action, while membrane filtration can fractionate the enzyme and its casein substrate (as plasmin naturally associates with the casein micelles) away from the inhibitors, which are lost in the permeate (Gazi et al., 2014). The implications of such processing considerations for the ultimate stability of casein in ingredients such as micellar casein concentrate (MCC) when later incorporated into formulated food or beverage products is the subject of ongoing research at UCC (France et al., 2021). In addition, collaborative studies between UCC and Teagasc are evaluating the role of such enzymes in the ripening of cheese made from such ingredients (Li et al., 2020).

Overall, the enzymology of milk remains an active area of research, and research teams in Ireland remain at the forefront of international study in this area; this is also reflected by the publication of a major new reference work in this field (Kelly & Larsen, 2021).

Residues

The significance of residues in global food production, international trade and consumer confidence is gaining momentum, as evidenced by increasingly complex legal and regulatory guidelines surrounding their presence and subsequent consumption in food. Vulnerable consumers such as the very young, old or those with compromised health status can potentially be at higher risk due to the presence of these compounds in dairy foods. A factsheet developed by The Food Safety Authority of Ireland (FSAI) for foods of animal origin advises on legislation at both national and EU levels, and on monitoring/analysis of residues (FSAI, 2015). Irish and international studies of residues in milk have included organic acids, quaternary ammonium compounds and iodine. This is supported by the achievement of high sensitivity in the detection methods applied to milk, such as high-resolution mass spectrometry, which can detect a wide range of residues in milk at very low limits of quantification. In recent years, research at Teagasc has focused on residues associated with the use of chlorine-based sanitisers and the entry, partition and fate of their disinfection by-products in milk/ dairy products and strategies for their mitigation. Cleaning and disinfection are critical aspects of good manufacturing practice within the dairy sector and are essential to ensure bacteriological quality of milk and subsequent dairy products through effective sanitation of contact surfaces. However, disinfection by-products formed by the reaction of chlorine with organic/inorganic compounds during dairy processing and their potential for accumulation within finished dairy products such as butter and milk powders (often used as ingredients in infant milk formula) has led to trichloromethane (TCM) and chlorate emerging as residues of significant concern.

Contact of chlorine with organic material, for example, milk, can result in the formation of organic chlorine disinfection byproducts (Tiefel & Guthy, 1997), consisting of volatile and nonvolatile organic chlorine. The most important of the volatile organic chlorine group is TCM (CHCl₃), which has an affinity for the fat fraction in milk and hence is preferentially enriched in high-fat derivatives such as cream and butter. Germany is currently one of the most important export markets for Irish butter, and German standards surrounding TCM levels in food govern specification compliance of countries exporting therein. Thus, target TCM levels of <0.002 mg/kg for milk and <0.03 mg/kg for butter were recommended to meet market requirements. The main factors influencing milk TCM levels were identified by O'Brien (2009) and included having sufficient rinse water volume, not reusing rinse water, and having adequate plant drainage after wash cycles, limited reuse of detergent solutions and adherence to recommended chemical usage rates. Many of these factors were addressed in the study of Ryan et al. (2013) who demonstrated the importance of adequate rinsing of both organic (milk) and detergent residues from the milking plant; these authors recommended a minimum rinse water volume of 14 L water per milking unit to meet TCM targets. Implementation of improved control strategies at farm and processor level surrounding chlorine use ensured that initial TCM target levels were met. TCM target levels were subsequently reduced from 0.002 to 0.00155 mg/kg to the current level of 0.00124 mg/ kg in milk, with a corresponding target of 0.0124 mg/kg in butter. Routine monitoring of milk supplies in Ireland indicates that currently this target is consistently surpassed (personal communication).

Chlorate (CIO3-) residue has become a growing concern within the dairy, food and beverage industries in recent years. In addition to organic by-products like TCM, disinfection with chlorine is also associated with inorganic chlorine species, formed through oxidation reactions. Chlorine can form an extensive number of oxidised inorganic disinfection byproducts, with chlorate formation being primarily associated with the decomposition of chlorine dioxide and hypochlorite solutions (Adam et al., 1992; WHO, 2005; Snyder et al., 2009). A maximum residue level (MRL) of 0.01 mg/kg for chlorate was applied to all foods according to EU Regulation 396/2005 (EC, 2005). However, EU surveys have identified chlorate residue levels in food products, including milk and milk-based products, greater than the MRL of 0.01 mg/kg (EC, 2005). From a food safety perspective, chlorate and other oxychlorine species have been associated with the inhibition of iodine uptake in humans and the formation of methaemoglobin, with infants and young children identified as a high-risk demographic. Thus, to ensure compliance with the EU MRLs with respect to chlorate levels in Irish dairy products, a critical evaluation of cleaning and disinfection procedures applied at farms and processor level was undertaken to assess the impact of chlorine-containing disinfectants on chlorate levels and to assess potential mitigation solutions.

The presence of chlorate in milk and dairy products arises primarily from the use of chlorinated water and chlorinated detergents for cleaning and sanitation of equipment at both farm and dairy processor levels (McCarthy *et al.*, 2018). At both farm and processing levels, degradation of hypochlorite and formation of chlorate occurs during storage of concentrated hypochlorite solutions and is dependent on concentration, product storage temperature and pH. Thus, entry of chlorate into the dairy production chain through cleaning/disinfection practices will depend on the level of chlorate formed in the stored hypochlorite solution and on the efficiency of removal of chlorate residues during the rinsing cycles after disinfection (Gleeson & O'Brien, 2016). While total removal of chlorine detergents at farm level solves the chlorate problem, this strategy could have negative implications for the microbiological guality of milk. Gleeson et al. (2013) demonstrated that chlorine-free cleaning was effective when examined over a 3-mo period, during which detergent usage rates, water temperature and rinsing protocols were closely monitored. New cleaning protocols were subsequently developed together with guidelines on the key steps required for cleaning milking equipment in a chlorine-free environment (Gleeson, 2018); this allowed an initial transition to chlorine-free cleaning on-farm without creating microbiological challenges. A further study by Yap & Cotter (2020) examined the microbiological and residue quality of milk from farms that had adopted chlorine-free cleaning and those that continued to use chlorine-based cleaning. Improved microbial quality of milk and reduced residue levels were evident on farms using chlorine-free cleaning methods.

Disinfection of water with hypochlorite and chlorine dioxidebased solutions has also been identified as an entry route for chlorate within the dairy process. A study by Paludetti et al. (2019) highlighted that within the production process in a processing plant, chlorate levels could increase 50-fold, due to the concentration of milk to product but also due to chlorinated rinse water. Potable water for in-process use, treated with hypochlorite or chlorine dioxide, often generates high chlorate levels therein. During equipment stabilisation, flushing and product pushout scenarios, there is high potential for comixing of water and product, risking enrichment of chlorate in finished dairy products. Alternatively, water treatment using chlorine gas does not contribute to chlorate levels in treated water (Nieminski et al., 1993). The dairy industry is now moving away from chlorine dioxide and hypochlorite solutions for water treatment, with widespread adoption of chlorine gas treatment now limiting potential cross-contamination of chlorate from water to product.

Today, partly based on the research at Teagasc, Ireland has instated a resolution to remove all chlorine-based detergents from both farms and processing plants from January 2021. This involves removing all chlorine-based products from cleaning protocols on the farm and in the processing plant and replacing them with alternative sanitisation approaches based on combinations of peracetic acid and hydrogen peroxide. While this approach broadly addresses the risk of chlorine disinfection by-products entering the dairy supply chain, vigilance surrounding emergence of other sanitation residues is essential to maintain the high safety standards to which Irish dairy products are held.

Processing technology and implications for milk and dairy product quality

The Irish dairy industry produces a range of commodities and high value dairy derivatives through a core platform of dairy technologies designed and optimised to produce the long shelf-life export products that define the Irish dairy processing sector as a whole. Key technology platforms include heat treatment, fermentation, mechanical, enzymatic, charge and size-based separations, evaporative concentration and spray-drving. The legal requirement for pasteurisation is normally met by high temperature, short time (HTST) heat treatment, which is widely used in liquid milk production using conventional plate heat-exchangers. Currently, commercial HTST pasteurisation usually refers to a heat treatment ranging from 72°C to 75°C for 15-20 s (Reich et al., 2017). However, meeting microbiological specifications in long shelf-life products necessitates sequential additional heat treatments of up to 125°C for 3-5 s. These sequential heat treatments often employ direct steam injection/infusion technologies and can cause deleterious effects to the nutritional and organoleptic properties of products, including changes in physical properties such as viscosity, colour and generation of Maillard reaction products (Van Boekel, 1998).

Mechanical separation initially focused solely on centrifugal separation of cream, but has evolved to incorporate removal of curd fines from cheese whey, clarification of cheese brine, separation of acid curd, bacteria removal and, more recently, cold separation of spores from liquid milk. The evolution from mechanical to size-based separation in the dairy industry was a gradual one, which diversified the product portfolio that could be generated from milk. Early plant designs based on dead-end and plate- and frame-filtration techniques have been replaced with separation processes which rely upon cross-flow filtration of a liquid through a semi-permeable membrane. Membrane filtration has become the workhorse of the dairy industry for the physical separation and selective concentration of milk components. In their current form, membrane filtration processes are applied within dairy processes for removal of bacteria and spores, de-fatting of milk and whey (microfiltration), standardisation of whole/ skim milk, protein enrichment and isolation (ultrafiltration), demineralisation, concentration of total dry matter (DM) and recovery of white water streams (nano-filtration and reverse osmosis). Filtration systems are now widespread in the dairy industry and drive creation of dairy ingredients with tailored functional and nutritional properties.

Commercially, dairy products are concentrated using fallingfilm evaporators, with earlier designs incorporating thermal vapour recompression, which are now mostly superseded by more efficient mechanical vapour recompression-based systems. Both systems exploit the indirect heating of a thin film of product under vacuum, removing up to 90% of the water. However, evaporation is an energy-intensive process, limited by product characteristics including viscosity and stability of heat-labile components (Hasanoğlu & Gül, 2016). To reduce energy consumption and/or maximise plant capacity relative to capital costs and plant footprint, dairy products are now often pre-concentrated using reverse osmosis and nano-filtration followed by evaporation to reach DM contents suitable for efficient stabilisation through spray-drying (Ramirez *et al.*, 2006). Spray-drying is by far the most frequently used technology for the manufacture of dairy powders. As the last major unit operation in the powder manufacturing process, it can have far-reaching effects on both the microbial and physical quality of products.

In general, hygienic design principles are well observed and safeguarded against the risk of contamination. The fundamentals of hygienic dryer design are reviewed by Masters & Masters (2006). However, in industry there is a continuous focus on improving hygienic design, driven largely by the European Hygienic Engineering and Design Group (EHEDG, 2018). A strong focus is placed on the integrity of drying surfaces to eliminate cracks or crevices in which microbes can proliferate, which is achieved through highquality fabrication and installation procedures, along with rigorous preventative maintenance. Clean-in-place (CIP) systems should be designed to ensure that product contact surfaces can be reached by cleaning reagents and allow for efficient post-CIP drainage and moisture elimination. This includes exhaust systems, with design of ever-more efficient and cleanable powder recovery systems (e.g. cyclones and bag filters) continuing on an ongoing basis (Masters, 2004; Cornall, 2020).

While product microbial quality is of paramount importance, many products are sold based on their physical functionality, for example, wettability and flowability. Here, the effect of preprocessing can be as important as the dryer configuration and the body of work investigating the interaction between wetprocessing and drying is continually growing (Murphy et al., 2011, 2013, 2014, 2015; McCarthy et al., 2013; Finnegan, 2021). A key feature of any spray-drying installation is the technology used for atomisation. Recently, high-pressure nozzles are more commonly used in new installations and can impart greater control over resultant powder properties such as span of particles and agglomeration (O'Sullivan et al., 2019), both of which are factors influencing key selling points such as wettability and flowability. However, due to the high operational cost of spray-drying, the main challenge lies in producing high-quality products while also maximising capacity. A commonly applied approach is to maximise water removal by pre-drying concentration steps (e.g. membrane filtration and vacuum evaporation) (Fox et al., 2010) which can be complemented by applying novel technologies to reduce the extent of viscosity development (Murphy et al.,

2013, 2015; Tanguy *et al.*, 2015). A detailed discussion on the interaction between energy optimisation and product physical quality was presented by Patil *et al.* (2021).

Nutritional security, sustainability and socioeconomic perspectives

The value of dairy exports in 2020 was €5.2 billion, increasing 3% on 2019, and the second year in a row in which dairy exports were greater than €5 billion. This was due to strong sales of butter, specialised nutritional and ingredient powders and cheese (Bord Bia, 2020). While still highly dependent on commodity production, over time, the dairy products portfolio in Ireland has evolved driven in part by demand from consumers for healthy and functional foods. The current diversity of products manufactured by the dairy industry in Ireland is shown in Figure 3.

Milk and dairy products are highly nutritious but perishable. Early shelf-life extension solutions were based on fermentation leading to soured milk and coagulated products like cheese and yoghurt. In Ireland, hard cheeses like Cheddar are most common; however, recent diversification into stretch curd cheeses like mozzarella has occurred due to market growth in particular in Asia and new market regulations. By contrast, large-scale yoghurt production has transferred abroad to super-factories, while small-to-medium-size production remains in the more specialised, including organic, sectors. However, global demand for commodities has remained strong, and the recovery of protein from milk and whey using membranes is now applied widely to milk separations. The range of protein ingredients that are currently produced in Ireland is shown in Figure 3.

The development of global economies and the requirement for nutritionally validated foods have come to the fore. The demand for ingredients with scientifically (clinically) proven health benefits aligns with the emergence of markets for functional foods. This has led to advancement in formulation for value-added ingredients that can be incorporated into foods and beverages to improve their technological and nutritional properties.

While research, and farm and processing plant management have accomplished very significant advances in milk and dairy product quality, some overarching emerging challenges include product substitution and sustainability. The industry is already being challenged by plant-based milk substitutes and this trend could potentially increase as consumers may consider such products more sustainable and better for health. Developments in fermentation technology-produced milks are progressing rapidly, and milks or milk components made using this process could potentially be used in some ingredient applications, as they may be considered more cost effective and sustainable than conventional milk. Thus, clear messages to key stakeholders are important regarding the

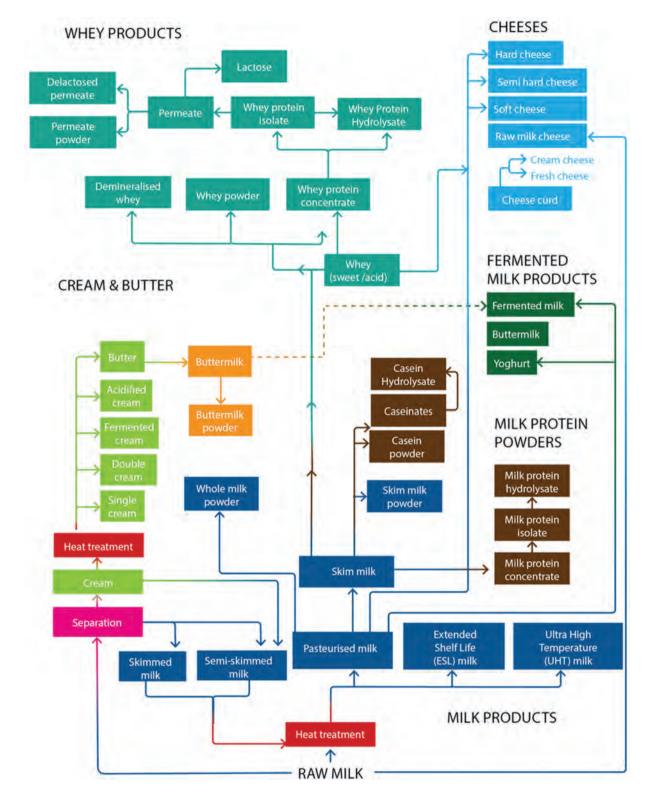


Figure 3. "Milk Map" of Ireland's Dairy Products (Adapted from the International Dairy Federation [IDF] milk tree: https://fil-idf.org/our-work/ dairy-science-and-technology/the-milk-tree-technology-and-use/.).

benefits of dairy from nutritional security, sustainability and socioeconomic perspectives.

Key pillars for the future

Evolution in analytical instrumentation

Fatty acids in milk directly impact milk quality in terms of nutrition, sensory and functional aspects and also have the potential to influence any derived dairy product in the same way. The FA composition of milk and dairy products is influenced by many factors, including breed, stage of lactation, diet and the health of the cow. Over 400 different FAs are known to exist in milk fat, varying in relation to carbon chain length, degree of unsaturation, chain branching, geometric and positional configuration and functional groups. However, most are present at trace levels, with only 15 FAs making up 1% or greater of the total amount (Mansson, 2008). The method of choice for FA quantification is gas chromatography flame ionisation detection (GCFID), where FAs are first isolated and then derivatitised to make them volatile and suitable for GCFID analysis. Separation is mainly achieved by the different FA affinities to a non-polar column stationary phase and through the application of heat, where FAs move from the stationary phase into the mobile or carrier gas phase and into the detector. Gas chromatography flame ionisation detection are reliable instruments, even though they require some expertise to operate, and their relatively low cost in comparison to gas chromatography mass spectrometers (GCMS) makes them ideally suited for routine quantification of FA. However, onedimensional GC analysis of FA is limited, as many FA isomers exist which are both structurally and molecularly similar and thus, very difficult to separate in a single chromatographic run. To date, most analysis focuses on quantifying the most abundant FA, or at least those from C4:0 to 22:0 (O'Callaghan et al., 2016b). In order to achieve sufficient separation of these FAs, long columns are required which also results in long run times, which significantly impacts the efficiency of the method. A main approach to circumvent this is twodimensional chromatography or GC×GC, where all or part of the eluent from the first column is passed to a second column of different polarity to enhance resolution of co-eluting FA. Two-dimensional chromatography is rapidly becoming a mainstream method to analyse semi-volatile and volatile components, as recent significant advances in hardware and software have made it more practical, easier to use and cost effective. A recent study managed to identify 51 individual FA (24 saturated, 13 monounsaturated and 14 polyunsaturated) in buffalo milk (Pegolo et al., 2017). The key element in GC×GC is the ability to modulate the flow of eluent between the two columns; traditionally, this was achieved using temperature modulation, but advances in flow modulation controlled

directly by the GC software/hardware make it easier to use and control, while also negating the use of cryogenics. The utilisation of GC×GC with MS further increases resolving power in tandem with sensitivity. GC×GC, in combination with time-of-flight MS or Orbitrap MS, offers the potential to identify volatiles derived from different feeding regimes that influence aromatic qualities of milk and dairy products that previously would not have been possible.

Process, products and functionality

Advances in data analytics, including chemometrics, have led to the development of predictive algorithms, generated through mid-infrared/near-infrared (MIR/NIR) spectroscopy data that can feed information into different stages of the dairy process. The emergence of process analytical testing (PAT) via sensors and their integration, data capture and increased connectivity through the industrial internet of things (IIOT) has fuelled artificial intelligence, facilitating quality by design and processes that can adapt remotely. Moreover, recent dairy manufacturing innovations are reliant on validated milk composition and functionality datasets to optimise processing parameter settings at different stages of the process, such as concentration, heating and dehydration. As discussed above, new scientific studies in this area include using MIR/NIR spectral data for analysis of milk components and functionality, animal health and nutritional traits.

Many of the most recent ingredients illustrated in Figure 3 are produced using some form of filtration. A relatively new technology, membrane filtration is now used widely in the dairy industry to physically separate and selectively concentrate milk components (IDF fact sheet, 2020). The ratio between nutrients can be altered to obtain a liquid or powdered ingredient with specific composition and functionality, suitable for use in the lifestyle beverages already mentioned. Some processors within Ireland use microfiltration as an initial step during manufacture, for the removal of bacteria and bacterial spores and meet composition specifications. Microfiltration can be used for de-fatting of milk and whey, protein enrichment and isolation, partial demineralisation, DM concentration and water recovery. The majority of milk protein-based ingredients shown in Figure 3 are selectively concentrated using ultrafiltration or microfiltration membranes; however, a more recent development is the production of micellar casein and corresponding serum proteins. Using microfiltration (with pore sizes of about 0.1–0.2 µm), it is possible to retain the casein fraction (in the retentate) and allow the serum proteins (65–95%) to pass through the membrane into the permeate stream, depending on the parameters used. The retentate is an MCC or isolate micellar casein (MCI), depending on the extent of processing (Figure 3). While MCC and MCI ingredients are not currently produced in Ireland, the technology is available in some processing plants. Further alteration of the functionality of protein ingredients can be achieved by pre- or post-processing treatments such as heat treatment or interaction with other ingredients, for example, specific minerals. Further fractionation is also possible using industrial chromatography, emulating what is currently being carried out in other dairy ingredient-producing countries. Finally, Irish dairy processors use enzymatic hydrolysis of proteins to improve functionality, reduce allergenicity and release targeted peptides. This has generated a new category of ingredients that require additional quality control to ensure that bioactivity in selected protein fractions and peptides is retained during processing.

Expansion in the number of dairy product streams has meant additional testing regimes, with advanced testing methodologies, for milk processors, in order to confirm quality specifications. Much research has been conducted over previous years, in Ireland, directed at milk quality and safety within the supply chain serving a global marketplace. Studies have included physical (e.g. functionality) and nutritional (bioactivity) parameters, as well as bacteriological parameters. Ireland's dairy sector continues to attain the highest standards for quality and safety, and is recognised for its excellence in milk and dairy product quality.

Digitalisation

Innovation in digitalisation is particularly important in this sector due to the level of international trade, health and safety and regulatory issues. Modest steps in digitisation have the potential to improve production and processing efficiency, quality, safety and traceability of dairy products. However, implementation is highly dependent on regulations and local infrastructure, including basic internet access. Connectivity is key, both in terms of allowing access to information and enabling capacity to share digital platforms and applications directly related to dairy topics/challenges; an example may include block chain technology, which requires increased interconnectivity between individual units within a supply chain and the associated financial and regulatory supporting services.

Examples of data management approaches within individual platforms may include the following: (a) effect of level of nutrition (grass intake) on milk protein (incorporating herd management and milk composition datasets); (b) effects of plate cooling on milk cooling costs at farm level; (c) effect of temperature and duration of milk storage on the microbial quality of milk in the silo at milk assembly stage; and (d) effect of curd cutting time in the vat on cheese yield at the processing plant stage. A further level of data management is the integration of data on these four platforms; this would involve using data generated on one platform to predict measured outcomes at a further platform, thus enabling changes in practice and potential improvement, thus benefitting from

"real-time" data to manage outcomes. An example may include the effect of milk protein level on cheese yield or the effect of milk SCC on cheese quality.

Evidence-based information could potentially be used to add value; examples may include evidence of milk originating from pasture grazing cows or evidence that could be used to justify payments for various grades of product, depending on composition of the raw material. A number of dairy farmers are already using digital technologies such as electronic milk meters to precisely measure milk production, pedometers to detect the increased numbers of steps linked to cows in heat and analyses of milk conductivity to detect mastitis. Internet of things (IoT) sensors with applications in milk quality are now also commercially available. They include wireless and portable NIR devices and handheld scanners that measure protein, fat, lactose and total solids and temperature. These microsensors use micro-electro-mechanical systems (MEMS) technology and can operate at wavelengths between 1,350 and 2,450 nm. However, studies are required to validate their use against current routine testing approaches. IoT sensors for temperature measurements are also commercially available. These infrared (IR) sensors are available for installation in milk bulk tanks and can monitor and store milk storage temperatures. Specifically, these systems can release an alert to farmers if temperatures are not maintained or begin to increase. All data are stored on a local system which can be connected to a tablet or phone device, where personalised data can be viewed via simple dashboards. The system can also send out alerts to a farmer in the event of temperature spikes. This approach may be more or less relevant to particular farms, depending on the farmer's disposition towards new technologies, the labour efficiency on the farm and the investment capabilities of the farm. However, it is crucially important in all cases, that the farmer has sufficient support from independent consultants or advisers, in the form of clear information on how to use the additional data available on-farm to best advantage.

Potential datasets that may be used by milk purchasers within the milk assembly platform include milk volume in different farm bulk tanks to allow efficient logistics for collection of milk; milk volume supplied by different farms; milk SCC and TBC supplied by different farms, as well as temperature and time duration in each tanker and in each silo.

With edge and cloud analytics, dashboards can be developed and shared between farmers and dairy processors for viewing milk quality parameters. There is also potential to develop suitable, accurate and user-friendly prediction models for farmers. The application of temperature sensor IoT systems allows full transparency in the storage conditions of the milk between the farmer and processor, which can be important for traceability or payment system. However, some challenges do exist, which include issues pertaining to the security and ownership of data collected and stored in the cloud, and these need to be addressed.

Conclusion

While milk quality may be considered a dynamic standard or concept, there are some predictions that can be made with a degree of certainty. The demand for dairy products is increasing, so markets will need to be supplied, but increasingly stringent consumer-related quality standards will represent an associated challenge. Therefore, it is important to focus on an evolving framework to address these standards and markets.

Much research has been described in the foregoing paper, which has played a significant role in developing and progressing the dairy sector to its current excellent status. Some of the long-standing issues have been addressed through science and technology developments. However, some gaps in knowledge and challenges remain. Research on grass-fed milk has highlighted and characterised the unique compositional and sensory attributes of this milk and dairy products, which is particularly important to Ireland. However, the need for legislation to distinguish and protect grass-fed milk products, ideally by rapid spectral methods, is clear. The complexity of enzyme systems and their diverse and sophisticated modes of action have been investigated in depth, but significant knowledge gaps remain, and work continues on their role in influencing processing efficiency and product quality. While the risk of chlorine residues has largely been eliminated from the dairy supply chain as a consequence of the moratorium on the use of chlorine-based cleaning agents, it is absolutely critical that microbial hygiene and quality is not compromised. In addition, there is an ongoing need for vigilance regarding the emergence of other potential residues from the use of replacement or other products.

Some key considerations for the future include new technologies, new instrumentation, standards, payment incentives and digitalisation. As quality parameters become increasingly important, detection limits within analytical methodology become vital, and likewise, as precision management of steps along the milk process line become standard practice, the development and use of new and progressive instrumentation is necessary. These instruments must be reliable and ideally not require comprehensive expertise to operate, and they should ideally be suited to routine quantification or determinations.

The International Dairy Federation (IDF) has contributed to the development of standards for the dairy sector over many years; the organisation and its members from different dairy research organisations globally (including Teagasc) participate in the development of science-based, globally harmonised standards, guidelines, codes of practice and related methodologies, to continually improve the regulatory environments of the dairy sector. These include food standards, animal health and welfare standards, standards for methods of analysis and sampling and various standards for milking machines. This is increasingly important in light of increasing international dairy trade.

Financial reward has been used successfully in the past to improve milk quality in terms of TBC and SCC. This could be complemented by putting a monetary value on more recently defined quality parameters or on achieving a suite of quality standards; however, this would need to be accompanied by fast and reliable measuring techniques. The whole area of digitalisation, data management integration of data platforms, the use of evidence-based information and real-time measures to improve predictability and control of manufacturing processes and decision-making will be crucial pillars for the dairy sector of the future. Digitalisation has potential to optimise logistical chains within the processing stages, and change the pattern of organisation from "inspect" and "reject" to "predict" and "prevent".

Even as international quality standards become more stringent, Irish milk has continued to achieve premium quality status as a direct consequence of greater scientific knowledge of the factors affecting it and the quality control measures implemented at farm and processing level, as well as training and education of farmers, improved hygiene, measurement systems, documentation and traceability. However, much still needs to be done, and whatever the future holds for consumer trends and markets, quality will be foremost.

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Irish Journal of Agricultural and Food Research

Current research and emerging tools to improve fresh red meat quality

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Abstract

A consumer's decision to purchase red meat is guided by a combination of many interacting factors including safety, nutrition, sustainability and perception of healthiness along with a variety of sensory characteristics such as colour, marbling, tenderness, juiciness and flavour. Red meat quality is complex and influenced by many intrinsic and extrinsic factors, spanning the chain from breed/genetics through to the final end product with key influences coming from on-farm management and post-mortem processing. As a result of various factors, including consumer demands, the importance of both red meat quality and safety has in recent times come to the fore for the meat industry, with steps to meet these requirements having a large bearing on profitability. Therefore, a critical review of steps which can help control these traits is very important. Accordingly, several processing strategies were proposed at the research and industry level aiming to improve fresh red meat quality traits. This review summarises the current methods applied to improve fresh red meat quality and safety, including the advances in management and prediction tools for carcass and technological and sensory quality traits. These methods are also relevant to the safety and microbiological status of carcasses and meat produced, along with the recent developments in sensory analysis, which aim to understand the sensory properties of red meat and consumers responses. The potential of foodomics approaches is discussed under the topics of genomics, proteomics and metabolomics, which help our understanding of the underlying biological mechanisms behind the variation of sensory and technological quality traits and their use for the discovery of putative biomarkers. We further considered the current and emerging sequencing-based methods used to understand microbial community composition of fresh red meat.

Keywords

Biomarkers • foodomics • meat and carcass quality management • meat quality evaluation • prediction tools • safety and microbiology of fresh red meat • sensory science

Introduction

Meat quality can be defined in many ways, but for the consumer, safety and sensory quality represent key criteria. These attributes are complex and are influenced by a multitude of both intrinsic and extrinsic interacting factors. These include, for example, genetics, production systems, feed, pre-mortem animal handling and stress at slaughter, post-mortem carcass handling, technological treatments and their interactions (Moloney *et al.*, 2001; Troy & Kerry, 2010; Hocquette *et al.*, 2012; Gagaoua & Picard, 2020; Terlouw *et al.*, 2021). Consumer demands for high-quality, safe, nutritious and healthier red meat products have recently provided an impetus into the development of several innovative and

non-destructive methods, sensory protocols and decision tools aiming to evaluate, control and improve the quality or to deepen our understanding of biological mechanisms underpinning the variation in technological and sensory quality traits of red meat. For economic considerations and consumers' satisfaction, red meat quality also constitutes an important concern for industry stakeholders who continually seek innovative and sustainable approaches to improve all the aspects of red meat quality.

This review, based on recent literature but not considering production systems or animal management, is organised into three main sections focusing on the current advances

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and emerging methods used to control and improve the sensory quality and safety of fresh red meat products (mainly beef and lamb). The first section discusses recent advances and the potential of foodomics (genomics, proteomics and metabolomics), rapid and non-destructive physical and imaging methods to improve and predict red meat quality as well as the emerging post-mortem intervention methods used to increase meat tenderness, mainly in beef. The second section focuses on the safety aspects of fresh red meat by describing the current interventions used to control microorganisms in the meat chain, the methods of characterisation and the potential of powerful sequence-based methods such as whole-genome sequencing, metagenomics and meta-transcriptomics to tackle the comprehensive assessment of red meat safety to ensure the health of consumers in a globalised market. Finally, the last section covers the recent advances in sensory analysis relevant to fresh red meat.

Recent advances in the management and prediction of technological and sensory quality traits of fresh red meat

Foodomics as a tool towards understanding variation in, and predicting, meat quality traits

During the last two decades, new OMICs technologies, referred to in this context as foodomics, have been applied to widen the scope of traditional methods and open up impressive possibilities to explore the unknowns relevant to meat science and quality variation of fresh red meat and processed meat products (Herrero *et al.*, 2012; Munekata *et al.*, 2021; Purslow *et al.*, 2021). Genomics, transcriptomics, proteomics, metabolomics and so on combined with chemometrics methods were further used to predict the potential quality of red meat quality traits (Gagaoua *et al.*, 2020a).

Livestock genomics and red meat quality

While natural variability in the genomic DNA sequence includes insertions, deletions, inversions and copy number variations of 10s to 1000s of bases, which can all contribute to variation in a trait of interest, DNA single-nucleotide polymorphisms (SNPs) are the most common type of genetic variation in the genome. Agrigenomics resources arising from genome sequencing projects include DNA chips containing thousands to hundreds of thousands of SNPs evenly spaced throughout the genome (Ghosh *et al.*, 2018). The ability to analyse genetic diversity in the population has been further expanded through important projects such as 1000 Bull Genomes, which involves whole-genome sequencing of pedigree bulls, facilitating the expansion of information that can be collected from these chips about the population, to levels way beyond the size of the chip, and even up to the whole genome level, through

imputation (Hayes & Daetwyler, 2019). While these chips are used to drive genomic selection, which accelerates the pace of genetic improvement in livestock due to early availability of the predicted breeding value of calves (Meuwissen *et al.*, 2016), they can also be used to identify the genomic regions associated with a trait in the population. Important initiatives relate to genome annotation and the need for standardisation of methods, ontologies and a common infrastructure for data sharing and acceleration of annotation such as the Functional Annotation of Farm Animal Genomes project (FAANG, https:// www.faang.org/) and a common resource for the repository of information on gene regions associated with important livestock traits (Animal QTLdb, https://www.animalgenome. org/QTLdb/).

Although next-generation sequencing (NGS) has resulted in huge progress in livestock genomics, read depths are variable and substantial gaps remain in genomes (Taylor et al., 2016). Current technological developments include the advent of third-generation (long read Nanopore and PacBio) sequencing approaches. Although not as accurate as short read sequencing, they seemed to be fast and sequencing reads are long (10-60 kb), hence they are leading to progress with livestock genome projects at the forefront, for example, goat (Bickhart et al., 2017) and water buffalo (Low et al., 2019) genome builds which each surpassed the human genome in contiguity. These technologies have high relevance in microbiome and pathogen sequencing and the Nanopore MinION technology has the capability to bring genome sequencing at the slaughterhouse level and to countries with more limited infrastructure for genome sequencing (Lamb et al., 2020).

Genetic regions and gene expression associated with meat quality

Meat quality traits are moderately heritable with recent heritability estimates ranging from ~ 0.1 to 0.2 for sensory traits such as tenderness, juiciness, flavour and chewiness (Berry et al., 2021). Single-nucleotide polymorphisms variants that are causative and impact on the phenotype, depending on their location in the genome, exert their effects on a given trait via different mechanisms. These include changing the amino acid sequence of the synthesised protein or activating, enhancing or suppressing the level of expression of a gene. The causative variants are in linkage disequilibrium with neighbouring SNPs, hence SNP chips can be used to map the trait to quantitative trait loci (QTLs) (Hu et al., 2018). At present, 19 sensory-related traits (including Warner-Bratzler shear force [WBSF]) are included in AnimalQTLdb with 759 QTL for these traits across all 30 chromosomes with notable representation on chromosomes 3, 7, 10, 18, 21-23 and 29, for which several biomarkers of beef tenderness and colour were confirmed (Gagaoua et al., 2020b, 2021b). Some genes

such as myostatin (GDF8) and insulin-like growth factor 2 (IGF2) harbour variants that cause major effects in livestock species, and they are master regulators in muscle growth and development (Van Laere et al., 2003; Aiello et al., 2018), These genes are robustly associated with muscle characteristics in diverse bovine breeds, although the DNA variation may differ per breed. For other genes, such as calpains, the regions harbouring these genes are also consistently significant in a range of genome-wide association studies (GWAS), though conclusive identification of causative mutations remains elusive (Aiello et al., 2018). Calpains represent an important family of proteolytic enzymes, with µ-calpain (CAPN1) involved in post-mortem tenderisation of meat, while calpastatin, its inhibitor, and the SNP in these genes have long been known to be associated with tenderness (Page et al., 2002; Casas et al., 2006).

It is widely considered that tenderness is the most important trait relating to palatability in meat quality, namely beef (Gagaoua et al., 2019a). However, recent studies have shown that once variation in beef tenderness is controlled, flavour becomes the most important driver of eating acceptability (Killinger et al., 2004; O'Quinn et al., 2018). The past 5 yr have seen numerous genome-wide association and transcriptomic sequencing studies, as well as the advent of new methods for targeted monitoring of gene expression profiles from specific pathways and candidate genes (Aiello et al., 2018). A genomewide analysis for an instrumental measure of beef tenderness, WBSF, conducted in five Bos taurus breeds revealed 79 QTLs associated with WBSF in at least one breed, with 37 QTLs identified in at least four of the five breeds, indicating a strong association with WBSF (McClure et al., 2012). Candidate genes present within the 37 QTLs, shared by four breeds, include µ-calpain and calpastatin on bovine chromosomes BTA7 and BTA29, respectively (McClure et al., 2012). Other candidate genes proposed by the authors include MYOD1 located on BTA15 which is expressed in muscle during growth and regeneration, fibroblast growth factor 2 (FGF2) regulating heat shock proteins on BTA17, gelsolin (GSN) on BTA8 and calmodulin (CALM1) on BTA10. A study on both Bos indicus and Bos taurus breeds which included a separate validation test population confirmed the QTLs for WBSF on BTA7 (Bolormaa et al., 2011). Recent studies on Simmental breed using HD chips (>777k SNPs) are also confirmatory of the QTL on BTA7 for shear force (Xia et al., 2016).

Progress in refining QTLs has been facilitated by recent developments, such as imputation of variants not present on the gene chips, which has led to the identification of 114 SNPs significant at the genome level and QTLs for marbling, meat colour, fat colour and texture in Hanwoo cattle (Bedhane *et al.*, 2019). Several of the QTLs for beef colour were confirmed in proteomic studies that identified candidate protein biomarkers (Gagaoua *et al.*, 2020b). On another hand,

a recent study focused on Angus examined a range of traits, but their tenderness analysis not only confirmed the known QTLs including the calpain gene, but of the most significant structural genes highlighted in the study, 81% were validated using *in silico* analysis to be substrates of calpains (Leal-Gutiérrez *et al.*, 2020c), illustrating the central importance of this proteolytic process in defining ultimate beef tenderness. Furthermore, experimental validation of the functional relationship of putative candidate genes with their proposed phenotype is a very valuable addition to GWAS. *S-myotrophin* is a novel gene for that was discovered in a GWAS study using imputed sequences in Simmental cattle, and was subsequently demonstrated to play a role in promoting muscle hypertrophy and inhibiting differentiation (Bordbar *et al.*, 2020).

Transcriptomic approaches have provided information on changes at the gene expression level which are associated with meat quality (Guo & Dalrymple, 2017). A synthetic index combining shear force, sensory tenderness, connective tissue and marbling score was created in an Angus-Brahman population, and RNA sequencing (RNA-seq) was applied to the most divergent animals (Leal-Gutiérrez et al., 2020a). Cytoskeletal and transmembrane anchoring genes were over-represented (Leal-Gutiérrez et al., 2020a). From this study, the most significantly differentially expressed genes were novel (e.g. ARHGAP10 and ARRDC4), while others had previously been associated with meat quality in GWAS (e.g. KIAA2013). A follow-up expression OTL (eQTL) study of the same animals uncovered a number of predicted master regulator genes involved in muscle and meat quality. For example, neurotrophic factor 3 (NTF3), which plays a role in the regulation of myofibre and myoblast differentiation, has previously been associated with cooking loss (Leal-Gutiérrez et al., 2020b). Of the 17 master regulators with specific functions, nine were membrane proteins, four were transcription factors, three were cytoskeletal proteins and one was a DNA methylase. Other noteworthy genes in the study included Titin and TEK (angiopoietin-1 receptor known also as a tyrosine-protein kinase), which appeared to be under substantial multigene regulation and also were located close to significant splicing cis-regulatory SNP. In another study, Fu et al. (2020) combined gene expression with GWAS and quantitative trait expression profiles to refine 180 candidate genes for fat-related traits down to just six, including known master regulators such as several PPARs (PPARG, PPARD and PPARA). New insights have been gained on the molecular pathways underpinning heterosis and its implications for growth, development and meat quality in sheep meat using RNA sequencing (Cheng et al., 2020). Allele-specific expression occurs where a single allele is expressed in a heterozygote and where this is driven by differential methylation due to parental effects, and it is termed imprinting. Many genes involved in growth and metabolism are indeed

imprinted (O'Doherty *et al.*, 2015). Recent studies examined allele-specific expression in the *Bos indicus* transcriptome, finding the phenomenon to be widespread, with imbalance in allelic expression of many genes known previously to be associated with meat quality such as the ryanodine receptor (*RYR1*), calsequestrin (*CASQ1*) in the same pathway (calcium homeostasis), myomesin (*MYOM1*) and myosin light chain 1 (*MYL1*) which interact with each other and are known as proteomic biomarkers of beef ageing (Gagaoua *et al.*, 2021c), and *ALDH5A1* involved in the pathway 4-aminobutanoate degradation, which is part of amino acid degradation that has previously been shown in a GWAS to be associated with tenderness, fat colour and water-holding capacity (de Souza *et al.*, 2020; Bruscadin *et al.*, 2021).

Future trends of genomics and transcriptomics in the field of red meat science

Even well-powered GWAS can lead to the identification of large genomic regions frequently containing hundreds of genes, and refining these regions down to putative candidate genes and ultimately quantitative trait variants for a trait is challenging. There is consensus around a need for the different types of OMIC approaches (e.g. genome/transcriptome/proteome/ metabolome) to be integrated together in a multi-omics approach (Da Silva Diniz & Ward, 2021). Recent studies have taken such an approach to refining genomic regions and lists of potential candidate genes in pork (Welzenbach *et al.*, 2016) and beef (Cardoso *et al.*, 2021) and it is likely to grow in importance in future livestock studies.

While SNP variation can be profiled with SNP chips and modern sequencing methods, other types of variation such as copy number variation and variation in low complexity repetitive regions are more challenging to routinely score in populations, and they potentially account for a substantial proportion of the so-called "missing heritability" observed in many livestock genomic traits, that is, heritability not accounted for by common SNP variants. With long read sequencing, there is hope that these alternative types of common genetic variation could be properly characterised and shed more light on the molecular regulation of meat quality (Gonzalez-Recio *et al.*, 2015).

When the causative genes and variants contributing to a trait are known, the future of agrigenomics is likely to include genome editing in a precise and targeted way and these approaches have been tested with successful introgression of a number of disease-resistant, welfare-related and muscling (myostatin) genetic variants in livestock (Tait-Burkard *et al.*, 2018).

In the era of big data and data analytics, and in a time when genomic information is easier than ever to collect, an important limitation on fully elucidating genomic features of relevance relates to the "shape" of data that is commonly generated. Within genomic data sets, and OMICs data in general, the number of data points recorded for each sample is vastly greater than the number of samples/phenotypes in a typical study and this challenges statistical inference.

Proteomics to study red meat quality and discover candidate protein biomarkers

Faced with the recurrent and increasing demands for consistent and high-quality red meat, farmers and meat industry stakeholders have changed their production methods and modernised breeding practices, leading to improvements in the potential of breeds and adaptability of the animals, which has an impact on the quality and variability of the meat produced (Gagaoua & Picard, 2020). Therefore, product quality prediction becomes an absolute necessity for the meat industry. In addition, meat quality assessment methods (whether sensory or mechanical) are considered destructive and not easy to implement routinely. In this sense, there is a need to find an alternative and to develop simple and fast decision tools that do not require large quantities of meat samples to classify and predict the potential quality from live animals, carcasses early post-mortem or cuts at the point of sale. Proteomics seemed to be an effective solution to this problem (Bendixen, 2013; Gagaoua et al., 2020a) through the global or partial study of the proteome (muscle tissue or fluids such as plasma) to propose explanatory mechanisms for the origin of the variability of red meat quality traits. Thus, a range of proteomics methods (gel-based and gel-free approaches coupled with mass spectrometry) have been applied to investigate important meat quality traits (Picard & Gagaoua, 2017; Picard et al., 2017; López-Pedrouso et al., 2020) including tenderness (Gagaoua et al., 2020a; Picard & Gagaoua, 2020; Gagaoua et al., 2021b; Zhu et al., 2021a, 2021b), colour (Nair et al., 2018a, 2018b; Gagaoua et al., 2020b), water-holding capacity (Di Luca et al., 2013, 2016; Tao et al., 2021), marbling (Ceciliani et al., 2018; Bazile et al., 2019) and pH decline (Gagaoua et al., 2015, 2021d; Poleti et al., 2018). In addition, proteomics was used to investigate the dynamic changes and modifications occurring in postmortem muscle proteome (Gagaoua et al., 2021c; Zhou et al., 2021).

The main research area where meat proteomics has been applied is in the field of protein biomarkers discovery (Picard & Gagaoua, 2020). Generally, the first phase in the pipeline of biomarkers discovery focuses on identifying differential abundances in proteins in groups of samples (mainly muscle biopsies and recently other biological sources such as plasma are tested) which are distinctly divergent for a phenotype of interest, such as tenderness (Picard & Gagaoua, 2020; Gagaoua *et al.*, 2021b; Zhu *et al.*, 2021b). It is important that conditions are standardised within the study, for example, muscle (e.g. M. *longissimus thoracis*), same animal type, same rearing conditions, same muscle preparation approach and so on, to analyse only the trait of interest. This first phase called "discovery" is composed of several steps from sampling and categorisation, protein extraction until the identification of the proteins of interest by mass spectrometry and their quantification. This strategy was extensively described by Picard & Gagaoua (2020) in their integrative beef tenderness proteomics study, which considered separately several important factors such as muscle, breed, gender as well as the evaluation method of meat quality. In our quest for beef tenderness biomarkers, a recent ground-breaking integromics meta-analysis based on 28 proteomics studies from the literature enabled us to propose the first atlas of 124 biomarkers from which 64 were found in a minimum of two studies, allowing then to shortlist a robust panel of 33 beef tenderness biomarkers identified in at least four experiments for validation (Gagaoua et al., 2021b). Moreover, protein network analysis delivered a functional annotation of the 124 proteins from M. longissimus thoracis and provided key insights into the interconnectedness among various pathways and processes in the muscle, which are pivotal in producing high-quality beef. There were six interconnected pathways identified to play a pivotal role in the determination of beef tenderness. Those were (i) muscle contraction and structure development; ii) energy metabolism; (iii) cellular responses to stress; (iv) response to oxidative stress; (v) proteolysis and (vi) regulation of cellular processes, binding, apoptosis and transport. Similar integromics proteomics studies were further conducted to create biomarker repertoires for beef colour (Gagaoua et al., 2020b) and the quality defect of dark, firm and dry (DFD) beef, otherwise termed dark-cutting beef (Gagaoua et al., 2021d). The ultimate objective of biomarkers discovery is to propose a robust list of validated biomarkers that would allow development of routine bioanalytical tools that can be used by stakeholders for testing the potential quality of the carcasses in the slaughterhouse, their management early post-mortem as well as for breeders to improve the potential merits of breeds.

Emerging use of metabolomics in meat quality analysis and authentication

Metabolomics can be defined as the study and analysis of metabolite molecules that have a molecular weight lower than 1,000 Da (including free amino acids and short peptides, monosaccharides, organic acids, lipids, vitamins or nucleotides). Such metabolites can be affected by several factors in the food-processing chain and these will be reflected in the metabolome profiles including in meat and processed meat products (for review: Muroya *et al.*, 2020). The profiles obtained for such low-molecular-weight compounds can be further correlated with sensory properties and functional and nutritional profiles, providing a deeper understanding of the factors affecting the final eating meat quality traits and the underlying mechanisms. This approach can further lead to the identification of potential biomarkers that can be used as indicators of those meat quality traits such as tenderness and flavour (Kodani *et al.*, 2017; King *et al.*, 2019).

The study by King et al. (2019) reported that a significant increase in the concentration of free amino acids (mainly methionine and tyrosine) was correlated with samples categorised as tender, and these values were higher as ageing time increased. A similar correlation was found for two glycolysis metabolites, namely glucose and glucose-6phosphate. On the other hand, glycerol-3-phosphate and 3-phosphoglyceric acid were observed to be significantly more concentrated in tough beef. Similar findings were reported when Japanese Black cattle was investigated over a period of 10 wk of ageing (Kodani et al., 2017). In fact, increasing amounts of free amino acids (Leu, Ile, Val and Ala) as well as acetic acid were detected. These studies revealed that nuclear magnetic resonance (NMR)-based metabolomics, for instance, has the potential to evaluate multiple parameters related to beef qualities. In another study, Ma et al. (2017) reported that an increased amount of free amino acids is related to the extent of proteolysis, which is indicative of more tender meat, but also it is related to more precursors of aromatic compounds that play a role in the sensory perception of cooked meat. These authors further correlated the concentrations of nicotinamide adenine dinucleotide (NADH) and its oxidised form NAD+ with the oxidative status of the meat, and its direct correlation with colour stability which deteriorated as these compounds were depleted by extended ageing. The relevance of carnitine, creatine and carnosine, as candidate metabolic biomarkers of meat quality (beef, lamb and yak), has been proposed (Jeong et al., 2020; Zhu et al., 2020; Wang et al., 2021). Such compounds have a relevant role in the muscle metabolism, associated mainly with oxidative pathways and lipid transformation into metabolic energy. Antonelo et al. (2020) reported a positive correlation between carnosine and consumer acceptance of beef steaks, while carnitine and creatine were strongly negatively correlated with consumer sensory traits (overall liking, tenderness and juiciness scores).

In light of these studies, it is important to note that the potential of metabolomics in the field of red meat science has yet to be unlocked. Indeed, further developments in metabolite analysis (lower detection limits, improved extracting protocols or faster sample handling) will lead to a more complete profiling of potential biomarkers. Applications for authentication, detecting spoiling-associated compounds, metabolic profile for meat processed products, acquiring a better understanding of ageing and post-mortem practices, detection of the impact of feeding and production practices, or for the investigation of the quality variations among breeds or for the study of certain meat quality defects are the current important and challenging topics. Metabolomics is well positioned to provide some important advances in this regard (for review: Goldansaz et al., 2017). A number of excellent examples were highlighted by these authors in their review including metabolome discovery for normal metabolite composition and concentrations, identification of biomarkers as well as production traits in dairy and beef cattle. Moreover, metabolomics is considered as an emerging tool for meat authentication. For example, an earlier study using an NMR-based metabolomics was able to discriminate beef originating from four countries: Korea. New Zealand, Australia and the United States (Jung et al., 2010). In this study, the major metabolites responsible for differentiation in orthogonal projection to latent structure-discriminant analysis (OPLS-DA) loading plots were succinate and various amino acids including isoleucine, leucine, methionine, tyrosine and valine. The use of a mass spectrometry-based untargeted metabolomics for differentiation of beef samples from different geographical origins, namely the United States, Japan and Australia, and feeding regimes was also found to be a relevant approach (Man et al., 2021). Another study by Osorio et al. (2012) investigated the use of an NMR-based metabolomics to authenticate beef on the basis of the preslaughter production system. The authors used both urine and muscle samples from animals fed either pasture outdoor, a barley-based concentrate indoor, silage followed by pasture outdoor or silage followed by pasture outdoor with concentrate over 1 yr. The results showed that separation according to production system was possible indicating the potential use of this approach in beef authentication. Identification of the major discriminating peaks in urine led to the identification of potential markers of the production system including creatinine, glucose, hippurate, pyruvate, phenylalanine, phenylacetylglycine and three unassigned resonances (Osorio et al., 2012).

Rapid and non-destructive methods to predict the quality of fresh meat

Rapid non-destructive spectrometric methods have shown potential in the context of objective carcass and meat quality assessment (Allen, 2021). Spectroscopy is the term given for the interaction that occurs between radiation and matter. When radiation interacts with a sample, the radiation may be transmitted, reflected or absorbed. The contribution of these three phenomena is dependent on the samples' physical specifications and chemical constitution (Nicolaï *et al.*, 2007). Near-infrared spectroscopy (NIRS) is a form of spectroscopy predominantly involved in the direct measurement of the vibrations of –CH, –SH, –OH and –SH bonds (Prieto *et al.*, 2017), whereas other vibrational spectroscopic techniques such as Raman spectroscopy are involved in the measurement of inelastic scattering of light (Cama-Moncunill *et al.*, 2020). When the sample is irradiated, its special characteristics

undergo changes through various wavelength-dependent scattering and absorption processes. NIRS combined with advanced multivariate statistical techniques has been shown to be an effective tool for the prediction of quality traits in many food applications, including in red meat (Prieto *et al.*, 2017; Moran *et al.*, 2018; Cafferky *et al.*, 2020). NIRS has also been proven as an effective method for species identification in meat, with Mamani-Linares *et al.* (2012) able to successfully determine cattle, Ilama and horse meat from homogenised meat samples with an accuracy of 89–100%. Using NIRS as an authentication tool in meat, Moran *et al.* (2018) were able to classify beef ageing time with an accuracy of 94–100%.

Major advantages of NIRS are the speed at which it can be applied, and its non-destructive nature as there is no necessity for sample preparation in most settings. NIRS technology has been used for determination of various quality traits in muscle foods at-line, on-line and off-line. Spectral information on final meat composition is also an effective tool to allow producers to adapt and optimise dietary supplementation and feeding regimes to suit the needs of their consumers (Weeranantanaphan et al., 2011), while rapid measurement technologies have the potential to be utilised by breeders as methods of improving meat quality traits during genetic selection. The use of NIRS for the prediction of textural traits such as WBSF values and trained sensory panel scores in meat is a topic which would have important application in meat plants, as both WBSF and trained sensory analysis are timeconsuming and destructive; however, due to the complexity involved in the prediction of these traits, the coefficients of determination presented in the literature are variable (De Marchi, 2013; Cafferky et al., 2020).

The potential of single-point, and to a lesser extent, multipoint, spectroscopy for the accurate and representative prediction of meat quality attributes on intact samples is dependent on the heterogeneity of the meat, which is a challenge due to the complexity of the tissue structure in any given cut, and the non-uniform distribution of its constituents (Savoia et al., 2020). Hyperspectral imaging (HSI) represents a more advanced approach with the potential to overcome this limitation. HSI can record images of the entire sample surface and at each pixel location a wide spectrum across defined wavelengths is acquired. HSI therefore records spatially defined chemical information. An HSI image can cover the chemical signature of the entire sample at different spatial and spectral resolutions, although the increase of the data accuracy requires more time, more complex and expensive instruments and a higher computational power for the management of bigger data sets. Therefore, several studies have examined the relevance and assessed the accuracy of HSI for the prediction and classification of meat quality traits. Already at the beginning of the decade, successful performances were shown for the assessment

of colour, pH, tenderness (both instrumental and sensory), major muscle constituents and water-holding capacity in beef (EIMasry *et al.*, 2011, 2012) and lamb (Kamruzzaman *et al.*, 2012, 2013). Most recently, Antequera *et al.* (2021) described the development of non-destructive methodologies (i.e. HSI, NMR and magnetic resonance imaging [MRI]) to determine quality characteristics of fresh meat that gave accurate and promising results. The studies on the applications of the HSI are mainly at laboratory scale and based on benchtop instruments, hence it is desirable that further advances orient towards factory solutions and applications to provide fast, accurate and real-time information.

Two hyperspectral systems for the image acquisition of ribeye muscle on beef carcasses in processing plants were proposed at 2 d post slaughter (Konda Naganathan et al., 2015a, 2015b). In these two studies, the classification of beef, based on tenderness at 14 d, gave promising results in terms of accuracy and scanning/processing times. Dixit et al. (2021) assessed and compared the performances of two spectroscopy and three HSI automated measurement systems on intact M. longissimus thoracis et lumborum sections in a meat-processing pilot plant. Prediction models for pH and Intramuscular fat (IMF) were presented and the HSI linescan provided prediction validation powers of 0.89 and 0.90, respectively. The development of HSI systems for the online implementation in slaughter and processing plant environments holds a lot of promise, though continued improvement of accuracy and reduction in scanning time are necessary.

Post-mortem interventions for beef tenderness improvement

The variability in beef tenderness is related to several factors ranging from farm to fork (Gagaoua et al., 2018b, 2018c, 2019a, 2019c; Holman & Hopkins, 2021) as a result of intricate interconnected biochemical mechanisms (Gagaoua et al., 2021b). However, it is well acknowledged that, outside of extreme situations such as much older animals, postmortem factors are the main influencers when we consider meat tenderness. The level of variability evident within a particular meat cut, especially the valuable pieces such as striploins, is a serious concern for both consumers and the meat industry (Maher et al., 2004). Therefore, several post-mortem interventions are outlined in the following text, which have made, or are expected to make, significant improvements in the tenderness outcomes. Not included in this review, but of interest, is the application of enzymatic treatments using exogenous proteases and the conventional (applied) methods for meat tenderisation such as electrical stimulation, mechanical tenderisation (blade/needle tenderisation, flaking, mincing) and contraction-prevention (stretching/tenderstretch/alternative hanging, tendercut[™], wrapping, rapid crust freezing) (for details refer Bekhit et al.,

2014; Bhat *et al.*, 2018). For details on the recovery methods (Hafid *et al.*, 2020; Gagaoua, 2021) and use of exogenous enzymes to tenderise meat, we invite the reader to refer to the recent review by Gagaoua *et al.* (2021a) on the latest studies and other emerging methods that combine proteases to physical intervention methods some of which are described in the following text (Santos *et al.*, 2020; Botinestean *et al.*, 2021).

Ageing methods including dry ageing to improve beef tenderness

After critical early biochemical events such as apoptosis, pH decline and *rigor-mortis*, the maturation period commences leading to improvements of both the texture and sensory aspects of meat (Ouali *et al.*, 2013). Ageing consists of a number of biochemical processes that are mainly related to the breakdown of muscle proteins, namely those of structure by endogenous proteolytic enzymes leading to the appearance of new protein fragments (Gagaoua *et al.*, 2021c). In fact, two main effects can be observed: a progressive increase in tenderness, as the muscle structure is disintegrated, and a release and accumulation of peptides and free amino acids. Such molecules have an impact on colour (Gagaoua *et al.*, 2020b) and other quality attributes, but more importantly as precursors of flavour (Kim *et al.*, 2018).

Ageing methods can be classified into wet and dry ageing. By far, the most relevant at the industrial level is the former, in which the moisture content is kept as constant as possible, while in the latter, water evaporation is desirable. Advances in packaging materials with high barrier properties for water allowed the development of the wet ageing process, in which primal cuts are vacuum packed and stored under controlled conditions. At the end of the ageing period, an improvement in yield, processing and shelf life is obtained when compared to dry ageing (Ha et al., 2019a). The most relevant processing factor for wet ageing is the required time. Typical ageing times are those between 14 and 21 d, with no huge improvement beyond this point but different muscles do respond differently (Nair et al., 2019). Dry ageing is less popular due to high processing cost, extended ageing times and lower sealable yields, leading to an increased purchase price; however, recent niche market trends indicate that dryaged beef is growing and attracting more consumers (Álvarez et al., 2021).

Dry ageing is described as the process of storing *post-rigor* meat, generally without protective packaging, under controlled conditions of humidity, temperature and airflow for a certain time, typically more than 4 wk (Álvarez *et al.*, 2021). As a consequence, there is a concentration of typical compounds responsible of the "dry-aged flavour" providing aromas such as nutty, roasted or buttery (Flores, 2017). According to Ramanathan *et al.* (2020), wet ageing flavours tended to be

described as sour, metallic and bloody flavours, which are not evident in dry-aged meat. There is still controversy whether dry ageing can improve beef tenderness when compared to wet ageing; in any case, the main reason for dry-aged beef is its differential flavour and aroma profile. Recent investigations have demonstrated that dry ageing could also improve the palatability of low marbled beef (Ha *et al.*, 2019b).

A third type of ageing has been recently developed, in which previous methods are combined in a stepwise dry/wet ageing process (Kim *et al.*, 2018). In this case, the meat was dryaged for 10 d and then packaged and wet-dried for extra 7 d.

Physical intervention methods to improve the texture of fresh meat quality

Other methods to improve beef tenderness (including muscle proteins digestibility) revolve around post-slaughter interventions using physical methods capable of manipulating the muscular, cellular or protein structure of meat (Bekhit *et al.*, 2014; Warner *et al.*, 2017; Bhat *et al.*, 2021). Among these, the most studied emerging methods include high hydrostatic pressure (HPP), pulse electric fields (PEF), ultrasound (US) and hydrodynamic shockwaves (HSW), although others such as electrical stimulation can also be effective (for review: Hwang *et al.*, 2003; Abhijith *et al.*, 2020).

Bolumar *et al.* (2021) recently reviewed in detail the mechanisms of action of HPP based on the pressure applied, ranging from 100 to 900 MPa. It seemed that HPP can influence muscle structure breakdown and in particular modifications at the I-band and M-line in addition of the fragmentation and polymerisation of myosin and the activation of the proteolytic enzymes. High hydrostatic pressure can be applied to prerigor muscles, with optimum tenderisation around 200 MPa, for 4 min and temperatures between 30 and 35°C (for beef and lamb), although higher pressures may be required for pork. When applied to post-rigor muscle, although it can be performed at lower temperatures, more consistent results are achieved at temperatures >25°C (Sikes & Warner, 2016).

The application of PEF in the meat industry has been recently reviewed (Bhat *et al.*, 2019), and the exact mechanisms by which PEF promotes meat tenderisation are not fully elucidated. As for HPP, it has been proposed that PEF can lead to a physical disruption of the muscle structure, although modification of the enzymatic system seems more plausible. Further, it has been suggested that PEF induces calcium release, which may influence the activity of certain proteolytic enzymes such as the calcium-dependent proteases, that is, calpains in addition to the impact on glycolysis rate (Warner *et al.*, 2017). However, the tenderisation effect of PEF is not immediate, and a further ageing process is required. When *post-rigor* meat is treated, contradictory results have been observed in the literature; while some authors did not find any significant improvement in the shear force (Suwandy *et al.*, 2015a, 2015b), other authors

reported an improvement of beef tenderness (Mungure *et al.*, 2020). A similar scenario was observed for hot-boned muscles (Warner *et al.*, 2017; Bhat *et al.*, 2019). Arguably, the final impact of PEF on *post-rigor* meat strongly depends on muscle type and processing parameters (frequency, number and duration of pulses and intensity).

Ultrasound is widely applied in food industry for several purposes, for instance, to improve meat quality traits by modulating pH, WBSF and water-holding capacity (Kang *et al.*, 2021), and also to induce structural changes in post-mortem muscle (Alarcon-Rojo *et al.*, 2019). The main mechanism seems to be through calcium release and the enhancement of the activity of lysosomal enzymes, hence leading to an increased overall proteolytic activity in post-mortem meat (Kang *et al.*, 2021). In addition, US seems to have an effect on connective tissue, by modifying its thermal characteristics, hence impacting the final tenderness.

Hydrodynamic shockwaves (HSW) was also recently proposed to improve tenderness of tough meat cuts by both inducing and accelerating the ageing tenderisation process (Ha & Warner, 2021). Very briefly, this technology consists of the generation of pressure waves (up to 1 GPa) using water as the transmission fluid; such a wave pressure passes through the liquid and the meat matrix. The wave can be generated mainly using explosive or electrical devices. Because of the mechanism of action and considering the very short treatment time (milliseconds), it can be considered as a non-thermal treatment, although the transmission fluid needs to be monitored. The few studies that applied HSW reported that muscle structure is disrupted (Zuckerman et al., 2013); however, further studies are required to ascertain the role proteolysis plays in this regard (McDonnell et al., 2021). In any case, as reviewed by Ha and Warner (2021), there is an agreement about the positive impact that HSW has to improve meat tenderness.

Recent advances in the management and prediction of safety and microbiology of fresh red meat

It is well recognised that ruminant animals presented for slaughter are an important source of microbial contamination into the meat plant and for the carcass. Most of these microorganisms are of faecal origin, with some originating from the environment. Microbial contamination of meat carcasses may occur during slaughter and dressing operations, through direct or indirect routes. Such contamination may impact on meat safety, if pathogens such as Shigatoxigenic *Escherichia coli* (STEC) or *Salmonella* are present, and on spoilage and shelf life of the meat, depending on both the total microbial load and the specific spoilage causing microorganisms which may be present (Mansur *et al.*, 2019; Ghougal *et al.*, 2021). The shelf life of packaged meat products has been shown to correlate with the number and types of microbes on meat primals at the time of packaging in the boning hall and on the lag phase and growth rate of microorganisms during storage (Kaur *et al.*, 2017).

Interventions to control microorganisms in the fresh meat chain

A range of intervention measures have been considered as a means to prevent or reduce microbial contamination of carcasses to reduce microbiological hazards further than what is achievable solely by adhering to good hygiene practices (GHP). Many of these interventions have been developed with the aim of reducing the level of STEC or *Salmonella* prevalence and concentration on beef carcasses and meat cuts (Buncic *et al.*, 2014), but most are broadly antimicrobial and will also impact on the total microbial load and its composition. To implement an intervention, it is necessary to consider the regulatory status in local and export markets. It is also essential to take into account the required purpose, cost, space availability and infrastructure of the plant, in addition to environmental factors, such as waste and effluent disposal.

The role of the animal coat (hide/fleece) in introducing microbial contamination into the slaughter plant is well acknowledged and many countries have policies around cleanliness of livestock, as well as management practices for dirty animals at the abattoir. In some jurisdictions, cattle hides may be washed with chemical agents in the lairage. A meta-analysis of the literature showed that the use of sodium hydroxide or lactic acid for STEC hide decontamination gave mean log reductions of around 3.66 and 3.22, respectively (Zhilyaev et al., 2017). Finalyse® (marketed by Elanco Food Solutions, Greenfield, IN, USA) is a commercially available bacteriophage cocktail which can be sprayed on cattle hides in the lairage to specifically reduce the load of E. coli O157. However, in a United States feed-lot trial, Arthur et al. (2016) reported no significant reduction using this approach, with a prevalence of 51.8% E. coli O157:H7 on cattle hides receiving phage treatment compared to 57.6% on untreated hides. Regulatory restrictions in the EU do not currently permit the use of chemical washes and bacteriophages on bovine hides. Slaughter facilities rely on good dressing procedures during de-hiding/de-fleecing to minimise contamination of the carcass. Additional GHP measures may be used to remove visible faecal material from carcasses pre-evisceration, including carcass washing and knife trimming. Evidence for their impact on pathogen reduction is limited. Steam vacuuming may be used for spot cleaning along the cut line after hide/fleece removal and before evisceration. This is a handheld device consisting of a vacuum wand with a hot spray nozzle, delivering water at 88-94°C to the carcass

surface under pressure, while simultaneously vacuuming the area. Research has shown that this treatment could reduce microbial counts on carcasses, but reported results are highly variable with aerobic plate count reportedly reduced by around 3 ± 0.14 log, and total coliform and *E. coli* counts by 4.0 ± 0.12 log (Dorsa *et al.*, 1996a, 1996b). A meta-analysis showed a mean log reduction of *E. coli* of 3.1 log10 cfu/cm² (Zhilyaev *et al.*, 2017). The success of the method is very dependent on both the training and performance of the operator.

Interventions may be applied to the carcass post dressing and pre chill to reduce microbial contamination on the carcass surface. Currently, only potable water (hot water and steam pasteurisation) and a lactic acid wash for beef carcasses are permitted for use in the EU. In other jurisdictions, however, there is regulatory approval for the use of a wide range of carcass interventions. Water at varying temperatures may be used to wash the dressed carcass at the pre-chill stage. The temperature achieved on the carcass surface is affected by the temperature of the water, the volume of water, the distance between the spray nozzles and the carcass and the pressure at which the water is applied. A commercial hot water wash cabinet at 74°C for 5.5 s was reported to reduce both total viable count (TVC) and Enterobacteriaceae counts by a mean of 2.7 log cfu/cm² and reduced the prevalence of E. coli O157:H7-positive carcasses by 81% (Bosilevac et al., 2006). The meta-analysis cited above estimated that increasing the temperature of water may also increase the effectiveness in reducing E. coli by 0.014 log cfu/cm² per °C (Zhilyaev et al., 2017). A study using hot water at 85°C in a spray cabinet at 15 lb/inch² (60 cycles) against a cocktail of STEC serogroups inoculated on to beef flank indicated significant reduction (3.3 to 4.2 log reduction) in STEC (Kalchayanand et al., 2012).

Organic acid (lactic, formic, propionic, citric, fumaric, L-ascorbic acid and acetic) washes have been applied to carcasses. Internationally, solutions of lactic or acetic acids (1-3%) are the most frequently used chemical interventions in commercial plants for both beef and lamb dressing. Lactic acid gives mean reductions of 2.07 log10 cfu cm² in E. coli (Zhilyaev et al., 2017) and about 1.1 log in total bacteria (Ransom et al., 2003). Regulations (EC) 101/2013 permit the use of lactic acid on beef, though not on lamb, for surface decontamination of whole carcasses, halves or guarters. It can be applied at a concentration of 2-5% and prepared in potable water under 55°C. It can only be applied at the stage before chilling or refrigeration and must be applied under controlled and verifiable conditions and integrated into a HACCP (Hazard Analysis & Critical Control Point)-based management system. Other chemical and physical interventions allowed on the carcass in some jurisdictions include the use of trisodium phosphate, chloride dioxide, acidified sodium chloride and cetylpyridium chloride, all of which give reported reductions of generally 1-2 log cfu/cm² in total bacteria and also give

reductions in pathogens such as *E. coli* O157 (Wheeler *et al.*, 2014).

The objective of chilling carcasses is to cool the meat quickly enough to prevent bacterial growth but not so quickly as to cause cold shortening of the meat. The higher the carcass surface temperatures the more likelihood there will be for bacterial growth, including spoilage bacteria. The length of time that carcasses are in the chill room prior to bone out will also impact on growth of psychrophilic aerobic bacteria and may result in primals that have higher bacterial counts (Bieche-Terrier *et al.*, 2019).

A variety of meat packaging systems are available, ranging from air-permeable packaging for short-term storage and retail display of raw chilled meat to modified atmospheric packaging (MAP), and vacuum packaging for longer-term storage. In terms of packaging materials, the oxygen and carbon dioxide permeability, water transmission rates, seal reliability, antifogging properties and resistance to puncture are key characteristics which, together with the temperature of storage, will have a significant impact on the shelf life of fresh meat (Mills *et al.*, 2014). It should be noted, however, that the shelf life of meat is limited not only by the microbiological load and profile, but also by organoleptic factors such as colour, odour, flavours and so on and should to be taken into consideration in terms of achievable shelf life.

Characterising microorganisms in fresh meat production

The spoilage of stored meat is mainly due to the growth and dominance of undesirable bacteria, and the composition of the microflora is as important as the total microbial load. The conditions during carcass chilling and during meat storage will greatly influence the lag phase and growth rates of bacteria, and may be selective for particular groups of bacteria associated with the spoilage of refrigerated fresh beef and lamb meat. Table 1 highlights the types of spoilage which may be caused by different groups of bacteria. There is, however, a need for improved knowledge about the composition of the total meat microflora, to allow a better understanding of meat spoilage development. While the use of culture-based methods can detect a limited range of bacteria, recent advances in molecular tools, such as sequencing, including amplicon sequencing which is most commonly based on sequencing the 16s rRNA region, allow the composition of the total microflora to be ascertained. Such information about the development and changes in the composition of the microbial community on vacuum-packed beef and lamb during storage will give a better understanding of how spoilage develops and improved shelf life prediction.

Sequence-based approaches for understanding microbial community composition

Recent years have seen a rapid improvement in the availability, accessibility and quality of DNA and RNA highthroughput sequencing methodologies (often termed next-generation sequencing), which have revolutionised microbiological studies and have many varied applications for food microbiology, including supporting product safety and shelf life assessments. Continued improvements in analytical pipelines and cost reductions are facilitating a movement from the use of sequencing solely for research purposes to more widespread applications within industry, including the agri-food sector. There are two predominant sequencing applications in food microbiology. Whole-genome sequencing (WGS) is utilised to provide the complete genomic sequence of individual microbial isolates (Bergholz et al., 2014). Microbial community compositional analysis, on the other hand, identifies all microorganisms, or subsets thereof, in a sample. It can be facilitated through either metagenomic sequencing, where all DNA in a sample is sequenced and the microbiome identified, or amplification of specific genes (e.g. 16S rRNA gene for bacterial analysis or the fungal ITS region) allowing taxonomic identification of the species present.

Table 1: The type of spoilage caused of different types of bacteria

| Microorganisms | Type of spoilage on beef and lamb |
|--|--|
| Pseudomonas spp. | Slimy appearance and sulphurous off odours |
| Clostridia spp. | Putrid sulphide smell with a metallic sheen on the meat with or without gas production |
| Shewanella putrefaciens | Sulphurous off odours and greening colour in vacuum pack |
| Psychrotrophic Enterobacteraceae including | Off flavours described as cheesy, malty/acidic, slimy appearance on meat, greening |
| Hafnia, Serratia, Rahnella aquatilis, Yersinia | of meat when vacuum pack is opened, unpleasant sulphide odours |
| Brochothrix thermosphacta, | Strong odours described as cheesy or dairy or eggy odours, bubbles in vacuum pack, |
| Brochothrix campestris | green drip in vacuum pack, meat discolouration |
| Lactic acid bacteria including | |
| Lactobacillus, Carnobacterium and Leuconostoc spp. | Souring |

Subtyping of bacterial pathogens is central to public health epidemiology, helping identify outbreaks, track transmission and identify sources of infection. Depending on the pathogen, a number of methods have been used for this purpose by regulatory authorities and public health agencies, such as pulsed field electrophoresis, multi-locus sequence typing, multiple-locus variable number tandem repeat analysis and others. However, these came with limitations, including suboptimal precision (Brown et al., 2019). Whole-genome sequencing has revolutionised this field, providing the possibility of sequencing a complete bacterial genome in a quick and cost-effective manner, providing unprecedented precision for comparing and tracking isolates. Concomitant improvements in the sequencing technology and associated bioinformatics pipelines, allied with increased accessibility and decreasing costs, have supported a rapid implementation of the technology to enhance food safety and public health worldwide and it is now used for prospective surveillance of bacterial foodborne pathogens in a number of countries (Jagadeesan et al., 2019).

In addition to its use in subtyping and comparing isolates, WGS analysis has also found applications within the meat industry, particularly for identifying routes of pathogen contamination within production facilities, or the presence of persistent isolates. Such studies support the implementation of targeted controls to provide enhanced food safety assurance. For example, a Norwegian study compared 252 *Listeria monocytogenes* isolates from four meat-processing facilities over an 8-yr period by WGS and was able to demonstrate the presence of this specific sequence type across a number of unrelated facilities, repeated detection of specific clones within specific zones over a number of years, the introduction of clones through the installation of second-hand equipment and cross-contamination routes (Fagerlund *et al.*, 2020).

In addition to WGS, advances in sequencing technologies have provided the opportunity to gain a far greater understanding of the total microbial community composition of different ecological niches and how they change over time. Not all microbial species within a given environment are culturable in standard laboratory conditions, but they may nonetheless have a significant impact on the microbial community function. Culture-independent technologies such as sequencing facilitate a more in-depth understanding of the species present and, with some approaches, their metabolic activity.

Many studies to date have focused on the use of ampliconbased sequencing for examining the bacterial community composition of meat carcasses and products, with 16S rRNA as the most commonly used target gene for sequencing. Other genes, such as gyrB, have also been proposed for such studies to provide greater discriminatory potential (Poirier *et al.*, 2018). Such studies have been used to examine the impact of various abattoir setups and practices (Stellato *et al.*, 2016; Korsak *et al.*, 2017) and the impact of storage and/or packaging conditions (Wang *et al.*, 2016; Kaur *et al.*, 2017). In some cases, such analysis has been undertaken with parallel analysis of metabolites such as volatile organic compounds to provide further understanding of spoilage (Mansur *et al.*, 2019). A recent study examining the impact of meat industry sanitation processes combined RNA-based 16S rRNA amplicon sequencing with plate counts to map the viable microbiota and to define any specific bacterial group inactivation (Botta *et al.*, 2020). Some amplicon-based studies have also used software tools such as PICRUSt to predict and compare metabolic activities of microbial communities from different sample types such as the abattoir environment or the meat itself (Stellato *et al.*, 2016).

Shotgun-based metagenomic studies, where all DNA in a sample is sequenced, allow for identification of individual strains, analysis of metabolic pathways, presence of antimicrobial resistance and virulence genes. Studies of this nature focused on the microbiome of meat and meat production and processing facilities remain rare to date. This is likely due to the increased cost and computational complexity in analysing the results in comparison to amplicon-based studies. A recent study utilised such an approach for pathogen detection along the beef production (Yang et al., 2016), but it is acknowledged that such studies are hampered by the absence of well-curated and high-quality databases relevant for food safety management, and the incomplete functional annotation of genes in public databases (Jagadeesan et al., 2019). Nonetheless, with an increased acknowledgement of the need to consider the complete microbial community, as opposed to single species, and the importance of ecological interactions in understanding food systems, it is likely that such studies will become more common. Meta-transcriptomics focuses on sequencing the RNA within a sample, enabling a focus on the viable microbial community and also gene expression within that community, providing an understanding of the metabolic activity of the microbial community. For example, Hultman et al. (2020) utilised meta-transcriptomics to analyse a modified atmosphere-packaged beef during storage and was able to identify changes in active metabolic pathways related to spoilage onset.

A number of challenges exist for the routine application of sequencing in the meat sector. These include, but are not limited, to the diversity of sample types and matrices, the presence of inhibitory substances, the viability of the microbial community present, low cell numbers, DNA concentration and quality, lack of standardisation in sequencing and analysis and the composition of available databases. Notwithstanding these challenges, however, the potential of the technology is immense in relation to meat safety and quality management.

Monitoring of microorganisms in fresh meat production

To support the goal of achieving consistently low microbial counts on meat carcasses and meat cuts, there is need for at- or near-line monitoring of microorganisms to support real-time process control and management as part of HACCP systems. While conventional microbiological methods including culturing and colony-counting can detect low numbers of cells, they require several days to obtain a result (Wang et al., 2018) and are thus unsuitable for online monitoring and process control in meat production processes (Wang et al., 2018; Achata et al., 2020). There are a number of emerging techniques which could be used near-line or atline based on fluorescent sensors, spectroscopic and spectral imaging techniques, such as infrared spectroscopy (IRS), Raman spectroscopy, fluorescence spectroscopy, HSI and multispectral imaging (MSI) for the rapid detection of total or specific microorganisms in meat. These are attractive methods due to the rapid, non-destructive nature of sample examination. Moreover, the potential for online monitoring in meat production facilities would provide a quicker method than the conventional time-consuming methods.

Optical oxygen microrespirometry assay, based on a commercial GreenLight[™] probe (Luxcell Biosciences, Cork, Ireland), is a microtitre-based plate assay providing a rapid high-throughput method to determine aerobic bacterial load assessment on fresh meat, based on analysis of microbial oxygen consumption (Fernandes et al., 2019). In this test, the probe produces a large increase in fluorescence on the depletion of dissolved oxygen by growing microorganisms, which occurs when a certain threshold of respiration is reached. The time required to reach this increase in signal can be used to calculate the cfu/g of the original sample, based on a predetermined calibration (Fernandes et al., 2019). The authors showed that the GreenLight[™] method enabled the detection and enumeration of aerobic microorganisms (TVC) within 12 h at contamination levels from 10³ cfu/g in selected raw meats, beef, lamb, and pork and showed good agreement with the standard conventional culture method (ISO 4833:2003) for the enumeration of aerobic microorganisms at 30°C with a Pearson correlation coefficient value of 0.96. The application of this promising method, however, requires further investigation in commercial meat plant settings.

Achata *et al.* (2020) assessed the potential of HSI in the visible (445–970 nm) and NIR (957–1664 nm) range with chemometrics in the prediction of TVC in beef. Partial least squares regression (PLSR) and principal components analysis (PCA) were compared, along with a variety of spectral preprocessing techniques and band selection methods before data fusion combined the information, which produced a more accurate model. Data fusion for both spectral regions successfully produced TVC prediction models for beef stored at 4°C ($R^2 = 0.96$), 10°C ($R^2 = 0.94$) or at either 4 or 10°C

($R^2 = 0.86$). Tao *et al.* (2015) used hyperspectral scattering imaging in the VIS/NIR range (400–1100 nm) combined with Lorentzian function to predict low-level bacterial contamination on beef. Data were modelled using multivariate statistical analysis methods including principal component regression (PCR), PLSR and back propagation neural network (BPNN). While the prediction models did not perform well using individual Lorentzian parameters, the combination of parameters yielded improved models for determining low levels of beef TVC by PCR ($R^2 = 0.86$), PLSR ($R^2 = 0.87$) and BPNN ($R^2 = 0.90$) methods.

Another spectral imaging technology is mass spectrometry imaging (MSI), which is based on HSI technology. In HSI, the three-dimensional (3D) hypercube is composed of full wavebands, providing a full spectrum for each pixel. MSI also provides a 3D hypercube; however, rather than obtaining a continuous full spectral range, MSI obtains discrete noncontinuous bands (Panagou et al., 2014). As a result of fewer spectral bands being examined, MSI systems do not provide the detailed fingerprints of HSI; however, instrument costs and complexity are reduced and data acquisition time is significantly lower than HSI. In MSI, the sample is placed inside a white sphere (Ulbricht sphere) which is illuminated by light-emitting diode (LED) lights which uniformly distribute the spectral radiation, and finally the reflection from a specific wavelength is recorded by a camera at the top (Gowen et al., 2015). Panagou et al. (2014) evaluated an MSI system in monitoring aerobically stored beef at chilled and abuse temperatures using 18 wavelengths ranging from UV (405 nm) to short wave NIR (970 nm). The beef samples were classified into three different classes based on the TVC values and PLS discriminant analysis (PLS-DA). PLSR models were also developed to predict the TVC (rp = 0.783, root mean square of error prediction [RMSEP] = 1.291), Pseudomonas spp. (rp = 0.837, RMSEP = 1.116) and Brochothrix thermosphacta (rp = 0.859, RMSEP = 0.996) levels present on the beef fillets. Estelles-Lopez et al. (2017) compared data from MSI, electric nose, high-performance liquid chromatography (HPLC), Fourier-transform infrared spectroscopy (FTIR) and gas chromatography coupled with mass spectrometry (GC-MS) using "MeatReg", a web-based application which identifies the best machine-learning regression models for microorganism prediction in minced beef under aerobic and MAP conditions. MSI data from 18 non-uniformly distributed wavelengths in the visible and NIR region (405-970 nm) were acquired. The prediction models obtained from MSI data provided accurate measures of TVC (RMSE = 0.584), Pseudomonas spp. (RMSE = 0.853), B. thermosphacta (RMSE = 0.685), Enterobacteriaceae (RMSE = 0.658) and LAB (RMSE = 0.495) using PLSR or random forests regression (RF-R) during aerobic storage, with similar results obtained for MAP samples.

Overall, these type of spectral technologies offer potential for at- or near-line measurements of microorganisms, supporting process- and hygiene-control measures as part of HACCP plans but they require further validation and robustness assessments within industrial conditions.

Future challenges and opportunities for the management and prediction of safety and microbiology of fresh red meat

From the above, it seems that a number of opportunities exist for beef and lamb processors to achieve the ambitions of significant shelf life extension of fresh meat with assured safety by incorporation of microbial decontaminants and inprocess microbial monitoring. However, there are significant challenges with regulatory barriers in EU, production systems and logistics of slaughter plants. There is clearly no single solution to achieve extended shelf life. Therefore, an approach based on a series of intervention and management strategies along the complete meat chain, from animal through to storage and distribution of the packaged meat, will reduce contamination on the meat and the sources of crosscontamination in the factory environment (air, meat contact surfaces such as conveyors belts, etc.). When applied in combination, this will enhance and ensure meat safety, reduce spoilage events and significantly extend the shelf life of beef and sheep meat.

Recent advances in sensory analysis applied to fresh red meat

Consumers' desire to purchase and consume red meat is mainly driven as highlighted previously by its sensory properties of which tenderness, juiciness and flavour are considered the most important traits (O'Quinn *et al.*, 2018). Indeed, it has been reported that few humans have an intrinsic distaste for meat, but rather an innate preference for the sensory sensations it imparts during eating (Frank *et al.*, 2017). Thus, the application of the human senses in understanding meat sensory attributes and their relationship to perceived eating quality has grown significantly over the past several decades (Djekic *et al.*, 2021).

Sensory analysis provides a set of scientific techniques to better understand the sensory properties of meat and consumer responses to these properties. In conjunction with instrumental and/or biochemical studies, human sensory data provide the best models for predicting how consumers are likely to perceive the eating quality of meat (Lawless & Heymann, 2010) as it was the case of the Meat Standards Australia system (for reviews: Watson *et al.*, 2008a, 2008b). Within the meat science community, sensory analysis of meat has been traditionally divided into two clearly defined areas: 1) analytical tests, aimed at objectively evaluating the sensory properties of meat using discriminative or descriptive techniques, and 2) hedonic tests, in which consumers provide information regarding their acceptance/preference (Warner et al., 2021). While these methods are recognised as valuable tools for generating data relating to various aspects of meateating quality, they are also time-consuming, costly and lack the flexibility required for successful commercialisation in today's fast-paced industry environment. Moreover, the need for sensory information is becoming more complex as consumer purchase decisions increasingly take account of extrinsic factors including environmental concerns, animal welfare, sustainability and perceived healthfulness, in addition to traditional intrinsic quality cues (Frank et al., 2017; Warner et al., 2021). As the industry continues to expand into new and emerging markets, there is a need to develop and adopt novel and rapid sensory techniques to generate data that are more reflective of consumer assessments in the real world without compromising the quality of results.

Therefore, several new rapid sensory techniques including check-all-that-apply (CATA), rate-all-that-apply (RATA), napping and flash profiling have been recently applied to study the sensory characteristics and consumer acceptance of a range of muscle foods (Pintado *et al.*, 2016; de Andrade *et al.*, 2018). While there has been little to no application of these methods to fresh red meat, the findings to date have been promising, with studies reporting sensory maps comparable to those obtained from traditional descriptive analysis with trained panels (Ruiz-Capillas *et al.*, 2021). However, as the application of these methods to fresh red meat is limited, research is strongly needed to establish the reliability and reproducibility of these new approaches for consumer sensory evaluations of beef.

Other recent advances in sensory analysis in the context of fresh red meat has been in the use of dynamic sensory methods such as temporal dominance of sensations (TDS) and temporal liking. The sensory properties of meat pieces perceived while eating change dynamically as they are broken down and manipulated in the mouth. Therefore, the sensory properties perceived in the earlier stages of eating are very different to those perceived at the end. Traditional sensory techniques typically provide a quantification of perceived intensity after eating, and thus fail to consider the dynamic aspect of in-mouth sensory perception. For example, TDS has recently been used to study the dynamics of sensory perception of Wagyu beef (Watanabe et al., 2019). The study showed that in addition to providing a good overall description of the sensory characteristics of Wagyu beef, the TDS method revealed new information regarding the dynamics of sensory perception as impacted by different cooking methods and fattening periods. In another study, a combination of traditional and temporal liking methods were

used to compare consumer liking of striploin beef steaks from three different feeding systems (Corcoran *et al.*, 2020). They reported that while consumers generally found the traditional method easier to perform, the temporal liking method provided more discriminatory data regarding the impact of animal diet on consumer liking during consumption. Taken together, these studies show that temporal methods can be applied to understand the dynamic nature of meat sensory attributes during eating and may provide information close to, or indeed superior to, that obtained using descriptive analysis, in a quicker and more cost-effective manner.

Beyond the application of new sensory methods, meat scientists should also consider the type of statistical approach used to analyse consumer sensory data. Consumers' mean acceptance ratings of meat and meat products are often used rather than comparing consumer segments as commonly done in marketing or consumer research (Miller, 2020). While popular multivariate techniques such as PCA and PLSR can account for some variation in consumer data, they often produce predictive equations that are not repeatable (Miller, 2020; Warner et al., 2021). The importance of taking into account consumer segmentation in consumer data analysis is based on the assumption that consumers have different likings and different drivers of liking, and thus using aggregated mean acceptance scores can conceal interesting and important findings. In addition, consumer segmentation or clustering techniques such as k-means, agglomerative hierarchical clustering or Gaussian mixture models (Gagaoua et al., 2018a, 2018c, 2019b) could be employed in conjunction with temporal assessment methods and open new research opportunities in meat science for segmenting consumers according to the evolution of their liking over time.

Across the meat industry to date, consumer sensory responses are collected using self-reported "explicit" measures, whereby consumers are typically instructed to assess a meat sample for liking in terms of tenderness, juiciness and flavour by indicating their response on a scale. However, consumer's purchasing decisions of meat are not solely based on sensory likes or dislikes and summarising all that complexity into a simple liking score is not sufficient to predict consumer response in today's market (Borgogno et al., 2017). Recently, considerable research efforts have been made to incorporate self-reported emotional measures in consumer sensory testing to better understand why food products that produce similar liking ratings perform vastly different in the marketplace (Crofton et al., 2019). Accordingly, Borgogno et al. (2017) used the EsSense25 method to investigate the emotions associated with beef consumption. The authors showed that presenting to consumers the same beef with different breeding information led to different emotions being evoked, and these differences in emotions were associated with different levels of meat liking. Within the meat industry,

this type of information could enable a deeper understanding of consumer perception of products by considering data that move beyond simple liking measurements.

While numerous studies have captured consumers' emotional response towards the sensory profile of different food products, the techniques applied have relied on the use of selfreported measures, and therefore the accuracy of the data is dependent on the individual's ability to articulate their hedonic and emotional response to different sensory sensations (Crofton et al., 2019). Research has indicated that consumers' sensory acceptability of beef during eating is strongly linked to expectation formed at the point of purchase (Polkinghorne, 2018), but consumer expectation at the point of purchase is almost never captured in meat sensory testing. There are reasons for this, one of which is that this type of information is very difficult to collect as most people cannot articulate or describe their expectations or why they choose one product over another. It has been estimated that somewhere in the brain of 95% of human decision-making occurs on a subconscious level (Crofton et al., 2019). So, when consumers are choosing meat products in a retail setting, they are heavily influenced by factors that do not enter their conscious thought process. In addition, there are many sources of variation in consumer sensory responses that cannot be controlled in a sensory test, and as a result, panels of humans are by their very nature heterogeneous instruments for the generation of meat-eating quality data.

Recently, researchers have suggested using implicit or "biometric" techniques to measure consumers' subconscious sensory and emotional response to foods (Crofton et al., 2019; Miller, 2020). The most commonly studied techniques to date include capturing facial expressions using either electromyography (EMG) (Beyts et al., 2017) or a facial action coding system (de Wijk et al., 2012); recording eye movements using eye-tracking technology (Siegrist et al., 2019); and to a lesser extent, recording brain wave rhythms using electroencephalography (EEG) (Viemose et al., 2013). Other measures of interest include involuntary physiological responses governed by the autonomic nervous system (ANS) such as heart rate, skin temperature, respiratory patterns and skin conductivity. In addition, a sophisticated technique called functional MRI (fMRI) has provided interesting insights into which areas of the human brain changed after differing qualities of beef steaks were consumed, and how these changes are driving consumers' perceptions of tenderness, juiciness, flavour and overall liking (Tapp et al., 2017). While the application of implicit techniques in meat sensory research is in its infancy, these methods have the potential to provide a complex product characterisation over the entire eating experience in relation to how the temporal sensory profile of meat products influences consumers' hedonic and emotional response on both a physiological and behavioural level.

In the comprehensive review by Crofton et al. (2019), virtual reality (VR) technology has been highlighted to provide an immersive and engaging opportunity for researchers to examine and manipulate the core structure of different food products. including meat. For example, using handheld controllers enables measurement data of different characteristics of foods' structure, by immersion into a VR setting (Crofton et al., 2021). Moreover, the work by Crofton and co-workers stated that VR could be applied as a context-enhancing technology, which will enable a more realistic consumer experience. Accordingly, Crofton et al. (2021) used VR as an emerging technological tool to understand the effects of eating context on consumers' sensory assessment of beefsteaks by comparing two different contexts, such as traditional sensory booths and a VR restaurant. It was concluded that consumers found the VR restaurant experience to be significantly more memorable in comparison to evaluating the beefsteaks in the traditional sensory booth. The results showed that the hedonic scores for all sensory attributes, including smell, tenderness, flavour and juiciness, were significantly greater for beefsteaks consumed in the VR restaurant, compared to the sensory booths. Further, overall liking scores were significantly higher for beef tested in the VR context.

Among the other emerging methods, Ross (2021) highlighted the benefits of using electronic tongue (e-tongue) in sensory food science. E-tongue was first used to discriminate the five basic tastes, therefore providing a valuable tool to food scientists, which will assist in enabling the evaluation of food quality, authenticity or the presence of residues. Tan & Xu (2020), who reviewed the applications of electronic nose (e-nose) and e-tongue in food quality-related properties determination, concluded that both e-nose and e-tongue are useful tools to help in refining evaluation of different types of food quality characteristics compared to conventional detection methods. These methods are relatively low cost, rapid and efficient; however, a strict control of sample preparation, sampling and data processing are required for obtaining robust data, which could be positively correlated with consumer data. For meat applications, e-noses can be utilised to determine meat quality throughout smell evaluation such as freshness (Chen et al., 2019) or spoilage (Kodogiannis, 2018).

Conclusion

Recent advances in management and prediction of red meat quality (technological and sensory) have been discussed throughout this review. Many novel opportunities are presented through the application of a variety of foodomics approaches, which help not only in understanding the underlying causes of variability, but can also aid in both management systems delivering consistency in quality and in the development of innovative markers for quality. Further research in rapid non-destructive methods for predicting fresh meat quality is leading to important innovations and developments. Post-mortem carcass interventions are key factors in the management of the final eating quality, with a focus on ageing methods and physical interventions. Management and prediction of the safety and microbiology of fresh red meat cover interventions to control characterisation of microorganisms of relevance, advances in sequenceapproaches and monitoring systems. based Manv advances are also evident in relation to sensory analysis and understanding consumer motivators - areas which are of high interest for further research are outlined which are focused on advancing commercially relevant research themes to aid in the delivery of sustainable meat products that meet consumers' expectations.

Acknowledgements

Dr. Mohammed Gagaoua (MF20180029) and Dr. Alessandro Ferragina (MF20170219) are Marie Sklodowska–Curie Career-FIT Fellows funded by the Marie Sklodowska-Curie grant agreement No. 713654. The support of Meat Technology Ireland (MTI), a co-funded Industry/Enterprise Ireland project (TC 2016 002), to the authors is greatly acknowledged.

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Special Issue Article • DOI: 10.15212/ijafr-2020-0146 IJAFR • 61(1) • 2022 • 168-183



Irish Journal of Agricultural and Food Research

'Come aboard' the systems-based approach: the role of social science in agri-food research and innovation

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Abstract

Increasingly, systems-based approaches are taken in agri-food research and innovation (R&I). Such approaches also align with changes in science governance and new policies related to research impact and responsible research and innovation. However, taking a holistic view of food systems to maximise impact from R&I in a societally acceptable manner poses theoretical and methodological challenges. How can diverse actors come to occupy roles in forming and pursuing common visions towards more sustainable food systems? This paper focuses on how social science can activate, mediate and add rigour to systems-based approaches. An overview is presented of the policy context in which greater attention is paid to systems-based approaches and we present a framework to theoretically and practically support systems-based approaches: transdisciplinarity and the "multi-actor approach" (MAA). These approaches explain practically how different scientific contributions and non-scientific actors can be engaged and unified in creatively addressing R&I challenges. Overall, because social science is used to inform and deliver R&I outcomes that take into account the whole system of actors, their different values and expectations and their interactions and knowledge exchange, it is a crucial source of knowledge for advancing and meeting the challenges of systems-based approaches. Illustrating this, we present a profile of projects where social science has been applied to enhance R&I within a systems-based approach. However, we also signal caveats, qualifications and provisos in applying such approaches. This paper will be of interest to researchers and practitioners planning to incorporate social science to systems-based R&I initiatives to avoid pitfalls and add rigour.

Keywords

MAA • multi-actor approach • research and innovation • responsible research and innovation • RRI • systems-based approach

Introduction

It is acknowledged that more holistic solutions are required in the face of Grand Societal Challenges and United Nations (UN) Sustainable Development Goals (SDGs) relating to climate change, food security and health and nutrition. In this context, transdisciplinary and systems-based approaches are increasingly being promoted by international research and innovation (R&I) policies. Ireland's (draft) AgriFood 2030 Strategy, reflecting the UN's current emphasis on food systems, describes its systems-based approach as itself "an innovation" (by comparison to previous strategies) (AgriFood Strategy Committee, 2021) through its acknowledgement of "the link between policies for food, climate and the environment, and health, and [focuses on] the role each part of the food chain has in delivering the 2030 vision. Sustainability in its three forms - economic, environmental and social - are at the heart of the Strategy" (AgriFood Strategy Committee, 2021). Developing this definition, the Food and Agriculture Organization (FAO) of the UN defines a sustainable food system as

"a food system that delivers food security and nutrition for all, in such a way that the economic, social and environmental bases to generate food security and nutrition for future generations are not compromised. This means that: it is profitable throughout (economic sustainability); it has broadbased benefits for society (social sustainability); and it has a positive or neutral impact on the natural environment (environmental sustainability)" (United Nations Food and Agriculture Association 2018).

AgriFood 2030 references the UN Food Systems approach, which relies on systems thinking. Systems thinking is

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explained as "a way of looking at the world. [inviting] us to think about a broader set of factors that can influence these outcomes; and to think about synergies and tradeoffs between all of these". Systems thinking is essentially a tool for broadening perspectives on food systems, and it is the basis for understanding and applying a food systems approach to R&I. Critically, systems thinking offers three main benefits: it provides a list of interdisciplinary topics that must be considered in designing a food systems approach; it identifies vulnerabilities in food systems, and root problems, in order to improve resilience; and it identifies limiting factors so that the most crucial interventions may be targeted (van Berkum et al., 2018). Aside from these three benefits, a further critical and distinctive benefit of taking a food systems approach is that it examines the interchanges and interdependencies between aspects of the system, but only in so far as the range of disciplinary perspectives brought to bear on the problem allows. Achieving the benefits of a systemsbased approach depends on reaching insights in relation to all human, physical, social, economic and environmental components of systems and their interdependencies; and in this context, the systems-based approach is described as inherently "interdisciplinary" and "non-linear" (van Berkum et al., 2018). Allied concepts, which are called upon to more holistically address wicked problems at the nexus between various aspects of sustainability are: One Health - a concept that recognises that the health of humans, animals and their shared environment are interconnected; OneWelfare a concept that highlights the interconnections between animal welfare, human well-being and the environment; and OnePlanet - a concept that recognises the connection and reliance that exists between different habitats on a global basis (Lueddeke, 2019).

For meeting the challenges of conceptualising, theorising, understanding and designing interventions for food systems, knowledge of transdisciplinary approaches is both relevant and useful. Transdisciplinary is defined as "transcendence of disciplinary perspectives ... into a broader framework in 'true systemic fashion' that involves practical engagement with 'local and regional issues of concern'" (Stock & Burton, 2011). Transdisciplinarity, consistent with the needs of systems-based approaches, involves collaborations between non-scientific (professional communities, civil society, etc.) and diverse scientific actors, but also the activation and facilitation of participatory processes with actors on the ground (Stock & Burton, 2011). Importantly, transdisciplinary theory and practice is informed by social science, which is capable of understanding social networks; the power structures that frame them; and the ways in which networks and structures may be transformed (for greater collaboration, etc.). Transdisciplinarity is at the heart of the "multi-actor approach" (MAA), currently pioneered by

the European Union (EU)'s Horizon 2020 programme and its successor, Horizon Europe. Growing state of the art in practically supporting the MAA on the ground stands to be crucially supportive of those designing and implementing systems-based approaches to agri-food development and innovation. Practical tools to engage diverse actors and incentivise collaboration, and to mobilise and facilitate cocreative innovation, are crucial requirements for the delivery of a systems-based approach. Social science directly informs many of these practical tools.

This paper presents existing frameworks informed by social science, that can inform how food systems approaches may be theorised and practically supported. In the following section, we describe new policies that have been introduced to science governance, including research impact and responsible research and innovation (RRI). These policy frameworks have become cornerstones of publicly funded R&I programmes at both national (e.g. Department of Agriculture Food and the Marine [DAFM], Science Foundation Ireland [SFI], Irish Research Council [IRC], Environmental Protection Agency [EPA]) and European (e.g. H2020) levels. We describe how these changes intersect with, and demonstrate the need for, systems-based approaches and transdisciplinary approaches. We present how these frameworks link to and support food systems approaches in the "Systems-based approaches: practical uses of transdisciplinarity and the MAA" section. In the "Applying social science to projects across food systems: a profile of cases and some caveats for agri-food research" section, we present a profile of agrifood R&I projects that occur across the food system and show perspectives both on how social science has been used as a support and on the caveats and provisos in applying social science. Finally, the conclusion section presents insights of interest to researchers and professionals seeking to incorporate social science into food systems-based R&I projects on the ground.

Science in transition: new paradigms in science governance

"Science today is in transition – from a relatively closed, disciplinary and profession-based system, toward an open and interdisciplinary structure where knowledge creation is more directly accessible to stakeholders across society". (Wilsdon *et al.*, 2017)

This citation from Wilsdon *et al.* (2017) explains the transition that is underway in agriculture and food research, providing an important focus for this special issue. The food systems approach is outcome-oriented but it is also values-aware. In this respect, it intersects with changes happening in the area

of science governance over the last number of decades where outcomes (the turn to research impact) and values (the turn to RRI) are concerned. Looking back over the past six decades since the establishment of the Irish Journal of Agriculture and Food Research, a very significant arena for change has been science governance. New paradigms in science governance have brought about a change in the manner in which science is funded and conducted. As the European Commission has noted, there is an "on-going evolution in the modus operandi of doing research and organising science" (European Union, 2015). Global challenges such as climate change, sustainability, food security and health and well-being increasingly dominate headlines and societal discussion (United Nations, 2015; International Food Policy Research Institute, 2016). The need to find solutions and develop new technologies and approaches to combat these challenges in an integrated manner has led, in part, to the emergence of a research agenda within Europe which increasingly prioritises the need for "research impact" (Stilgoe et al., 2013). At the same time, science governance policies such as RRI argue that any techno-scientific progress needs to be tempered by a consideration of the moral, social and ethical expectations and requirements of society as a whole (von Schomberg, 2013). In combination, these policies have ushered in a new era of science governance that aims to encourage greater multi-actor participation in science and to ensure that science is acceptable to, valued and used by society. This new era of science governance is important to signal in this anniversary issue of the Irish Journal of Agriculture and Food Research.

The overarching common thread of these policies is that as a result of their integration to and increased dominance within European research policies, research practices are in transition. Through institutionalised mechanisms (e.g. regional research policies, funding stipulations, university policies and so on), scientists are increasingly encouraged and even expected to do research in a different way. The nature of the change required is wide-ranging and varied but includes changes to the manner in which actors develop and design R&I projects (e.g. user-led research/MAAs), the manner in which data are stored (e.g. collaborative and open repositories), how research is published (e.g. open access) and how research is evaluated (e.g. demonstrating impact and socially responsibility). There is considerable literature dedicated to the terminology and defining of science governance-related concepts, as well as exploring and mapping their ontological beginnings and growth (Stilgoe et al., 2013; Mayer, 2016). In this section, with respect to two primary policy concepts research impact and RRI - we provide a brief introduction on key changes to science governance and the implications this has for contemporary research practice. We elucidate how these key changes are clearly aligned with and supportive of the food systems approach to R&I.

The turn to research impact

The food systems approach places a particular emphasis on outcomes, which is consistent with the "turn" in science governance towards an emphasis on research impact, where policy has attempted to lessen the gap between research and practice. The "European Paradox" suggests that although Europe has been a leading global player in producing highquality scientific output, there has been a failure to translate these scientific advances into tangible economic and industryrelevant impacts (Acosta et al., 2011), with a perception amongst policymakers that the occurrence of impacts are "too few, and poorly targeted with respect to their needs" (Midmore, 2017). Although some commentators question whether this paradox is actually supported by empirical evidence (Dosi et al., 2006), over the last two decades, the need to generate and demonstrate "research impact" has been increasingly emphasised in the European research agenda (Wouters et al., 2015) and in national research agendas (e.g. Innovation 2020 - Ireland's Department of Business, Enterprise and Innovation, 2019). Publicly funded research streams are dominated by problem-oriented R&I (Henkel, 2005; Stilgoe et al., 2013). With high expectations of accountability for public funding, research funders and society more broadly are requiring researchers to provide evidence of the social, cultural, environmental and economic returns from science (Gibbons, 1999; Bornmann, 2013; Dinsmore et al., 2014). Notwithstanding Midmore's conclusion, following a content analysis of the UK's 2014 REF Impact Case Studies, that researchers have "a nascent conservatism that focuses on research that can be shown to have impact, rather than research impact itself" (Midmore, 2017), providing such evidence is particularly important where food-related research is concerned.

Food is at the heart of the SDGs (United Nations, 2015), with more than half of the 17 goals emphasising the need for a safe, nutritious and sustainable food supply (International Food Policy Research Institute [IFPRI], 2016). Researchers who work in publicly funded food-related research projects are thus increasingly aware of the growing pressure to demonstrate that their research supports the development of sustainable global food systems. Scientists are now working within a "policy framework geared towards the exploitability of science" (Henkel, 2005). There are increasing demands on publicly funded researchers to provide evidence of the impact of their research beyond traditional scientific key performance indicators (KPIs), such as scientific publications. Research funding is no longer awarded on the basis of research excellence alone - funders are demanding that researchers demonstrate the social, cultural, environmental and economic returns from research (Bornmann, 2013). Furthermore, research impact is a highly gendered topic. Horizon 2020 funding rules stipulate not only that a minimum

threshold of females should be involved in R&I consortia. but that R&I programme design should consider both female and male populations to enhance wider societal applicability of outcomes. The same logic applies to promoting diversity in innovation and research processes, such as youth, new entrants and LGBTI+ (AgriFood Strategy Committee, 2021). While the value of achieving and demonstrating research impact to society is clear, effective mechanisms and metrics to provide evidence of such research impact are less clear (Midmore, 2017). How to operationalise, capture and/or measure impact has been a topic of much discussion. Research impact is a complex, multi-dimensional and valueladen construct; the term conveys multiple understandings and meanings within different scientific and policy circles. In this regard, it can be viewed as an "essentially contested concept" (Ferretti et al., 2018; Regan & Henchion, 2019); therefore, evaluating and evidencing research impact is a challenge. To support this challenge, research impact frameworks have been developed by research funding bodies to assess whether R&I is technology-ready, policy-ready and/ or socially-ready (Harland & O'Connor, 2015; DAFM, 2021). For such assessments and to achieve impact readiness, social science is needed to understand end-user contexts and to engage a variety of actors (including end users) in the (co) design and testing of outcomes. Systems-based approaches need to be impactful; they need to go beyond systems-based theory (research) to systems-based thinking, which is oriented to action and impact.

The turn to responsible research and innovation

Providing evidence of the value and impact of science demonstrates accountability for public spending and acts as a means for continued investment in future funding, as well as building trust in science more broadly amongst general society (Gibbons, 1999; Bornmann, 2013; Dinsmore et al., 2014). Assessing societal impact in particular acts as a reflexivity exercise throughout R&I processes - it encourages those involved to periodically stop, reflect upon and critique how and where research is generated and used, the value society places on research and guides the formulation of future research questions and research plans (von Schomberg, 2013). Approaches fostering societal impact feed into the growing trend for governance approaches such as RRI. Responsible research and innovation encourages a multi-actor co-creation approach in tackling global challenges and to ensure that R&I meets the values, needs and expectations of society (von Schomberg, 2013). Responsible research and innovation, thus, is in keeping with the key principle of the food systems approach, which is that food systems must be sustainable - economically, socially and environmentally - and that any interventions must be "proofed" for responsiveness to public values, and according to multi-dimensional sustainability criteria.

In this respect, established approaches for RRI intersect with the pillars of (economic, social, environmental) sustainability that serve as the foundations of the systems-based approach. Responsible research and innovation encourages agendasetting based on societal needs (Fitzgerald et al., 2016), highlighting the need to reflect on the motivations and purpose of research before embarking on it and considering how these motivations and purposes align to societal thinking. Responsible research and innovation encourages upstream engagement and responsiveness during the R&I process (Khan et al., 2014). This type of thinking is reflected in "just transition" approaches that have been prioritised in environmental policy decision-making in particular (Harrahill & Douglas, 2019). Just transition approaches are dependent on innovative ideas for rural economic activity that are opportunistic for and acceptable to diverse societal cohorts. Responsible research and innovation is linked to the "science in society" programme where Public Engagement (PE) and Education and Public Engagement (EPE) initiatives encourage researchers to move from communication to dialogue with the public. However, the importance of PE and EPE and its integration to research practice is often lost. As argued by Stilgoe et al. (2014), "reflexivity", at the level of researchers and research institutions, is needed in order to instil esteem in and commitment to PE and EPE practices.

"Social science explains reflexivity as a way of reflecting or thinking, 'In a way that turns back upon, and takes account of, itself' (Hardy *et al.*, 2001). In supporting RRI (European Commission, 2021), reflexivity is a fundamental success factor: 'Einstein (...) was successful partly because he doggedly and constantly asked questions with seemingly obvious answers. Childlike, he asked Why? How? What? Rather than accepting givens.' (Bolton & Delderfield, 2018)" (Macken-Walsh, 2020)

Responsible research and innovation is aimed at linking "social and ethical desirability to the 'responsibility' of those involved in innovation and research processes (scientists, innovators, policymakers, interest groups, end users, etc.)" (Pelle & Reber, 2015). It requires researchers to consider, negotiate and potentially redefine their responsibilities and duties beyond those associated with the traditional role of their profession (Stilgoe et al., 2013). For some, this may manifest in the form of reflecting on societal concerns to reconsider their notions of research integrity (Stilgoe et al., 2013). What does all of the above mean for researchers? It means their role is changing - they are increasingly expected to engage with diverse disciplinary and professional actors in order to ensure their research agendas meet with societal needs; that they will not cause public outrage; that they can anticipate public reaction and interest; and to ensure that their research makes

a valuable addition to society. Contemporary researchers are challenged with contributing to meaningful and valuable innovation, and with producing tangible products, policies or processes from their research output.

It has been suggested that RRI should not be viewed as a goal, but rather as a way of organising social interactions (Asveld et al., 2015). Such social interactions do not just imply engagement with the "general public" but also with actors who play a direct role in supporting and implementing innovation, for example, industry, regulators and policymakers. Innovation requires more than the mere dissemination of research to target audiences; it requires collaborative efforts of different actors in combining new and/or existing tacit knowledge (Hansen et al., 2014). All of this draws attention to the importance of the transdisciplinary approach and the MAA where knowledge exchange and a bottom-up approach to research are prioritised. Research communities can help shape how science transitions in this period of fluidity rather than waiting for top-down approaches (Mayer, 2016). Social science has a role to play by providing ethical and methodological frameworks and tools to enhance the responsiveness of R&I to its clients and public.

Systems-based approaches: practical uses of transdisciplinarity and the MAA

Food systems approaches are characteristically "non-linear" and "interdisciplinary" (van Berkum et al., 2018). Because they rely on taking a holistic view of food system activities, socio-economic factors and environmental factors, a wide range of disciplinary perspectives is required to understand the whole system. Furthermore, however, because food systems approaches are also characterised as being highly outcome-oriented, engaging with non-scientific actors on the ground in putting an architecture on the process and populating it through the interactive design processes of coinnovation is also critical. Achieving successful collaboration between all the required actors in the food systems is hugely challenging, a challenge that is itself a caveat for systems-based approaches. While its application is not without challenges, social science is a necessary partner in systems-based initiatives (van Berkum et al., 2018) and it also provides valuable knowledge on how collaboration between the scientific and non-scientific actors required for a systems-based approach may be conceptualised, theorised and practically supported.

Social science assists in providing frameworks for understanding different forms of disciplinary collaborations. Where the different forms of collaborative multi-intertransdisciplinarity (MIT) are concerned, Stock & Burton (2011) explain, "While the basic principle across all these approaches is similar (i.e. focusing on integrated complex problem solving by crossing disciplinary boundaries) there are often subtle, but significant differences between the terms [multi-, inter- and transdisciplinarity] which mean they cannot (or should not) be used interchangeably".

Put simply, multi-disciplinarity involves different scientific disciplines (life, social sciences, etc.) working alongside each other and interdisciplinarity involves layering results and conclusions from different disciplines, with little cross pollination of knowledge arising. Transdisciplinarity is vastly more challenging, because, by definition, it,

"is the highest form of integrated project, involving not only multiple disciplines, but also multiple non-academic participants (e.g. land managers, user groups, the general public) in a manner that combines interdisciplinarity with participatory approaches" (Stock & Burton, 2011).

While transdisciplinarity is challenging to achieve authentically (Stock & Burton, 2011), systems-based approaches rely on achieving transdisciplinarity to achieve an accurate understanding of the whole food system, based on integrated understandings of sub-system components. Even in contexts where diverse disciplinary scientists (and professionals) have willingly engaged in cooperative arrangements to work together, significant challenges can arise from their differing epistemological and empirical world-views. Even within branches of science, there can be significant differences between disciplines and fields of study. This is true also of social sciences, where it has been noted that quantitative positivist economics, for example, can face difficulty integrating with sciences dominated by interpretivism, such as sociology and anthropology (Harvey, 2004). Unless deliberate strategies are employed to coalesce their views around mutual topics of interest, the transcendence of disciplinary boundaries (described by Stock & Burton [2011]) is jeopardised. We profile some of these deliberate strategies, in the following section. In a context where transdisciplinarity is increasingly called for, it remains rare by comparison to multi- and interdisciplinarity approaches, which fall short where the required level of integration for a thorough food systems approach is concerned. In order to move beyond them, social science is a helpful enabler. For example, social network analysis provides an evidence base for understanding who is/not involved in social networks; the extent to which actors are/ not connected; the extent to which they knowledge/resource share, etc. (see Figure 1). One of the main cited benefits of taking a systems-based approach is to identify weaknesses and opportunities in the whole system. Social network analysis can identify opportunities and weaknesses in system

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Degree and betweenness centrality of actors in the Irish bioeconomy social network

Figure 1. Social network analysis: Ireland's bioeconomy. Source: Harrahill et al., unpublished analysis.

networks to ensure that all the necessary actors are involved. Figure 1 profiles the range of transdisciplinary actors involved in Ireland's developing bioeconomy. The inner ring refers to the number of connections each actor holds. The outer ring demonstrates the ability of actors to fulfil the role of broker, connecting other actors to the bioeconomy social network. By illustrating differing proportions of the rings and how the outer ring connects with the inner, Figure 1 identifies the actors who are dominant and the extent of cooperation and contact between different actors.

Furthermore, at the more micro relational level, social science-based understandings of human value systems are critical for food systems approaches. "People's values matter for how food systems thinking is shaped" (UN Food Systems Summit, 2021) and social science can not only uncover the values that different actors hold but inform tools to mediate value systems in engendering collaboration. Effective approaches to mediate relationships in networks and human value systems - including in group or collaborative contexts - are informed by theories of power, inequality and social positioning more generally. Gender and diversity are identified as critical for effective systemsbased approaches (UN Food Systems Summit, 2021; AgriFood Strategy Committee, 2021) and require strategic advocacy. Tools to continuously evaluate the inclusiveness of networks involved in making systems-based interventions are critical for increasing the rigour of interventions, their impact and the extent to which they adhere to principles of RRI. A toolbox recently produced by the LIAISON Horizon 2020 project is of direct use in enhancing actors' reflexivity in assessing the inclusiveness of their networks (Figure 2). The toolbox draws from five main methodologies - social network analysis, participatory impact pathway analysis, positive social change, developmental evaluation and social impact management planning. These methodologies are attentive to the network-oriented, relational and reflexive dimensions of transdisciplinary approaches and how processes of innovation within them must employ strategies to be socially responsible. Figure 2 lists the array of individual tools within the toolboxes, which can be used (by wide-ranging scientific and professional actors) to practically enhance the innovation process with respect to improving the rigour of interactivity and transdisciplinarity. Social science has informed a range of state-of-the-art practical tools to support transdisciplinary work. While participatory modes of working emerged over half a century ago and were practiced originally in developing world contexts, the "multiactor approach" has been mainstreamed throughout much of Europe's Horizon 2020 programme and the forthcoming Horizon Europe programme. The MAA, consistent with transdisciplinarity, emphasises the need for non-scientific actors to contribute to development and innovation in order for the development and innovation process to benefit from their knowledges and to ensure the process is relevant to the "real world". The principles underpinning the approach are supportive of transdisciplinarity and also systems-based approaches. Practical toolboxes to support different actors to work together are available from the range of Horizon 2020 projects that have been operational for over 10 yr. As illustrated in Figure 3, a key challenge is to first engage and incentive actors to become involved (according to their cultural, social and economic values). Scientific and non-scientific actors must be also facilitated to interrogate knowledge sources outside of their own fields, as a necessary step before combining their knowledges. Furthermore, actors must be facilitated to create new innovations, to address problems

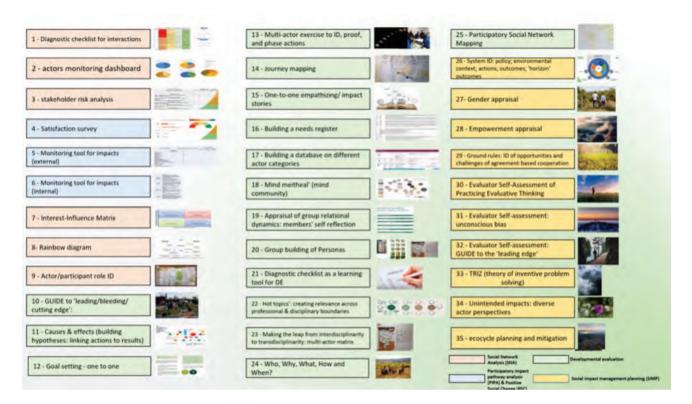


Figure 2. LIAISON H2020 toolbox.

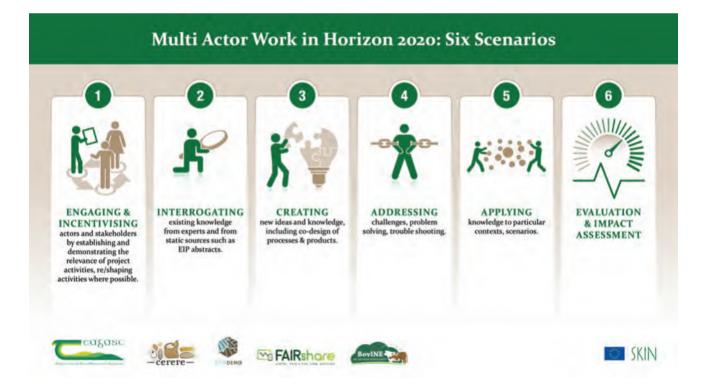


Figure 3. The multi-actor approach.

and troubleshoot and to apply new innovations in new contexts.

Applying social science to projects across food systems: a profile of cases and some caveats for agri-food research

A profile of research and innovation projects: examples of systems-based approaches

In Figure 4, we present a profile of cases that either apply an explicit systems-based approach (e.g. Ploutos and AgroBRIDGES) and those that are transdisciplinary/employ the MAA (e.g. Surveillance, Welfare and Biosecurity (SWAB), *safe*food AMU, CERERE, BovINE, BioÉire and NIVA). The figure highlights the complexity of the systems approach and the levels of diverse interactions that are required. While the complexity or "messiness" of cross-cutting relationships in transdisciplinary, systems-based approaches may be confounding to many scientists and other actors seeking to engage in such approaches, it is important to note that tools informed by social science are capable of addressing many of the associated challenges. Similar to other systems approaches used to tackle societal challenges (e.g. the Obesity Systems Map), such maps serve to communicate the complexity involved in a systems approach, while at the same time helping to make sense of such complexity and supporting the development of strategies to intervene within complex systems (Vandenbroeck *et al.*, 2007). In line with the food systems approach, all projects profiled make a strategic effort to enhance R&I impact and/or RRI.

The projects applying a systems-based approach focus not only on diverse parts of the food systems discretely, but, critically, on the ways in which these parts inter-relate and are possibly mutually reinforcing where the design and implementation of new initiatives are concerned. Ploutos, for instance, takes "a systems-based approach, looking at the overall impact of changes at any point in the value

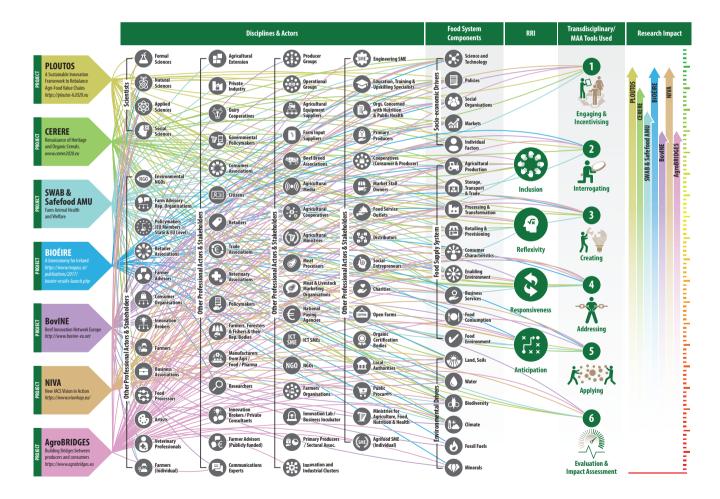


Figure 4. Profile of sample of systems-based agri-food research and innovation projects.

chain... [It takes an] explicit focus on identifying and creating opportunities for changes that can rebalance the value chain in the agri-food system towards a more environmentally, socially and economically sustainable system" (Ploutos. 2020). In taking a systems-based approach, it includes diverse scientific and professional actors that comprehensively represent many aspects of the food system (Figure 4). This has the ultimate aim of approaching the design of sustainability-oriented changes in the food chain in such a way that accounts for system-wide effects of interventions and trade-offs between parts of the system, etc. Ploutos utilises an EU-wide network of Sustainable Innovation Pilots (SIPs) to co-design/adapt, trial and test new innovations in realistic settings and involving multi-actor participation in a 'living lab' approach. While the project is in its first year, the Ploutos SIPs are already producing technologies (such as sensors at farm level) that have been adapted through a process involving farmers, scientists, farm advisors, etc. Incorporating a social science "behavioural innovation" work package, Ploutos ensures that the innovation process evolves in such a way that is responsive to the needs and value systems of actors involved across the chain, which is necessary for innovation outcomes to be wanted and used by actors and, thus, impactful and socially responsible. That innovations are proofed according to environmental, social and economic sustainability indicators enhances the RRI of the project's R&I activities.

AgroBRIDGES is another example of a project that employs a systems-based approach. It aims to build bridges between producers and consumers, rebalancing farmers' market position within the system by empowering them with knowledge about new business and marketing models. It will develop "a holistic, systemic agroBRIDGES Toolbox", to connect producers and consumers in new business and marketing models for short food supply chains (SFSCs). In doing so, it considers the role of markets (with a particular focus on public procurement), science and technology [particularly information and communications technology (ICT) and digitisation], policies (e.g. relating to agriculture, rural development, food quality, public procurement, labelling), social organisations (networks, communities) and individual practices (including the needs and challenges of primary producers and consumers) as key drivers of the system. Engaging all food system actors, it has built a multi-actor platform in each of 12 diverse regions across Europe. These platforms are connected through one central stakeholder reference group (SRG), comprising one representative per regional multi-actor platform (MAP). The resulting structure and associated activities (including workshops and training sessions) will ensure that a minimum of 400 diverse actors from the agri-food sector across Europe will directly participate in knowledge exchange, cocreating and co-developing project outputs together with project partners. This will ensure potential for pan-European roll-out of solutions that are appropriate to regional contexts. Social science-based approaches are deployed throughout the project with a specific work package dedicated to the development of the multi-actor framework that guides the operation of the project, and analysing the key drivers of the system that will impact the feasibility of the proposed models. The RRI aspect of the project is enhanced through assessing the proposed models according to their environmental, economic and social impact. This will lead to the co-creation of a Multicriteria Decision Assessment (MDA) dashboard to enable users to calculate the "SFSC sustainability" potential of the different models.

Where transdisciplinary/MAA projects are concerned, while they focus on discrete aspects of a number of food systems components, they make explicit and methodical efforts to integrate disciplines and professions. The SWAB of farmed animals project, for instance, is an Irish project targeting a subset of food system components, which are inter-related and mutually dependent when it comes to designing and implementing impactful results. The project incorporates a "TransActions" (transdisciplinarity for action) platform, led by social scientists, where different disciplinary scientists and professions identify "hot topics" of mutual interest, and cross-pollinate their different perspectives, experiences and knowledges in relation to these topics. Following the various multi-actor scenarios of Figure 3, the transdisciplinary team has taken concerted action in co-designing innovative approaches for extension, veterinary practice and for communicating new ideas, knowledge and values to the general farming population. As well as generating impactful, practice-ready outcomes, it is also notable that the diverse pool of collective knowledge of the TransActions platform was holistic, rounded and the discursive process within it kept "silo" thinking in check. In such a way, in addition to SWAB being led by international state of the art where topics such as animal welfare is concerned, the process within the TransActions platform was also supportive of RRI (itself dependent on holistic, comprehensive solutions for society).

Similar to SWAB, BovINE identifies hot topics. In this instance, they reflect European beef farmers' most urgent needs in addressing economic, environmental and social aspects of sustainability affecting their sector, as identified by themselves. It then uses participatory multi-actor processes to identify solutions from research and practice, blending knowledge from different sources and different levels in terms of readiness for application in practice. Solutions from research are challenged in terms of their potential for application in practice, as well as their potential impact on each dimension of sustainability (economic, environmental and social), through transdisciplinary thematic working groups, national

and international multi-actor workshops and evaluation of results from commercial on-farm demonstration. In this way, technologies are progressed along the technology readiness level scale to practice-ready solutions with involvement not only of end users but also of the wide range of actors that may influence its operation and feasibility in practice. Gender aspects are considered throughout, from a pre-proposal participatory workshop where the focus of the project was defined based on personas that included male and female farmers, to evaluation of gender representation within the project consortium and participation in project activities, to the communication and dissemination activities organised within the project and consideration of the relationship between gender and potential uptake of the proposed solutions. It is equally important to take into account other diversity factors such as ethnicity, class and sexuality. The LIAISON evaluation and impact assessment toolbox provides approaches to address these important factors, which if unmitigated can hamper the richness of transdisciplinary, systems-based approaches.

Exploring OneHealth issues in the food system is the aim of the all-island AMU project. This multi-actor project draws together scientists, vets, farm advisors, farmers and supporting actors (e.g. Animal Health Ireland) to develop and progress ideas for improving herd health and reducing the need for antimicrobials on farms. Behaviour change theory and animal health science have been combined with practical and local knowledge through the use of participatory research methods to develop a behaviour change intervention to tackle the issue of antimicrobial resistance on farms. The resultant AMU-FARM intervention will train key practitioners such as farm advisors and vets in specialised communication techniques (motivational interviewing, behaviour change techniques) and empower them to work collaboratively with farmers to make positive farmer-led changes to animal health practices. Using social science methods in this manner allows for the development of *bottom-up* interventions, which are particularly important where top-down interventions already exist (i.e. the incoming 2022 veterinary medicines regulations). Bottomup approaches, which bring together multiple expertise and knowledge types, can better prepare the farming community to navigate the changes that will be brought about by legislation, support them through this major transition and empower them to positively engage with change on their terms.

The CERERE project, like SWAB, focused on a subset of the food system, related to the renaissance of heritage and organic cereals. It included diverse actors – ranging from primary producers to end consumers to public artists (Figure 5). The EU-wide project strategically approached its research agenda by not only understanding, through social science research, the various challenges and opportunities from the perspectives of all the various actors, but also incorporated participatory methods to actively stimulate the development of collaborative alliances within the value chain. For instance, a Mind Meitheal approach (Figure 5) was taken, which brought together different actors and presented visually how they may collaborate together to achieve successful results (e.g. a scientist collaborating with a grower: and a grower collaborating with a processor or restaurateur). A "match making" event at a public arts festival (Tulca) involved actors placing colour-coded stickers on their name badges and networking to identify potential partners to combine different resources for achieving their goals. That the event took place at a mainstream festival, with no proprietary link with the agri-food industry, diversified the range of participants involved and increased public attention to the topic of heritage and organic cereals. In such a way, partnering with an arts festival addressed the challenge of bringing more and new knowledge to and augmenting the impact of activities, echoing the call of Harvey (2004) to focus less on "agri" and more on "culture" when aspiring towards more integrated approaches.

A sister Horizon 2020 project, SKIN, took another approach in responding to the same challenge of coalescing different actors around common interests for collaborative action. It engaged different disciplinary scientists and professionals in participatory exercises to identify "hot topics" of current and common interest, and once a comprehensive list of topics was identified, different professional and scientific perspectives and ideas were combined to address them.

Impactful results were generated by these projects, including new cultivation of produce that was utilised by influential chefs and restaurants, generating public attention to and new demand creation for the cereals. Environmental integrity and biodiversity were key principles of the project, as was scientific knowledge in efficient crop production and processing. As an example of RRI, CERERE adhered to these principles and good scientific practice, while also relating to the "real world" scenarios of farmers, processors, consumers, etc., generating highly valued, publicised and celebrated outcomes.

Also focusing on specific food systems components is the NIVA project, which is tasked with embedding e-governance in agriculture. This EU project is developing nine interconnected digital innovations to improve the system used to administer and control payments made to farmers under the Common Agricultural Policy. With a strong emphasis on both impact and RRI, the project incorporates an MAA to ensure the development of these technologies in a way that will provide ultimate value to both the agricultural sector and society more broadly. Given the centrality of data to these systems, a work package incorporating social science aligns with RRI principles to explore data governance issues from multiple perspectives and values and to resolve issues of possible contention and inequity. Social science also plays

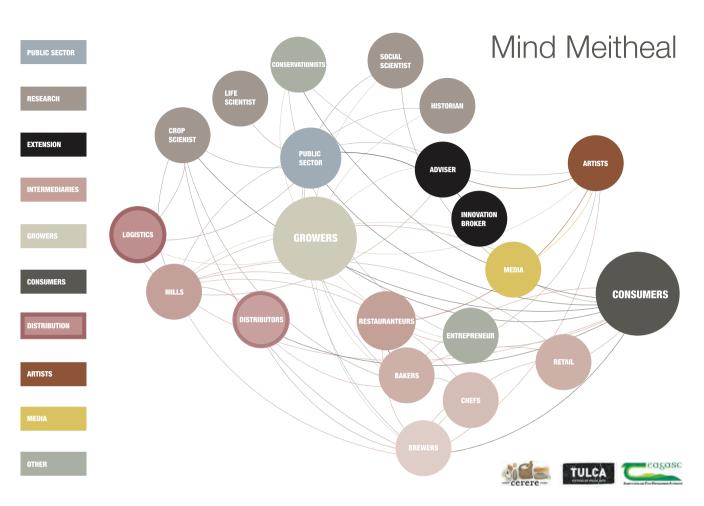


Figure 5. An impressionistic diagram of the heritage cereals value chain, Tulca Arts Festival, Ireland.

an activating role in the NIVA project with the Irish-led use case embedding a design thinking methodology to develop a geotagged photo app that will more efficiently resolve claim queries by empowering farmers to send digital photos of land parcels in lieu of on-farm inspections. The design thinking methodology has facilitated a co-designing of the app between the NIVA scientists, farmers, farm advisors and DAFM staff, ensuring that the technology itself and the processes surrounding the technology meet the needs of end users and generate a sense of co-ownership amongst the involved actors.

The Irish project BioÉire moved beyond food production, processing, marketing and consumption to address the waste and non-food bio-mass that is produced within the food system. Similar to the projects outlined above, it focused on using social science-based knowledge to design participatory methods to enable multiple actors to co-design a shared vision for the Irish bioeconomy. Working with diverse disciplinary perspectives and multiple actors, it provided clear direction for the Irish national bioeconomy policy statement. Given the evolving nature of the bioeconomy in Ireland and elsewhere, a reflexive exercise was undertaken to reflect on the actors that had been involved in the process (Devaney & Henchion, 2018), and thus to consider which actors would require greater attention in the future. This thinking has informed policy developments at European level, feeding into the Horizon 2020 Commission Expert Group to support the implementation of Bioeconomy Policy Support Facility organised by DG Research and Innovation in 2020. It has also contributed to related public consultations at European level (e.g. the Teagasc submission to the Bio-Based Industries Joint Undertaking [BBI-JU] public consultation on their Strategic Innovation and Research Agenda in 2020). In such instances, the need for greater involvement of innovation intermediaries and primary producers in particular has been emphasised. Current research undertaken within BiOrbic (the Irish bioeconomy research centre) builds upon this work by mapping the social networks, identifying actors who are not currently involved, entry points for such actors, etc. (Figure 1).

Caveats, qualifications and provisos in applying social science-based approaches to implement a food systems approach

At its most fundamental level, implementing a food systems approach within R&I requires supply chain actors' understanding of, and active engagement in developing, a holistic conceptualisation of sustainability in terms of economic, environmental and social sustainability, and consideration of concepts such as OneHealth, OnePlanet and OneWelfare. The case studies profiled above show how social science-based approaches can assist in this process. However, if implementation of a food systems approach is to be transformative, allocation of time and resources to a social science-based task needs to be sufficient: tokenistic or shallow involvement of actors is not sufficient. While this is so. it should also be acknowledged that social science research typically does not require capital investments in, for example, laboratory equipment, which can make investment relatively low cost and good value for money. Furthermore, social science approaches can activate and enable knowledge exchange, social learning and mutual respect within and across the elements of the system, which adds value to the work of diverse disciplinary scientists. Without these elements, knowledge will not be unleashed and brought together to develop impactful, socially responsible solutions that take account of the different elements of the system. Applications of social science-based approaches in several of the cases profiled in this paper indicate tools that can practically support the MAA, which is conducive to the required intensity of knowledge exchange. Yet for transformation to occur, significant change is likely to be required starting from the definition of a sustainable food system. This is where social science-based approaches have potential to have even more significant impacts. This thinking is implicit within the participatory processes encompassed by the national and independent dialogues in the lead up to the UN Food Systems Summit.

Because the nature and operation of a food system is determined by many factors, not only biophysical characteristics, what constitutes a sustainable food system is likely to vary from place to place. It is important to note also that it is not a purely scientific or theoretical construct. In the context of a discussion on planetary boundaries, which is implicit in conceptualising a sustainable food system, Pickering & Personn (2020) acknowledge the role of science in informing the establishment of a boundary but argue that the establishment of a boundary is a normative judgement. They state that "what is considered tolerable, acceptable or safe will depend on a range of normative or value judgements such as: the intrinsic or instrumental value that society places on the system compared to other social goals; how society values the well-being of the current generation compared to that of future generations; and social preferences about risk

aversion". Following these arguments, it is clear that defining a sustainable food system can be informed by science but it should be conceptualised along the lines of a boundary object or, "a set of arrangements that allow different actors to cooperate on a basic common understanding while keeping the diversity of their views". To account for such diverse perspectives, it follows that R&I projects that seek to implement a food systems approach need to undertake early and continuous actor and stakeholder engagement. Pre-proposal participatory workshops (such as undertaken in BovINE) and tools that enable participatory impact assessment on an ongoing basis are likely to be relevant.

Implementation of a food systems approach can be considered an innovation in its own right and like any innovation, how transformation towards a more sustainable food system can be achieved will vary. This is because transformations are "inevitably normative endeavours that explicitly (or not) carry with them ideas of desired futures" (Holmgren et al., 2020). Thus, who is/should be involved in defining desirable futures, the values of diverse actors, the instruments that they use to implement the change as well as the nature and extent of change required are key factors to be considered (Devaney & Henchion, 2018). Furthermore, as cautioned by Macken-Walsh (2019), those who will advocate for the co-designed vision within their communities may not be the same as those who were directly involved in the co-design process that created the vision. Consideration of such factors will have a significant impact on how the risks and costs, as well as the benefits, of such a transformation are socially and economically distributed. Pickering & Persson (2020) argue that developing appropriate processes, involving a division of labour amongst experts, citizens and policymakers, to open up space for deliberative contestation about value judgements, enable negotiations about various targets, while safeguarding the ability of experts to issue warnings about issues that they believe reflect unacceptable risks, can enable effective democratic decision-making in such contexts. The NIVA project mentioned above, which integrates considerations of ethical implications of data governance with design thinking methodology used during development of digital technologies, provides some inspiration for such processes.

Elaborating on who is involved in such decision-making requires consideration of not only who should be involved but also who is willing and able to be involved. Democratic legitimacy requires that those who are affected by a decision have the opportunity to participate in deliberations that substantially influence the decision. Supports, from, for example, innovation support services and farm advisory services, may be required to assist actors to occupy the decision-making space. In addition to responding to normative arguments relating to democratic legitimacy, involvement of citizens and other "non-experts" has a vital role in providing practical, local and other forms of knowledge that may not be available to experts and helping to ensure that developed solutions are responsive to their values and preferences, ultimately leading to higher likelihood of acceptance of co-designed solutions. While great care can be taken in identifying and selecting participants to achieve co-creation, there are significant pitfalls where participation and meaningful representation is concerned (Javornicky & Macken-Walsh, 2021). Although the MAA approach has been part of H2020 projects for several years and many tools are available to help with its implementation, its implementation can depend on a "coalition of the willing and able", that is, actors who are willing and able to contribute and are involved in co-planning, cocreation, co-design and co-decision-making.

The authors of the current paper have experience of research projects, not just those profiled here, that overcome many of the common pitfalls. Where actors were unwilling to share knowledge for reasons relating to commercial sensitivity, lack of trust and conflicting objectives, and where important actors were be unable to participate due to a lack of various forms of capital, these issues were identified, addressed and mediated using social science knowledge. An absence of enabling structures can also be a barrier to knowledge flows and, in this regard, reflexive processes within BovINE resulted in a review of management structures within the project and the establishment of an additional working group. While structures had been put in place to facilitate knowledge exchange between diverse actors, the creation of an additional structure that enabled practitioners to exchange knowledge within their own community resulted in improved knowledge flow. Moreover, it should be recognised that implementing a food systems approach might not be a comfortable process. As highlighted by Macken-Walsh (2019), co-creating interventions that are challenging to society rather than popular are required for RRI in addressing Grand Societal Challenges such as climate change. These are significant barriers to be overcome.

Unexpectedly, in many ways, considering traditional emphases on in-person interaction in participatory innovation processes, coronavirus disease 2019 (COVID-19) has resulted in the adoption of digital tools that can enable greater participation by some actors Gutierrez and Macken-Walsh (2021). For example, several BovINE multi-actor workshops were held through online digital platforms with the transnational meeting in December 2020 held online with simultaneous translation from Polish to English. Ploutos, following the example of EIP-Agri Focus Groups, held multiple online participatory workshops to establish value systems that drive actors throughout sustainable innovation value chains. Online participation allowed many actors who otherwise would be unable to participate (because of time constraints, caring duties and other factors) to engage in interactive innovation; and the low cost of participating online was also identified

as a factor conducive to participation (Gutierrez & Macken-Walsh, 2021) While online participation functioned extremely well, availability of internet and computer infrastructure was a pre-cursor for participation. Thus, while one of the arguments in favour of a food systems approach is that it is more likely to result in workable solutions, a consistent argument is that implementation of the approach will require capacity development – in many different ways – to enable stakeholders to become active participants. It also requires consideration of issues such as insufficient time, insufficient competences or participation fatigue (Schneider *et al.*, 2019) as well as trust and confidence-building so as to enable collaboration.

Implementation of a food systems approach has to be able to accept that it is not possible to know all possible outcomes. Hence, implementation will require decisions to be made in the absence of a complete evidence base, thus some failure is inevitable. This needs to be accepted, provided that it is built upon reflexivity and thus feeds into an ongoing process of continuous improvement. Indeed, following the argument of Schneider et al. (2019) that transdisciplinary approaches "seek to accommodate the complexity, uncertainty, and contested nature of current societal challenges as well as to contribute to their transformation", it is also clear that accepting and communicating about uncertainty is required in implementing a food systems approach. The RRI approach encourages a values-based questioning of the future we collectively desire to see and so, uncertainties about what will unfold as a result of specific R&I trajectories are deliberately anticipated, teased apart and reflected upon before further action is taken. This has been exemplified in the participatory approaches of the SWAB and AMU projects where diverse actors have been facilitated to consider the impacts and practicalities (economic, social and environmental) of changing animal health practices changes which are increasingly expected from food consumers and citizens, or demanded from policy and regulation. This allows for the development of more targeted supports which explicitly communicate and address these uncertainties and thus, navigate transitions in animal health practices in a more effective, empathetic and equitable way.

Conclusions

There is no doubt that the agri-food sector faces many challenges in providing sustainable diets for the growing global population. These challenges are embodied in targets to address many sustainability challenges set out in the Green Deal, Farm to Fork and other strategies at European level, as well as in policy ambitions and goals associated with the UN Food Systems Summit, the Paris Agreement, etc. at global level. While science and technology can contribute to providing solutions, no single discipline can develop holistic, implementable solutions of the nature and scale required. Social science has a significant role to play in facilitating different disciplinary researchers to work together and to exchange knowledge effectively. This will not only enable synergies to be achieved, it will also enable the identification of trade-offs and unintended consequences that may not come to light readily otherwise. However, more critically in terms of systems thinking and issues relating to just transitions, social science is needed to co-create solutions in a transdisciplinary way to result in solutions that will be deployed in an integrated manner by a diverse range of actors all across the system. This will require a shift in the positioning of social science in many R&I projects, moving it beyond investigative studies/ basic research to enabling and activating research impact. This will need to be accompanied by a growing awareness of the contributions of social science by other disciplinary communities and of their own very valuable potential roles in implementing facilitation tools to support multi-actor work (as evidenced in the AMU-FARM project above). In parallel, it will require an appreciation by social scientists that facilitation tools to support multi-actor work, although informed by social science, are not only implementable by social scientists. Thus, while social science/participatory sciences can facilitate implementation of a food systems approach as a basic level, deployment of a food systems approach will only succeed if there is co-ownership of all plans, decisions and actions. Familiarity with principles and tools of multi-actor work will thus be part of the skillset of all impactful agri-food researchers. However, as argued in Schneider et al. (2019) in the context of transdisciplinary research, "far-reaching structural and institutional changes are needed in the way academic organizations are managed, organized, and funded", in the way research is evaluated (Roux et al., 2010) and the way researchers are rewarded (Regan & Henchion, 2019) to achieve this as current science policy does not favour transdisciplinary modes of knowledge production.

While this paper has largely focused on the publicly funded R&I system, reflecting discussions in relation to research policy, it is recognised that R&I activities receive substantial funds from private and philanthropic sources. Given that the food system approach needs to be applied beyond the publicly funded research domain, it is important to consider the role of social science in such contexts. These authors believe that the frameworks, principles and tools discussed above are relevant for the governance and operation of R&I in such situations also.

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Special Issue article • DOI: 10.15212/ijafr-2020-0144 IJAFR • 61(1) • 2022 • 184-200



Irish Journal of Agricultural and Food Research

Potatoes in Ireland: Sixty years of potato research and development, market evolution and perspectives on future challenges

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Abstract

Potato is often considered synonymous with Ireland, due to the great Irish famine in 1845, and remains the most important primary food crop in Ireland. Over the last 60 yr, the area of potatoes has reduced from 86,000 ha to 9,000 ha. This trend has occurred in most developed countries but in Ireland it is due to decreasing consumption, increasing yield, decline in seed production and potatoes no longer being use for animal feed. Significant specialisation occurred in the industry during the 1990s, with improvements in agronomy, on farm investment in storage and field equipment, consolidation of packing facilities, and a significant shift in cultivar choice, with Rooster becoming the dominant cultivar. These developments led to an increase in yield from 20 tha in the mid-1980s to over 40 t/ha today. Potato research in Ireland has focused on breeding, pathology and agronomy, while there have been significant changes in how knowledge is communicated to growers and the industry in this period. The industry faces many challenges in the future, largely framed by climate change, the need to reduce fertiliser and plant protection products as part of the EU Farm to Fork Strategy and industry size constraints. New superior potato varieties and novel breeding techniques will have potential to help address many challenges in combination with integrated pest management principles. Multi-actor approaches will be necessary to address all challenges but particularly to aid the industry grow and exploit emerging opportunities.

Keywords

Breeding • market • pathology • potato

Introduction

The potato is often considered synonymous with Ireland and more than any other crop has had a formative effect on society and the Irish economy that is felt to this day. Introduced to Europe at the end of the 16th century from South America via the Canary Islands, potato is well suited to Irish conditions and produced more food with fewer resources than cereals, leading to its widespread adoption (Bourke, 1993). The arrival of late blight (Phytophthora infestans) in 1845 (Fry et al., 1992; Griffin et al., 2002) caused the Irish potato famine with widespread loss of life and emigration (O'Grada, 1999). The potato is the third most important food crop globally and late blight still remains the most significant disease challenge to potato production in Ireland (Dowley et al., 2008) and worldwide. Data from the Central Statistics Office (CSO) reveals that in 1848 when official records began, the area of potato had reduced significantly to 258,000 ha compared to the pre-famine area due to lack of seed and confidence in the crop. The area recovered to a peak of 359,000 ha in

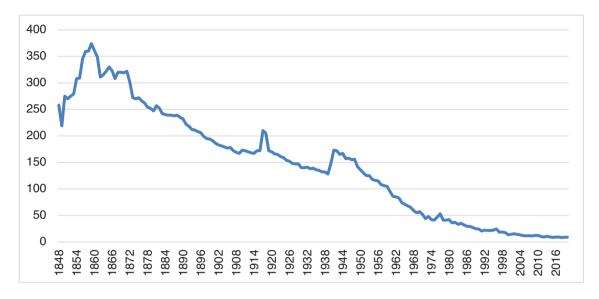
This transition has been supported by ongoing research and development, promotions to support consumption and large changes within the industry along the supply chain to retail outlets. This paper sets out the current market situation and developments in the industry that have led to this point. The paper will review the main scientific advancements associated with the potato crop under the areas of agronomy, pathology, breeding and genetics over the last 60 yr, and the knowledge transfer mechanisms to action this information. It reviews current and imminent challenges facing the domestic crop and market, largely framed by consumer preferences, climate change and the European Green Deal. Finally, the application of new technologies and innovation strategies to underpin

¹⁸⁵⁸ before beginning a gradual decline to the current area of approximately 9,000 ha (Figure 1). Over this period, the potato moved from being a subsistence crop grown on almost every farm in Ireland to a high-value specialist producer cash crop.

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sustainable potato production in the future to meet these challenges is discussed.

Current market situation

In 2019, food crops accounted for almost €400m of the total €467m value of horticultural crops in Ireland. The potato sector was worth almost 25% of horticulture output, valued at €111m at the farm-gate level. There are c. 700 Department of Agriculture, Food and the Marine (DAFM) registered potato growers in Ireland, with about 300 larger commercial farms supplying the majority of volume to retail and foodservice channels. Production was estimated to be 382,000 t in 2019, while the sector is focused around 10-12 central intake points for large-scale washing, selection and packing of potatoes. These potato packers supply the majority of the fresh potatoes to the retail sector. Other potato operations support foodservice "prepared" peeled/sliced potatoes, crisp manufacturing and the chip shop trade. The early potato market is another distinct market restricted to growers with suitable land and milder localised climates, whilst seed potatoes account for a small volume of the total tonnage¹.

Rooster is the dominant cultivar grown for the washed and prepacked sector, representing 62% of the household purchases (based on Kantar World Panel data) and c. 58% of plantings at the farm level (based on the 2019 annual Irish Farmers Association [IFA] survey Table 1). Consumer preference heavily influences the varieties retailed in Ireland and Kerr's Pink, Golden Wonder, British Queen and Record (Figure 2) are traditional varieties dating from the early 1900s that dominated Irish production until the late 1990s. All are high dry matter "floury" varieties with excellent taste. Before the introduction of refrigerated storage (discussed further in the following text) Home Guard, British Queen and other early varieties were traditionally marketed from late May to August, followed by Kerr's Pink and Record and finally Golden Wonder in the late season, traditionally from January/ February. Importation of new potatoes from Mediterranean countries in late spring to meet demand was common. Traditionally, potato varieties must meet both producer and consumer requirements and are difficult to displace from the market. Rooster was released in 1991 by Irish Potato Marketing Ltd. from the Teagasc potato breeding programme. It was an immediate hit with consumers as it combined taste preferences with skin finish benefits that eased preparation while being suitable for boiling, baking, chipping and mashing. As a cultivar, Rooster has excelled in this supply chain model.

Early knowledge-based advancements

Specialisation of potato growers, changes in consumer preference and advances in cultivar development

By 1961, the start of the focus period for this paper, the area of potato in Ireland was c. 86,000 ha (CSO data). The population of Ireland was beginning to urbanise and most potato production was still small scale, locally marketed and with a large proportion of the crop being used on farm for animal feed. The island of Ireland also exported a significant quantity

¹https://www.kantarworldpanel.com/ie.

| Cultivar | Rooster | Kerr's Pink | British Queen | Golden Wonder | Record | Earlies | Fresh chip & peeling | Crisping | Salads | Whites |
|-------------|---------|----------------|------------------|------------------|--------|---------|----------------------|----------|--------|--------|
| % Area 2019 | 57.8 | 6.4 | 5.8 | 2.1 | 0.6 | 0.8 | 5.8 | 11.1 | 2.7 | 6.9 |

Table 1: % Potato area in Ireland by cultivar or use

Source: IFA Potato Grower Survey 2019.

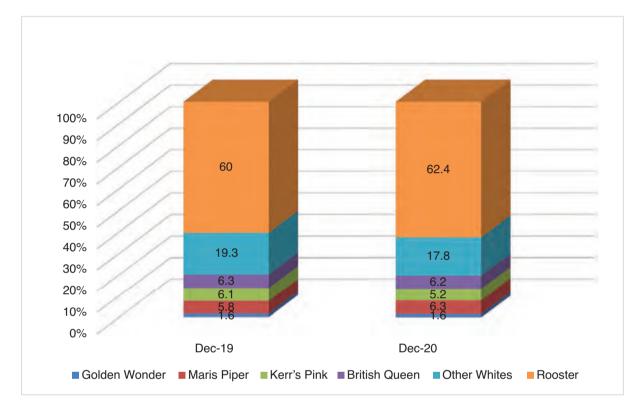


Figure 2. Proportion of Irish fresh potato market measured by household value spend for different potato varieties, figures reflect spend in €'000 by variety across all retail outlets from December 2019 to December 2020 (52 weeks) (Source: Kantar World Panel).

of seed potatoes to the Mediterranean region (Davidson, 1936; Proudfoot & McCallum, 1961). The decline in the area of potatoes grown in Ireland over the following 60 yr was linked with immense restructuring of the industry at both farm and retail levels, coupled with technological developments and shifts in cultivar choice which, in line with consumer preferences, increased yield and reduced production and storage losses.

Training and advice for potato farmers from the AKIS (Agricultural Knowledge Information/Innovation System) at this point was focused around general advice and awareness and it became widely accepted that state-supported agencies should ensure newer farmer practices were adopted (Keenan, 1965). Specialist advisors were deployed by the state from 1980 to act as an interface between research and advisory

(Kirley, 2008). Teagasc (a semi-state research and advisory body) was formed in 1988, with advice being delivered on a fee-paying basis. This resulted in knowledge transfer (KT) and advisory services focusing on more commercial farmers who could afford the fee (Phelan, 1995). The increased use of fertilisers and plant protection products which became part of the AKIS on many potato farms from the 1980s onwards was supported by commercial advisors or merchant agronomists. In addition, changes in the potato supply chain over this period, with a shift to supply of fresh table potatoes through supermarket chains, resulted in the necessity to produce crops to a higher specification, something that challenged growers. To support this, specialised potato farmers now use a mix of advisory services from state-funded organisations such as Teagasc, private consultants (from Ireland and the UK), subject matter specialists (e.g. potato storage) and also commercial advisors.

Research agronomy work conducted during this period also led to a greater understanding of potato physiology in Irish conditions particularly for new potato varieties such as Cara and Barna (Barry *et al.*, 1990; Burke *et al.*, 1998). Further research was also undertaken into the agronomy of producing potatoes suitable for french fry production (Burke *et al.*, 2005). Agronomy KT to potato farmers has evolved from general to specialised advice over the past 60 yr and this interaction continues to evolve. This level of specialisation is likely to increase as advisors in the AKIS (and farmers) are increasingly challenged to respond to environmental challenges such as decreasing chemical fertilisers and pesticides while at the same time increasing biodiversity and putting in place more environmentally friendly practices on farms.

Increased specialisation has been accompanied by a requirement for improved equipment and infrastructure. As demand for quality potatoes increased, Irish farmers looked to the UK, the Netherlands and further afield for new innovations, initially focusing on machinery, but also for changes to field agronomy practice. The introduction of centralised distribution centres by the retailers since 1998 also greatly influenced the scale and specialisation of potato producers. A major shift towards modern production techniques and market structure began in Ireland in the 1990s when the "Operational

Programme for Rural Development, Investment Aid for the Potato Sector" and FEOGA (Fonds Europeen d'Orientation et de Garantie Agricole or European Agricultural Guidance and Guarantee Fund) grant schemes were funded by the Department of Agriculture and Food. This allowed large investments in potato equipment including refrigerated stores, potato boxes, handling and packing equipment graders and field equipment (Gerry Doherty, DAFM personal communication).

The substantive changes in potato production during the period since national yield monitoring was introduced by Bord Bia and Teagasc through sample digs in 1985 are highlighted in Figure 3 (CSO). The total area of potatoes in Ireland remained relatively static from 1985 to 1996 while there was a steady increase in yield from 20 t/ha to 30 t/ha. This increase in vield was largely due to better agronomy and increasing specialisation of growers. While the change in potato area planted fell from 30,000 ha in 1985 to under 9,000 ha in 2019, the subsequent yield reduction in total annual production was not linear due to increasing yield and has fallen from over 600,000 in 1985 to between 330,000 and 400,000 t per annum currently. This reduction in production mirrors the scenario experienced in other developed countries between 1960 and 2008, where production fell from c. 18 million ha to just over 8 million ha (with rising yields). In contrast, many developing countries are exhibiting significant growth (Haverkort et al., 2009).

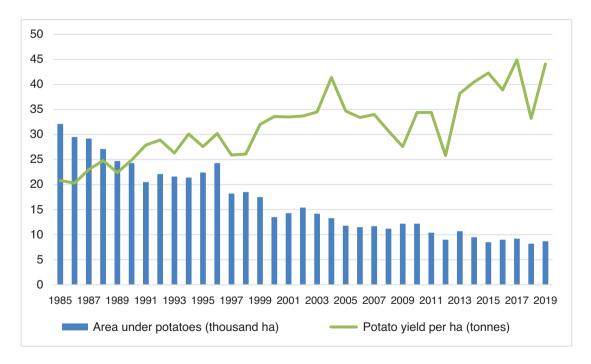


Figure 3. Area under potatoes, and average yield per hectare 1985 to 2019.

It was gradually recognised that more modern cultivars were required to improve yield and disease resistance while still serving the preferences of the Irish consumer. The release of the cultivar Rooster, developed in response to this demand. was transformational, when coupled with the development in the industry. In the period between 2000 and 2019, the national average yield also increased to just over 40 t/ha (excluding drops in 2012 and 2018 due to severe weather events). This is largely due to the increased yield and widespread cultivation of Rooster, which increased its overall proportion of the potato area to 58% in this period. Results from the Teagasc/IPM Potato Group breeding programme breeding trials show a 20% yield increase of Rooster over Kerr's Pink, the next most popular and highest yielding cultivar in Ireland. Whilst Rooster's superior yield and disease-resistance characteristics were important features of its success, it also exhibits other traits more characteristic of modern varieties, including uniformity of size and superior skin finish. The changing market requirement for potatoes with a very good skin, which could be sold year round, gave Rooster a distinct advantage over traditional varieties. The impact of a single cultivar bred to address the specific needs of the Irish market underlined the importance of cultivar development in addressing the challenges of potato production in Ireland; this theme will be revisited later in this review.

Potato research in Ireland: review and state of the art

Pathology, late blight in Ireland

Due to the destructive potential of late blight, which is one of the few diseases that can reduce yields of untreated crops to zero, research into *P. infestans* has been fundamentally important to support production in Ireland. A review of 25 yr of late blight trials at Teagasc Oak Park Carlow from 1983 to 2007 by Dowley *et al.* (2008) highlighted that losses during the period averaged to 10.1 t/ha in both marketable and total yields, representing almost 25% of potential yields in untreated crops. Research has primarily focused on three areas: *P. infestans* biology (and its relationship to disease severity and fungicide sensitivity), disease forecasting and control, and breeding for late blight resistance.

Annual monitoring of *P. infestans* populations has been a critical area of research. *P. infestans* was inadvertently introduced to Ireland and Europe over 200 yr after its host in 1845, on imported seed potatoes from the United States (Fry *et al.*, 1993). Similar to potato, only a fraction of the genetic diversity of the pathogen was introduced from its centre of origin leading to a single strain of blight dominating the global population (Goodwin *et al.*, 1994). Further migrations of *P.* infestans occurred during the 1970s and 1980s. Toolev et al. (1993) showed the arrival of new strains in the late 1980s. The first population change noted was in 1981 with the emergence of phenylamide resistance (Dowley & O'Sullivan, 1981). Two mating types (A1 and A2) of the pathogen are required for sexual reproduction. The first reports of the A2 mating type in Ireland occurred in the early 1990s, which is significant for two reasons (O'Sullivan & Dowley, 1991; Cooke et al., 1995). Sexual hybrids of late blight can be fitter and more aggressive, and oospores, the result of sexual reproduction, can overwinter in soil, leading to the potential for early infection of healthy crops from soil. Genetic-fingerprinting studies have confirmed that the P. infestans population of Ireland is now a subset of the wider European population but so far have not identified sexual hybrids of P. infestans (Carlisle et al., 2001; Griffin et al., 2002; Stellingwerf et al., 2018).

The vast majority of commercial cultivars are late blight susceptible and heavily dependent on the use of fungicides to maintain stable yields (Cooke et al., 2011). The majority of new fungicides for blight control are very efficacious, but are only active at a single biological site, which leads to a risk of resistance development. Even in the absence of sexual reproduction, the environmental conditions that prevail in Ireland are highly conducive to the development of late blight and random mutations can arise and quickly propagate. The notable emergence of phenylamide resistance in the Irish P. infestans population in 1981, with the complete loss of control provided by this class of fungicides (Dowley & O'Sullivan, 1981), was a major setback to late blight control at that time. In recent years, population monitoring has confirmed the presence of the fluazinam-resistant genotype EU_37_ A2, initially detected in the Netherlands. The importance of the link of research to KT was highlighted by the fact that communication of this change to Irish growers mitigated crop losses (Schepers et al., 2018). Fungicide resistance management will be more difficult as the older multisite fungicides such as Mancozeb and Chlorothalonil have been withdrawn from the EU market where they were often used as partner products to help prevent resistance development. This highlights the necessity to continue fungicide efficacy testing and development of fungicide control programmes which takes place every year in Teagasc.

The development of late blight is highly dependent on local weather conditions, in particular temperature and relative humidity. This produces a degree of predictability that can be used as a control measure, and disease forecasting based on these parameters has been a major target for control of late blight. Disease forecasting originally developed when scope to control the disease was limited to a small number of protective fungicides per season and therefore it was important to identify periods conducive to late blight in order to maximise the utility of the timing of these applications. Bourke (1955) originally

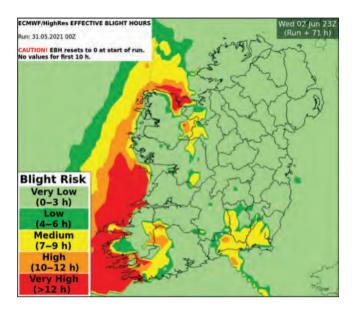


Figure 4. Sample map showing effective blight-hour risk prediction based on the revised model by Cucak *et al.* (2019).

developed the rules underlying late blight forecasting for Ireland, with subtle changes to these subsequently made by Keane (1982). Whilst these undoubtedly reduce the frequency and quantities of fungicides, they underestimate late blight infection events as reported by Hansen (2017) and Cucak et al. (2019). Both Leonard et al. (2001) and Cucak et al. (2021) highlight how this results in inadequate protection of the potato canopy and reductions in yield. Dowley & Burke (2004) have demonstrated that potential does exist for the role of such forecasting or decision support systems, although the methods the authors used were based on infield weather stations which were problematic in Irish potato production given the transient nature of production. More recently, Cucak et al. (2019) have revised the rules originally developed by Bourke (1955), increasing their accuracy and predictability. It is envisioned this will be used in the future by Met Eireann to provide local disease risk assessments in a graphical map format as shown in Figure 4. These revisions were further evaluated by Cucak et al. (2021) in conjunction with an increasing emphasis of the employment of varietal resistance. This scenario, which is an important support tool for Integrated Pest Management (IPM), demonstrated that a substantial reduction in fungicide usage can be achieved without compromising disease control and yield or adversely impacting local P. infestans populations in terms of their aggressiveness (Cucak et al., 2019; Cucak et al., 2021).

Potato virus Y epidemiology

Potato virus Y (PVY) remains the most important virus disease of potato globally (Valkonen, 2007). The disease is

particularly problematic in seed production for certification. In recent years in Ireland it has become the dominant virus partially due to its non-persistent mode of transmission which makes it more difficult to control using insecticides and also due to newer variants of the virus emerging in Ireland which produce less visible symptoms (Hutton et al., 2015). Reports from growers suggest the virus is spreading more quickly than in the past. Hutton et al. (2013) confirmed the presence of the PVYNTN and PVYNO strains that cause potato tuber necrotic ringspot disease (PTNRD), although the tuber symptoms are rarely if ever seen due to lower temperatures exhibited in Ireland. More recently during 2017 and 2018, many recombinant PVY isolates were detected in Ireland, with PVYNTNa being the predominant genotype (Della Bartola et al., 2020). Teagasc has recently invested in a network of aphid monitoring towers at several locations across the country to aid virus prediction and aphid transmission risk for a range of agricultural and horticultural crops². It is envisioned this system will assist with risk prediction for PVY and other potato viruses associated with potato seed certification in the future.

Cultivar development

Potato breeding and advances in marker-assisted selection (MAS) and genomic selection (GS)

The potato breeding programme in An Foras Talúntais at Oak Park Co. Carlow was set up in 1961 to breed cultivars suitable for the domestic market with enhanced resistance to late blight. There were many plant breeding programmes in Ireland at that time including programmes in perennial ryegrass and clover breeding (which are still in existence), and now defunct programmes in cereals (DAFM) and sugar beet (An Foras Talúntais (AFT) and Irish Sugar). It soon became apparent that commercial partnership and access to diverse international markets were necessary to support a viable breeding programme. The introduction of plant variety rights (PVR) and the creation of the Union Internationale pour la Protection des Obtentions Végétales (UPOV)³ in the same year enabled breeders and holders of PVR to exclusively produce and market their new improved cultivars. The income stream generated from royalties could then be reinvested in breeding research and further cultivar development. Irish Potato Marketing Ltd. were already an established exporter of seed potatoes from Ireland and recognised the opportunity created by PVR. Informal collaboration between AFT and Irish Potato Marketing Ltd (now IPM Potato Group Ltd.) since the late 1960s developed into a formal partnership agreement in

²https://www.teagasc.ie/tillagemonth/establishing-a-bydvand-aphid-monitoring-network-/. ³http://www.upov.int.

1976 and subsequently a collaboration agreement between the two parties to breed and market new potato varieties. Fifty-six cultivars have been released to date and 34 of these are either still in full commercial production or in early market development. While Rooster remains the best known cultivar in Ireland, Cara was the first successful cultivar released from the breeding programme in the early 1970s, while Nectar and Electra are well-established cutivars in the United Kingdom. Burren and Slaney are widely marketed across the Mediterranean region. This collaboration is one of the few commercially successful public–private partnerships remaining in European plant breeding.

One of the major challenges in potato breeding is the number of characteristics, or traits, that need to be combined in order to produce successful, competitive varieties that serve all of the actors along the value chain, from grower to consumer. Potato breeding involves selection of over 40 different traits, the combinations and specifications of which depend on the specific market class, use of the potato varieties and agroecology in which they will be grown (Bradshaw, 2017). In order to combine these traits, a cycle of potato breeding begins with the creation of a very large breeding population initiated when parents (generally current varieties) are crossed to produce progeny, from which one or two varieties are identified over 12-14 yr. In the Teagasc/IPM Potato Group programme, a cycle of breeding is generally initiated using approximately 200 parents, which are crossed in pairwise combinations to produce between 100,000 and 200,000 true seed progeny, each of which is a candidate cultivar (Milbourne et al., 1997). After 12 yr of selection usually only one or two candidate cultivars remain, and these are submitted to the official trials (lasting 2 yr) required to gain PVR and variety status.

Potato breeding is viewed as somewhat inefficient because the number of traits that can be combined into a new cultivar in a 12-yr selection cycle is limited; for example, in the area of disease-resistance breeding. For many pests and pathogens of potato, varietal resistance is based on individual resistance genes (*R*-genes) from cultivated and wild potato relatives from Central and South America. The cultivar Cara was an early success that was partially based on its resistance to the major strain of the potato cyst nematode (PCN) species *Globodera rostochiensis* in the UK at the time, conferred by the *H1* gene from *Solanum tuberosum* ssp *andigena*.

For many plant pathogens, resistance provided by single *R*genes is short lived. *R*-Gene breakdown due to adaptation by the pathogen population of late blight, as evidenced with *Solanum demissum* genes in the 1960s, led to a focus on partial "field resistance" (Malcolmson & Black, 1966) which was thought to avoid major resistance genes and be more durable (Collins *et al.*, 1999). The varieties Colleen (1991), Orla (1998), Setanta and Galactica (2004) are examples of cultivars released which exhibit significant levels of field resistance to late blight. However, over time, it became apparent that much field resistance was also at least partially based on R-genes (Gebhardt & Valkonen, 2001). One important idea based on this increased understanding is the concept of stacking multiple R-genes for the same pathogen into single cultivars (Ghislain *et al.*, 2019). Several well-known potato cultivars/lines that have exhibited durable broad-spectrum blight resistance have been shown to harbour combinations of strong and partial R-genes (Kim *et al.*, 2012; Rietman *et al.*, 2012). However, the process of introgressing R-genes from their wild species donors, and accumulating multiple genes in an individual cultivar over multiple selection cycles, is a multi-decadal process. Increasing the speed of recurrent selection is an important feature in resistance breeding, to enable the "stacking" of multiple Rgenes in varieties in as short a period as possible.

The Teagasc/IPM Potato Group breeding programme has adopted a genome-based approach to overcome this limitation, using DNA-based MAS which allows tracking of beneficial genes in a breeding programme. An experimental programme for MAS was established in the period between 2004 and 2008 using a single genetic marker for a gene conferring partial resistance to the PCN (or eelworm) species *Globodera pallida* (Moloney *et al.*, 2009). Currently, MAS is performed for over 20 different full and partially effective *R*-genes using the KASP genotyping platform. These markers target *R*-genes for the two major PCN species (*G. pallida* and *G. rostochiensis*), late blight, PVY and potato wart disease, with a general goal of adding several *R*-gene diagnostic markers to this set every year through a parallel marker development programme (Meade *et al.*, 2020).

Most significantly, MAS can be combined with "rapid cycle breeding" approaches to help shorten the effective selection cycle and accumulate R-genes in high-performing cultivar candidates more quickly. There are numerous possible schemes for this, but in the Teagasc/IPM Potato Group breeding programme, the approach is to target crosses between parents with complementary R-genes at the beginning of every selection cycle, and to use MAS to identify progeny individuals with multiple R-genes in the fourth year of the 12-yr programme. These candidate varieties can then be recycled for use as parents in another round of crossing. This effectively shortens the breeding cycle to as little as 4 yr for the resistance genes under selection using MAS, and up to three cycles of selection can be performed in the same time as a single 12-yr cycle of conventional selection. This is graphically represented in Figure 5.

The recently released potato varieties Java (late blight, PVY, wart and *G. rostochiensis* resistant) and Buster (dual species PCN *G. rostochiensis* and *G. pallida* resistant) highlight the ability of MAS and rapid cycle breeding to speed the process of *R*-gene stacking. Buster is the result of three separate rounds of crossing, initiated in 2004, during which MAS

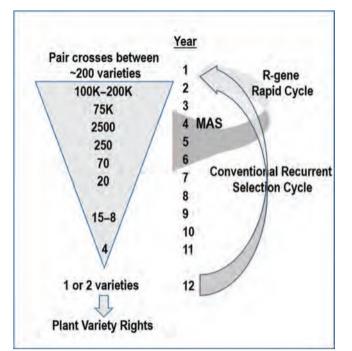


Figure 5. A representation of the Teagasc/IPM Potato Breeding Programme and how MAS and rapid cycle breeding can shorten the selection cycle. A cycle of breeding is initiated (every year) by pair crosses between approximately 200 varieties and breeding lines. The grey triangle represents the decreasing number of cultivar candidates present as selection intensifies each year. Trialling starts in one field location, and by Year 11, candidates are being trialled in Ireland, the UK, the Canaries, several locations in Europe and northern Africa. At the end of this cycle, one or two candidate varieties are advanced for PVR. In the Rapid Cycle scheme, specific crosses between R-gene-containing varieties are incorporated into Year 1. Progeny from these crosses containing multiple R-genes are identified in Year 4. These continue through the programme, but may be recycled as parents at any time over the next several years if they perform well in the field. This shortens the selection cycle. Repeating this rapid cycling process within the conventional programme eventually yields high-performing varieties with multiple R-genes.

and rapid cycle breeding were used to stack four partially effective resistance genes to *G. pallida* (*GpalV*, *Gpa5*, *Gpa6* and *Grp1*) and the *H1* gene into a single, high-performing cultivar. Previous research at Teagasc had demonstrated that combining the two strongest effect genes, *GpalV* and *Gpa5*, resulted in an additive effect in which very high levels of resistance to multiple field populations of *G. pallida* Pa2/3 were observed, and that MAS was an efficient way of identifying plants containing multiple genes (Dalton *et al.*, 2013; Rigney *et al.*, 2017). Under normal circumstances, stacking this many *R*-genes in a single cultivar over three rounds of selection could have taken in excess of 30 yr.

Many important traits in potato, such as yield, tuber quality characteristics and resistance to stresses such as drought,

are under complex genetic control, influenced by the expression of many genes (polygenic). Selection for these traits suffers from similar limitations to resistance genes in terms of the speed and efficiency of the recurrent selection cycle, but MAS is not suited for identifying complex polygenic traits. This problem has been addressed in animal breeding, where practically all important traits are polygenic, by the widespread adoption of GS. First proposed by Meuwissen et al. (2001), GS is a form of MAS that uses thousands of markers across the genome to predict the likely value of traits in cultivar candidates and parents. Significantly, because marker sets scan the entire genome, traits under polygenic control can be predicted. The application of GS to potato breeding for polygenic traits in potato was modelled and it was concluded that it was potentially cost-effective, and could increase the rate of genetic gain for these traits (Slater et al., 2014; Slater et al., 2016). More recently, the application of GS for the selection of fry colour, an important trait for potatoes destined for French fry and crisp production, was successfully tested using breeding material from the Teagasc/IPM Potato Group breeding programme (Byrne et al., 2020). This study concluded that while GS has potential, the current cost of genotyping assays could limit its applicability for many breeders. Work in the potato genetics and genomics programme at Teagasc is currently focusing on the development of low-cost approaches for genotyping that will allow the benefits of GS to be applied to the breeding programme, hopefully mirroring the success of MAS.

Genetic modification and novel breeding techniques

Much of the focus on biotechnology-based approaches to augment plant breeding over the last two decades has revolved around the collective technologies that have historically been referred to as genetic modification (GM). Genetic modification is defined as the use of recombinant DNA technology to introduce DNA elements from one species into another. The approaches under this banner can be broadly divided into two categories: transgenic, and cisgenic. Transgenic refers to the insertion of genetic elements that do not occur in the species being modified (the elements either come from an unrelated species, or are engineered constructs that do not occur in nature). Cisgenic refers to the transfer of genes within a genus (e.g. from a wild potato to a cultivated potato). Both approaches are subject to regulation in the same manner and the primary EU legislation (Directive 2001/18⁴ and Regulation

⁴Directive 2001/18/EC of the European Parliament and of the Council of 12 March 2001 on the deliberate release into the environment of genetically modified organisms and repealing Council Directive 90/220/EEC – Commission Declaration.

2003/1829⁵) governs both the cultivation and import of GM crops.

Although there has been a long history of use in a global context, the regulatory landscape and polarisation of public opinion has meant that no GM potato products have made it to market in the EU. For example, in 2010, the European Commission approved the transgenic BASF starch potato Amflora[™] that had been engineered to produce amylopectin starch, in the absence of amylose, a feature applicable to a range of industrial applications. In spite of regulatory approval. BASF pulled this GM potato from the market in 2012 due to intense political reaction⁶. Around the same time, BASF also ceased their commercial plans for a cisgenic GM potato, engineered with resistance to late blight. The Fortuna™ potato was based on the successful processing cultivar, Fontane, modified to contain two genes (Rpi-blb1 and Rpiblb2) from the wild species Solanum bulbocastanum, and had demonstrated strong resistance to late blight based on studies in Belgium. BASF closed down the commercialisation of Fortuna citing the uncertain regulatory environment within the EU as the primary justification for its action.

Recognising the need to demonstrate the potential societal benefits of GM technology in potato, some public sector research has adopted a more nuanced approach. From 2006 to 2015, Wageningen University in the Netherlands ran the "DuRPh" (Durable Resistance to Phytophthora infestans) Research project (Haverkort et al., 2008; Haverkort et al., 2016) which focused on developing a proof-of-concept that existing potato varieties could be made durably resistant to late blight when provided with stacked R-genes through cisgenic modification (Jacobsen & Schouten, 2007). DuRPh focused not only on the production of resistant plants, but also their use in combination with IPM to develop low fungicide input control strategies for late blight. This study received broad public support (Haverkort et al., 2016) because it was publicly funded and free of commercial bias; the material was generated via cisgenics as opposed to the transgenic GM technique used previously by BASF; and most importantly because the research team actively contributed to a programme of proactive societal engagement. Hence, the generic dialogue that was standard for GM debates was countered with factual and objective commentary. As a result, the potential benefits of cisgenic GM potatoes were succinctly explained in the context of the challenge of trying to reduce fungicide inputs, while maintaining an economic return for farmers and a high-quality product for consumers.

More recently, similar approaches were employed as part of the EU-funded project "Assessing and Monitoring the Impacts of Genetically-modified plants on Agroecosystems" (AMIGA). In Ireland, as part of AMIGA, Teagasc completed field evaluations of a cisgenic GM potato, developed through the DuRPh programme. The engineered potato displayed robust resistance to late blight disease through three successive seasons of field trials at Oak Park (Stellingwerf et al., 2018) with a comprehensive environmental assessment confirming there was no significant difference between the cultivation of the GM line and its non-GM comparator cultivar (Ortiz et al., 2016; Kessel et al., 2018). Indeed, using the internationally recognised and publicly available Environmental Yardstick for Pesticides to quantify the environmental impact of chemical crop protection on water life, soil life and groundwater, the cultivation of a conventional cultivar under current practice scored over 700 environmental impact points. In contrast, the cisgenic-resistant cultivar scored less than ten points (Kessel et al., 2018). As a result, the IPM control strategy adopted in the study, based on the use of the cisgenic potato line, reduced the average fungicide input by 80-90% across the three different years, without compromising control efficacy or yield. Similarly, as observed through the DuRPh project, it was evident through AMIGA that proactive public engagement ensured a greater understanding of the challenges faced by potato growers and the need to consider new technologies to reduce the environmental impact of potato production (Mullins, 2019).

In parallel to the public discussions on the applications of GMO approaches, biotechnology-based breeding initiatives have developed considerably over the last two decades. Numerous different approaches have been developed (reviewed by Schaart *et al.*, 2016) with a diversity of technical features that make it questionable whether EU legislation originally formulated several decades ago, largely based on the features of the transgenic-based approaches of the time, is relevant and fit-for-purpose (Zimny *et al.*, 2019; Turnbull *et al.*, 2021).

One breeding technique called gene editing has been central to a re-evaluation of both public attitudes and current legislation. Gene editing is a set of approaches that introduce precise edits in DNA of a target genome using enzymes guided to the target site using, for example, pre-coded RNA strands. Using this type II clustered regularly interspaced short palindromic repeat (CRISPR-Cas9) system, the precision of the approach to functionally alter single/multiple genes has resulted in its rapid application by the community to address important challenges in agriculture (Chen *et al.*, 2019). Significantly, it has been argued that when gene editing approaches simply introduce mutations in plants, they are functionally equivalent to other forms of mutagenesis breeding that are not subject to regulation, and have, in fact, formed the basis of thousands of plant varieties to date.

⁵Regulation (EC) No 1829/2003 of the European Parliament and of the Council of 22 September 2003 on genetically modified food and feed.

⁶https://www.dw.com/en/basf-stops-gm-crop-development-ineurope/a-15671900, accessed 01.06.2021.

In 2018, the European Court of Justice (ECJ) ruled that gene editing should be regulated as per current GMO legislation under Directive 2001/18. The ECJ judgement elicited a swift reaction from the plant science and seed trade communities in Europe due to the non-recognition of equivalence with mutagenesis breeding (Hundleby & Harwood, 2019). The gap between the structure of EU legislation on GM approaches versus the dynamic, continuous development of novel breeding approaches by the research community was clear. Subsequently, the European Commission commenced a lengthy multi-agency study in 2019 to review the status of new breeding techniques (NBTs) under EU law. Published in April 20217, the study concluded that current EU legislation was not fit-for-purpose and that NBTs have the potential to contribute to a more sustainable food system as part of the objectives of the European Green Deal and the Farm to Fork (F2F) Strategy. Significantly, the report followed with details outlining the pathway to commencing a consultation process with the goal of designing a new legal framework for NBTs such as gene editing and cisgenics.

The future of potato breeding is bright, but what it will look like is unclear

There are many limitations (some discussed previously) in potato breeding, arising from the genetic architecture of potato and its clonal reproduction through tubers. Biotechnologybased approaches such as MAS, GS and GM (cisgenesis and transgenesis), and gene editing overlaid on to current conventional breeding schemes are not the only approaches that are being developed to address these limitations. Diploid hybrid potato breeding, in which the genetic and reproductive architecture of potato is effectively re-engineered (using conventional breeding methods) to allow much more efficient genetic gain, was originally suggested a decade ago (Lindhout et al., 2011) and may revolutionise genetic improvement of potato in the next decade (Stokstad, 2019). The potential of this approach was recently underlined in a study by Zhang et al. (2021), who combined genome-based breeding approaches to help minimise and purge deleterious mutations from inbred lines, which were crossed to produce a hybrid line that gave plot yields equivalent to ~40 t/ha, which is on a par with many tetraploid cultivars. This is new technology and at the time of writing no diploid hybrid cultivar has been released. From a breeding point of view, the advantage of diploid hybrid potato is better precision and speed in cultivar development relative to current tetraploid-based breeding programmes. Hybrid potato also has another defining feature in that resulting cultivars can be propagated through true potato seed (TPS) rather than tubers. While many practical considerations

have vet to be worked out for this mode of propagation, it has potentially revolutionary ramifications for seed production. TPS is considerably less bulky than tubers and can be stored at ambient temperatures for long periods. Botanical seed is also subject to a much lower pathogen burden than seed tubers, making maintenance of seed health much easier. All of this could radically change potato seed production, and may have consequential effects on agronomy and management of potato crops. Whilst diploid hybrid breeding has great potential, its development requires a considerable investment of time and resources. Teagasc is part of a consortium with Wageningen University (The Netherlands) and other institutions and commercial potato breeders to develop an approach called Fixation-Restitution (Fix-Res) breeding, which has the potential to reduce this burden. Fix-Res breeding takes many of the advantages of diploid hybrid breeding, but makes it more compatible with current tetraploid breeding programmes, reducing its development and implementation costs.

Potato breeding is entering a period of disruptive advancement based on the development of the numerous powerful technologies and approaches that have been mentioned here. The future of genetic improvement in potato is likely to involve a combination of these approaches, and while the specific shape or shapes of these future programmes in unclear, what is clear is that breeding will be better able to respond to future challenges at exactly the time when this need is most pressing.

The next 60 yr: challenges and opportunities

The potato in industry in Ireland has changed dramatically over the last 60 yr. Specialisation of the industry, investment in technology, a reduction in the number of growers, changes in cultivars and decline in area of both seed and ware have been the most visible challenges. The next 60 yr are likely to be equally, if not more, challenging. Climate change will impact the physical growing environment for all crops, and potato growers will have to adapt accordingly. This is reflected in policy at EU and national levels and numerous challenging policy targets have been set that will affect potato production. Finally, consumer preference continues to evolve, presenting both challenges and opportunities and this is mirrored in EU policies with an increased emphasis on holistic quality-of-life aspects of consumer citizens. The question is: how will the innovation and knowledge community in Ireland respond to support the potato industry in facing these challenges and opportunities?

Predicted changes in physical climate may alter the face of potato production in Ireland

Potato growers worldwide will encounter the effects of climate change. From an agronomic perspective, Ireland will experience more benign effects than other regions, with a

⁷https://ec.europa.eu/food/plant/gmo/modern_biotech/ new-genomic-techniques_en, (accessed 01.06.2021).

predicted 0.5°C to 1°C of warming, drier summers and warmer wetter winters. However, weather events are predicted to be more extreme (Fealy, 2018).

Gradual and predictable changes to potato agronomy can be relatively easily accommodated. Increased summer temperatures, accompanied by drought, especially in the east of Ireland where potato production is concentrated, are an expected consequence (Holden et al., 2003). Whilst heat stress per se is unlikely to be an issue (productive potato cultivation takes place in both warmer and drier climates than those currently predicted for Ireland), there is likely to be a need for increased irrigation and drought-resistant cultivars. Some cultivars with enhanced drought or heat tolerance already exist; indeed, the Teagasc/IPM Potato Group breeding programme has a track record of producing such varieties for southern European and Northern African export markets; however, there will be a need to develop new cultivars with characteristics that suit the Irish production system and consumer preferences.

More extreme, unpredictable weather events are much more difficult to deal with. As shown in Figure 3, prolonged extreme weather patterns did affect potato yield in both 2012 (delayed planting due to very wet spring) and 2018 (prolonged drought after crop emergence in June and July), and these illustrate the potential effect of weather instability. Other potential consequences of predicted changes include crop damage due to late frosts, and wet autumns/winters that will impede harvesting, particularly on wetter soils where damage and soil loss may be an issue.

Disease control is a major component of potato production, and climate change may also impact this significantly. A small gradual change for a warmer climate in Ireland may increase the host range of several pests and pathogens of potato already present in slightly warmer neighbouring EU countries but which have not established in Ireland. The most notable of these include Colorado potato beetle (Wang *et al.*, 2017), potato tuber moth (*Phthorimaea operculella*) and bacterial wilt or brown rot caused by *Ralstonia solanacearum*. The latter has already been shown to be moving outside its normal range to higher altitudes in both Africa (Abdurahman *et al.*, 2017) and South America where global warming has been proposed as a cause (Castillo & Plata, 2016).

One problem in dealing with the physical effects of climate change is addressing a complex set of events in a complex system – resulting in combinations of effects that may act as ameliorative trade-offs. For example, a corollary to the potential emergence of new pests and pathogens might be a reduction in the pressure from major existing pathogens. For instance, drier spring and summers could lead to easier and earlier plantings in Ireland and may actually ease disease pressure from late blight. In another example, increased atmospheric CO_2 concentration actually has the potential to increase yields in potato production (Finnan *et al.*, 2005),

but these may be offset by lower natural precipitation. Future innovation systems to support potato production will have to be agile and responsive to the actual consequences of climate change that may or may not happen from a list of predicted possibilities.

The regulatory environment to deal with climate change may make it even more challenging

The Green Deal strategy is the EU response to climate change and environmental degradation. At the heart of this plan is to have no net emissions of greenhouse gases by 2050, and to decouple economic growth from resource use. This strategy spans all parts of the economy across Europe⁸. As part of the Green Deal strategy, in May 2020, the EU published the Farm to Fork Strategy and the Biodiversity Strategy for 2030 which are particularly important for agriculture. Key targets set out in these strategies are for agriculture to have a neutral or positive environmental impact, with the ambition of reducing use and risks of pesticides by 50% and reduce fertiliser use by 20%, and to increase organic agriculture to at least 25% of EU agricultural area by 2030. While potato as a food for primary consumption has a low carbon footprint of 540 kg CE/ ha per year (Hillier et al., 2009), with a relatively low water and nitrogen input in comparison to many other crops, it is still heavily reliant on plant protection products (PPPs) and fertilisers. The reduction in fertilisers and especially pesticides, if implemented in full, will have a huge impact on the potato sector. As previously discussed, Ireland's maritime climate is very conducive to potato blight and any significant reduction in these fungicides would need to be matched by improved varietal disease resistance to maintain yields and viability of the sector in Ireland.

Legislation to ameliorate the impact of agriculture is not new to potato growers. Existing national directives such as the Water Framework Directive⁹ and the River Basin Management¹⁰ plans are designed to protect and improve the water environment. Arable farming, including potato production, is associated with identified problems in a number of river catchments such as nitrate losses to waterways and sediment loss. Issues of bare soil, especially on sloping land, during establishment and post-harvest can give rise to overland flow of water and soil to rivers. Existing mitigation strategies such as non-cultivation buffer zones may be strengthened in years to come to mitigate the risks outlined previously. In terms of PPPs, the recent loss of diquat (used in haulm

⁸https://ec.europa.eu/info/strategy/priorities-2019-2024/european-green-deal_en.

⁹http://www.irishstatutebook.ie/eli/2003/si/722/made/en/ print.

¹⁰https://www.gov.ie/en/publication/429a79-river-basin-management-plan-2018-2021/.

destruction) and mancozeb (broad-spectrum blight control) has caused problems for which imperfect solutions have had to be implemented. For instance, the loss of diquat, with no equivalent replacement, has forced growers to use heavy equipment to top potato haulms late in the season which is not advisable where soils are saturated as damage to the growing potatoes is common in these situations as is soil damage (Phelan, 2020)¹¹. Continuing to deal with existing regulatory changes whilst responding to the ambitious policy targets of the EU Green Deal will be a major challenge for potato growers, highlighting the importance of continuing investment in research and development to support innovative solutions to these challenges.

It is not just the climate that is changing: the challenges and opportunities of evolving markets

The potato industry has a high farm-gate value of over €100 million per annum and from a food security perspective, domestic potato production is incredibly important. The Irish sector, while specialised, profitable, technologically advanced and supplying most of our fresh consumption needs, suffers from a lack of critical mass in comparison to other agricultural enterprises due to the relatively small production area. The industry has focused on the fresh consumption markets which, due to the Irish preference for higher DM potatoes, has largely isolated the Irish market from European commodity markets for processing and seed potatoes. Across the decades, competition from other sources of carbohydrate such as rice and pasta have reduced the consumption of potatoes, not just in Ireland but in the developed world in general. As mentioned earlier, this is reflected in terms of the declining national crop production (Figure 3).

There is already a strong recognition of the need for the industry to diversify and expand to maintain viability. In recent years, notable business innovation projects in the Irish potato sector have seen some potato packer operations diversify from their traditional packing business into ready meals, alcohol and potato starch manufacturing, while several others have begun new crisp brands which require specific varieties. Further opportunities exist for the industry in the area of import substitution, particularly of chipping potatoes and baby/salad potatoes. For instance, despite Ireland's potato production capacity, over 80,000 t of fresh potatoes for the fresh chipping market are imported each year. Theoretically, these could be produced in Ireland, but limitations include the availability of suitable, Irish-adapted chipping varieties and competition from keenly priced imports. The recent exclusion of UK seed potatoes from the EU due to Brexit (Robb, 2021) offers

opportunities for Irish certified seed for the domestic market in the short term and possible re-invigoration of the seed export market in the medium term. Ireland is one of five high-grade seed potato regions¹² due to the absence of quarantine pests and also has a large bank of virgin potato land that could be used to grow seed potatoes; however, much of this land is unavailable due to long-term leases in other farm enterprises.

Conclusions: Given these challenges, where do we go from here?

Cultivars are the answer to a lot of the problems

New cultivars can significantly contribute to the challenges across all three of the major aforementioned areas of diverse markets (such as organic and conventional), reduced PPPs and fertilisers, and biotic stress due climate change. This will be especially true if potato breeding can become faster and more precise. Breeding can address tolerance to abiotic stresses such as drought, disease and pest resistance, changing consumer preferences for products such as salad and baby potatoes, and the need for locally adapted varieties supporting all market sectors such as fresh processing and specialist markets. Potato breeding has always had the potential to deliver this in theory, but in practice, conventional potato breeding suffers from numerous limitations in terms of precision and timescale preventing the realisation of this ambition. However, as we have described in this review, we may be entering a disruptive and productive period for potato breeding. Technologies such as GS, MAS and other NBTs, combined with novel potato breeding schemes, have the potential to give breeders unprecedented levels of control in combining multiple traits in high-performing varieties. More importantly, most of these technologies increase the speed with which this can be performed, meaning that the timescale between identification of the required "ideotype" (e.g. a drought- and disease-resistant, white-skinned chipping cultivar) and the ability to produce a cultivar fitting this profile will shorten. Given that some of the impacts of climate change will become apparent over a relatively short time horizon, the ability of breeding to quickly respond to these emerging situations will be more important than ever.

While this "next-generation potato breeding" has enormous potential, there are factors that will need to be addressed to help it realise its potential. Precision breeding approaches are built on a base of basic and strategic research. Approaches such as GS, MAS and gene editing require a deeper

¹¹https://www.teagasc.ie/media/website/crops/crops/potatoes/ Potato-newsletter-September-2020.pdf.

¹²https://unece.org/fileadmin/DAM/trade/agr/meetings/ ge.06/2015/ExtBureauMtg_Finland/High_Grade_Region_ Finland2015.pdf.

understanding of the genetic control of important target traits in order to be successfully deployed. Teagasc has a good track record in participating in multinational initiatives such as the effort to sequence the potato genome (The Potato Genome Sequencing Consortium, 2011) which has driven many of the innovations in molecular breeding worldwide. The Irish research community will need to continue to engage in these initiatives and similar precompetitive collaboration efforts to maximise their ability to effectively deploy these approaches. Given the lack of large multinational companies in potato breeding, cooperative precompetitive publicly funded research remains an important source of innovation in the potato industry (the Bioimpuls project in the Netherlands to develop late blight-resistant germplasm for organic production [Almekinders et al., 2014] is an excellent model of this type of collaborative research).

In addition to this, for NBTs such as gene editing to fulfil their potential, an aligning of regulations for these technologies to the current situation is essential. As demonstrated in AMIGA and DuRPh, cisgenesis can augment existing and new potato varieties with the ability to reduce PPP use by more than 50%. The Commission's commitment to develop a new regulatory framework has to be welcomed and provides an expectation that future varieties developed through NBTs can be adopted on a case-by-case basis, supporting the EU to meet its goal of reducing the environmental impact of food production while also ensuring a stable supply of safe food for its citizens.

Multi-actor approaches really are the answer

In reality, whilst single solutions like improved cultivars are important, it is their use as a component of multi-actor approaches to address challenges facing the potato sector that has the greatest potential. We can use the specific example of management of late blight through augmented IPM to demonstrate this. As previously described, *P. infestans* is a dynamic pathogen capable of rapidly overcoming both cultivar resistance and PPPs. Given the added challenge of reducing the applications of fungicides by 50%, how might we address control of late blight using the developments described in this review? An augmented IPM approach that was initially proposed by Kessel *et al.* (2018) but adapted for Irish conditions might look like the following:

- Rapid cycle breeding and/or other NBTs give us the potential to create durable blight-resistant varieties by stacking multiple *R*-genes from wild species in highperforming varieties.
- (2) Active monitoring of *P. infestans* field populations using molecular methods, to determine the potential of strains to overcome both the *R*-genes present in varieties and the PPPs being used.
- (3) Development of low spray programmes that trigger a "decision-to-spray" based on the presence of *R*-gene

breaking strains in the local environment (based on *P. infestans* monitoring), combined with real-time climate data as the primary predictors of epidemic potential.

(4) Design KT support processes (e.g. cloud-based blight warning app available to registered growers) that enable growers to effectively take decisions based on these available resources.

In this model, advances in plant breeding, molecular plant pathology, modelling and data analytics are combined with well-developed KT networks to enable the challenge to be addressed. Importantly, all of this is based on the starting point of the current state of the art as outlined in previous sections. In the interim, such a model can be used with existing varieties with lower levels of resistance. Given the complexity of the challenges faced by the sector, similar multifaceted approaches combining innovations and actors across a range of disciplines will have to be developed.

Climate change will be more difficult

As previously mentioned, predicted gradual changes in climate will be gradually adapted to by the industry. However, extreme weather events which may become more common will present a greater challenge and will impact production. The Irish potato industry is highly mechanised in comparison to other countries to allow timely field operations if weather is inclement. Site and soil selection for growing may become more important in the future, both in the case of extreme weather events and also if autumns/winters become wetter, to ensure growers can avoid unsuitable heavier soils. Land access to ensure sustainable rotations particularly for seed production is currently perceived as an issue by growers. Long-term leases coupled with expansion of other agricultural areas have intensified the problem. A mechanism to make suitable land available through rotation and exchange should be explored. Continued climate prediction and horizon scanning to determine what the effects of climate change may be, such as modelling the establishment of new pest and diseases, will be key to ensuring the industry is prepared.

Market development

The Irish market is currently relatively stable in terms of demand, which has increased from a low point in 2012, attributable to two back-to-back EU-funded potato promotion campaigns¹³. Opportunities to expand the industry and reduce certain imports do exist. This in turn would lead to increased critical mass, increased service and support, and investment in research and development. Innovation in this area requires a true multi-agency co-operation and strong

¹³www.potato.ie.

partnership between public agencies and the private sector. Recent cooperative projects between Bord Bia, Teagasc and the IFA under the auspices of the Irish Potato Development Group are a good illustration of this. A good example of this is the knowledge transfer-led Salad/Baby potato project, which provided the technical know-how to produce specialist crops (Teagasc) combined with strong liaison with growers and packers (IFA) and strong market research/development (Bord Bia). The project increased production by over 200%¹⁴ from approximately 3.000 t per year to over 7.000 t. A current project, involving the same organisations, seeks to increase the volumes of fresh chipping potatoes grown in Ireland by developing technical expertise, engaging chip shop owners and their suppliers while creating demand for local sustainable produce. Future innovation initiatives will have to be similarly multidisciplinary, but perhaps even more ambitiously so, integrating research, KT, market development, strong partnership with private companies and growers and strong public engagement to maintain and expand a healthy and vibrant potato industry.

Acknowledgements

The authors wish to thank Carmel Hinchion, Central Statistics Office for provision of data on potato yield and planting areas in Ireland, Colm McDonnell, IPM Potato Group Ltd. and Prof. Garry Lanigan for helpful comments on the text, and Gerry Doherty, Department of Agriculture Food and the Marine for provision of information.

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¹⁴https://www.teagasc.ie/media/website/publications/2019/ Teagasc-Annual-Report-2018-web.pdf.

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Irish Journal of Agricultural and Food Research

Benchmarking a decade of holistic agro-environmental studies within the Agricultural Catchments Programme

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Abstract

Meeting sustainable food production challenges requires efficient ways to manage nutrients and mitigate the losses of nitrogen (N) and phosphorus (P) to water. Future nutrient management therefore requires a clearer understanding of the relative influence of soils, geology, farm practice, landscape and weather on the propensity for nutrients to be lost to water. Within the Agricultural Catchments Programme (ACP), environmental, agronomic and socioeconomic data have been gathered since 2009, using the same experimental methodology in five mesoscale river catchments, and one karst spring zone, covering a range of soils, landscapes and farming systems. The ACP has contributed to a better understanding of nutrient mobilisation and transfer pathways and highlighted the influence of the physical and chemical environment as well as agricultural and meteorological drivers on diffuse nutrient loss to ground and surface waters. The environmental quality standards were breached for N and/ or P in some of the catchments, but for different reasons and not always clearly linked to the source pressures within the catchment. There are clearly no one-size-fits-all solutions for mitigation of nutrient losses to water. A better understanding of the underlying processes is required to identify critical source areas, to select mitigation strategies, when to implement them and to build realistic expectations of their impact. Sustainability in an agricultural setting is not confined to environmental issues, but also includes social, economic and innovative aspects. To maximise farmers' uptake of environmental measures, the actions should encompass all these aspects of sustainability. Integrated knowledge transfer is key.

Keywords

Agriculture • knowledge transfer • socioeconomy • water quality • weather

Introduction

Sustainable food production is required to meet the demand of a growing and more affluent world population in combination with a changing climate (Smith & Gregory, 2013), a challenge which will require efficient ways to manage nutrients and mitigate the losses to water (Schoumans et al., 2014). Phosphorus (P) and nitrogen (N) are the main nutrients driving eutrophication, which has a detrimental effect on water ecology (Carpenter et al., 1998) and has negative implications for the food chain (Withers et al., 2014). To achieve the challenge of reducing nutrient loss to waters, we need a comprehensive understanding of how both agronomic and climate drivers influence nutrient loss along the whole nutrient transfer continuum and what the impacts are, both over time and space, and for catchments with different physical settings. We also need to understand the economical drivers' and farmers' attitudes and willingness to adapt to changes (Arbuckle et al., 2013).

The European Union (EU) member states are required to monitor their Nitrates Regulations or the National Action Plan (NAP), under Article 5 (6) of the EU Nitrates Directive (ND) (Official Journal of the European Community [OJEC], 1991). In Ireland, the Department of Agriculture, Food and the Marine (DAFM) monitors the implementation of the NAP through the "Good Agricultural Practice for Protection of Waters" regulations (GAP). The DAFM has funded the Agricultural Catchments Programme (ACP) to monitor the effectiveness of the GAP measures since 2008. Catchment monitoring is required to support Ireland's derogation (farming at higher stocking rates 170-250 kg livestock manure N/ha) under Article 8 of the Commission's Decision granting a derogation requested by Ireland (Official Journal of the European Community, 2007/697/ EC). Therefore, the ACP provides a scientific basis for policy review of the NAP, its derogation across different soil types

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and land use and the influence of agriculture on the Water Framework Directives objectives (OJEC, 2000).

The ACP is a collaboration with over 300 farmers in six small river catchments in Ireland and is currently in its fourth 4-yr cycle of funding. The programme has taken a whole catchment approach. By using the "nutrient transfer continuum" (Haygarth et al., 2005) as a conceptual framework, an extensive monitoring programme of nutrient sources and hydro-chemo-metrics have been implemented similarly across all six catchments. This facilitates an understanding of how nutrients are lost from agricultural sources, how they can be mobilised and transferred via different hydrological pathways, how they are delivered to water and where there may be a negative impact on water quality and aquatic ecology. The whole catchment approach was agreed upon during the first phase of the programme by the ACP Expert Steering Group composed of internationally leading scientists and national policy makers.

A strength of the ACP is the long-term and high-frequency monitoring. The programme uses simultaneous highfrequency monitoring of streamflow and stream water chemistry, which provides many advantages that increase as the technology quickly advances (Rode et al., 2016). High-frequency data have facilitated the use of analytical methods that allow us to identify and quantify nutrient transfer pathways, such as concentration-discharge hysteresis (e.g. Bieroza & Heathwaite, 2015), loadograph recession analysis (Mellander et al., 2012a, 2012b) and methods to evaluate the effectiveness of water management interventions such as concentration-discharge slope (Bieroza et al., 2018) and extended end-member mixing analysis (Jarvie et al., 2011). The long-term aspect is required to encompass time lags in the system, as well as changing weather and policy drivers. At the regional catchment scale, time lags can vary widely in magnitude from weeks to decades, depending on the underlying catchment geology (Fenton et al., 2011). The dominant mechanisms for nutrient mobilisation and the dominant transport pathways for nutrient transfer depend on the spatial and temporal scales considered (Fenton et al., 2011) and this will in turn dictate the time lag. This often means that it is difficult to assess the impact of diffuse pollution abatement programmes as the impacts of changes in management practice may not be observed until several years or decades after implementation (Benettin et al., 2013). Both anthropogenic warming (Schaller et al., 2016) and changes in the large-scale climate systems over the North Atlantic influence the weather in Ireland (Yiou & Nogaj, 2004). During the programme, there have been changes in air temperature, rainfall patterns and more extreme weather events. Examples are the severe summer drought of 2018 (Falzoi et al., 2019) and the wettest decade in 300 yr (Murphy et al., 2018). Despite difficulties in directly linking climate

change with water quality (Michalak, 2016), recent findings have stressed the importance of shifts in climate and weather conditions for agricultural nutrient loss. For example, in Great Britain up to 80% reductions in agricultural P loss are required to offset the projected increased P loss associated with climate change, and current mitigation efforts will not be sufficient (Ockenden *et al.*, 2017). A dynamic modelling study in Ireland found that changes in climate had the potential to influence the total P loads more than changes in either population or land use (Jennings *et al.*, 2009).

The ACP links the socioeconomic element with the biophysical component. This allows for the development of a deeper understanding of the processes related to policy changes and farm management decisions. After more than a decade of holistic agro-environmental studies within the ACP, the objective of this paper is to review the research output from the ACP and projects linked to the programme, to summarise the key biophysical, socioeconomical and knowledge transfer (KT) findings and support further research, environmental policy and nutrient management planning (NMP).

Experimental design

The ACP consists of six meso-scale catchments, five river catchments and one karst spring zone, ranging in size from 3 to 30 km² (Figure 1, Table 1). These were selected by a multi-criteria analysis (Fealy et al., 2010) to represent intensively managed agricultural land on different physical settings and dominating land use (mainly grassland or arable land). The six catchments therefore represent different types of riskiness for N and P loss in terms of dominating transfer pathways (leaching to groundwater or runoff with surface water). The catchment size was chosen to be large enough to encompass the range of hydrological conditions from headwaters to the main river channel, allowing for normal N and P transformation and mobilisation processes to occur, and also to integrate the impacts of a realistic range of farm practices within a typical farming system (Wall et al., 2011). Individual farmer preference did not influence catchment site selection, and the areas were chosen prior to notifying landowners. However, active engagement with farmers is key to the programme, and this is achieved mainly through the provision of an advisory service, where each catchment advisor deals with approximately 80 clients. Catchment and farm boundaries do not align. Consequently, many of the 300 farms across the six catchments also have significant areas of land outside the catchment boundaries.

Knowledge exchange occurs frequently *via* the specialised farm advisors, either one-to-one or in discussion groups. The programme also arranges public events and farm walks, and several research dissemination events are held annually.

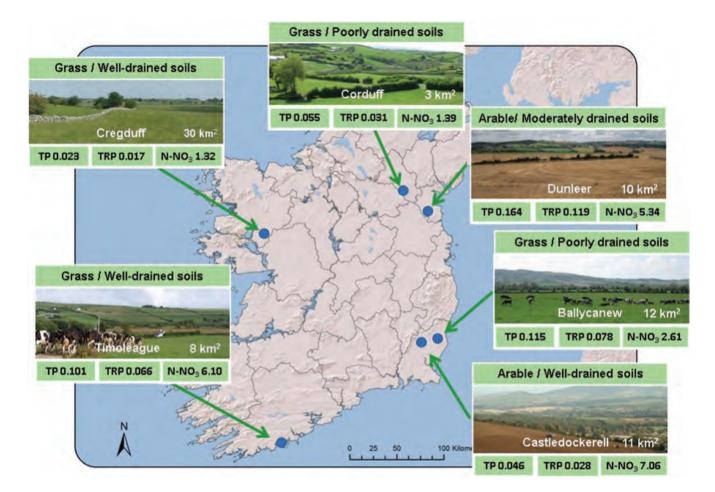


Figure 1. Overview of the six river catchments monitored within the Agricultural Catchments Programme. The figure includes the 10-yr annual average total phosphorus (TP), total reactive phosphorus (TRP) and nitrate-N (NO₃-N) concentrations in mg/L.

 Table 1: Summary of the main physical characteristics of the six catchments monitored within the Agricultural Catchments Programme.

 The annual average total rainfall, total river flow, runoff coefficient, mean river flow and flow "flashiness" Q10/Q90 (10th flow percentile/90th flow percentile) for data 2010–2019

| Catchment | Size [km²] | Geology | Elevation (range) [metre above sea level] | Rainfall [mm/yr] | River flow [mm/yr] | Runoff Coeff. | Mean flow [m³/s] | Q10/Q90 |
|-----------------|---------------|--------------------------------|---|---------------------|-----------------------|------------------|---------------------|---------|
| Ballycanew | 12 | Rhyolite, Slate | 19–230 (211) | 1037 | 506 | 0.49 | 0.194 | 73 |
| Castledockerell | 11 | Slate, Siltstone | 18–215 (197) | 1015 | 528 | 0.52 | 0.188 | 26 |
| Corduff | 3 | Greywacke | 110–221 (111) | 1051 | 559 | 0.53 | 0.063 | 67 |
| Cregduff | 30 | Limestone | 27-62 (35) | 1195 | 170 | 0.14 | 0.162 | 18 |
| Dunleer | 10 | Greywacke, mudstone | 26–223 (197) | 869 | 419 | 0.48 | 0.126 | 54 |
| Timoleague | 8 | Sandstone, siltstone, mudstone | 2–122 (120) | 1100 | 679 | 0.62 | 0.163 | 27 |

The experimental design was similar across all six catchments. The biophysical and socioeconomic data collection started in 2009 and include the following:

• Surface water in the catchment river outlets: river discharge (Q), electrical conductivity (EC), temperature,

turbidity and nitrate-N, total reactive P (TRP), total P (TP) and total organic carbon (TOC, since 2018) concentrations (every 10 min).

Surface water in multiple sites along the river networks: nitrate-N, TP, total dissolved P (TDP), TRP, dissolved

reactive P (DRP), dissolved organic carbon (DOC), EC, pH, dissolved oxygen (DO), oxidation–reduction potential (ORP), turbidity and metals (monthly).

- Groundwater in focused study sites: piezo-metric water level (every 30 min), and nitrate-N, TP, TDP, DRP, DOC, EC, pH, DO, ORP, turbidity and metals sampled in multilevel monitoring wells (monthly).
- A weather station is located centrally in each catchment, from which current data are publically available at www.acpmet.ie: air temperature, soil temperature, relative humidity, rain, solar radiation, wind speed/direction for estimation of potential evapotranspiration (PET) (every 10-min) and additionally, a second rain gauge located at higher ground.
- Aquatic ecology is surveyed twice a year in multiple sites along the river networks: diatoms and macroinvertebrates are assessed (every May and September).
- Soil sampling at the field scale (every 4 yr, maximum sampling unit 2 ha, to 0–10 cm depth): pH, liming requirement (LR), P, K and Mg content.
- Land management data supplied by the DAFM are added to more detailed information collected by advisors and data recorders.
- Socioeconomical and attitudinal surveys of catchment farms have been compared and supplemented with data from the National Farm Survey (NFS).

Additionally, each catchment has been surveyed for soil type, topography (LiDAR <1 m) and geology (EM3/EM37, two-dimensional resistivity, seismic refraction and ground-penetrating radar on representative fields).

Why so much data?

High-frequency monitoring of streamflow and stream water chemistry was recognised as a requirement to target the knowledge gaps for the underlying mechanisms to nutrient loss to water (Bol et al., 2018). The approach allows the capture of the full dynamics of nutrient loss to water over a year, without being skewed to specific sampling events or periods, and provides insights into water quality during both low-flow and high-flow conditions (Cassidy & Jordan 2011; Jordan et al., 2012a; Jung et al., 2020). Synchronous highfrequency water quality and discharge data provided new possibilities to analyse nutrient transfer pathways. The loadograph recession analysis was introduced to identify and quantify nutrient transfer pathways (Mellander et al., 2012a, 2012b). It was further used to detect subtle changes in water quality, needed for analysing the influences of large-scale weather systems on water guality (Mellander et al., 2018). High-frequency monitoring of hydrochemistry has also proved useful for interpreting low-frequency sampling, validating and designing sampling strategies (Cassidy et al., 2018), and to develop empirical models using low-cost surrogate variables

for more costly monitoring of P concentrations (Minaudo *et al.*, 2017) and load apportionment models based on low-frequency sampling (Crockford *et al.*, 2017). Within the ACP the setup of high-frequency monitoring is also often used as an educational platform for visiting students, scientists and stakeholders.

Soil analysis and nutrient management

Soils are one of the fundamental elements of the experimental design in the ACP. In the context of the nutrient transfer continuum, they are both the source and a recipient of nutrients and their impact is influenced by the physical setting, land management and climate. The difference in physical and chemical properties of soils regulates the flow of water through a catchment, and the transfer of nutrients and contaminants. The soils are therefore also crucial for the mobilisation potential of nutrients in each catchment.

Spatial and temporal soil sampling

The ACP has highlighted the importance of a multi-scale monitoring approach to decrease N and P losses. These include national, catchment, farm, field and soil process scales, for a complete overview and understanding (Wall *et al.*, 2012). Trends in soil P status, fertiliser P inputs and surplus P availability can be misrepresented at larger scales (national, catchment, farm scale) due to incomplete availability of data and information and may be better represented at smaller scales (field, soil process scale) where management and soil factors can be quantified and accounted for.

Almost the entire area (79–88%) of the ACP catchments is audited on a field scale, or at least *ca*. 2 ha, as a part of a soil sampling campaign, taking place approximately every 4 yr. The agronomic soil samples were collected using the standard operating protocol to the depth of 0–10 cm and analysed for the basic soil fertility status. The basic soil test includes soil pH, available P and K (Morgan's reagent) and lime requirement.

The resulting high-resolution soil database has multiple functions in the ACP. It provides information on both nutrient use compliance regulated by the NAP and the ongoing trends in nutrient status of soils. For example, the soil data from ACP catchments showed a large spatial variability in soil test P (STP) at the farm and field scale, indicating scope to correct imbalances with better nutrient management and redistribute P to lower status soils, potentially increasing P use efficiency and decreasing P loss risk (Wall *et al.*, 2012). Furthermore, long-term trends in soil P status supplemented by farm-gate P balances suggest that the regulations outlined in NAP have a positive effect. This was reflected in a decreased proportion of P index 4 soils (excessive P) and improvement in on-farm P use efficiency (Murphy *et al.*, 2015). The data also show scope

for improvement; however, soil P responses and trends differ between catchments and land use (McDonald *et al.*, 2019). The soil census data were also combined with additional studies carried out in catchments, where ancillary soil chemical and physical information provides the links relating to nutrient loss pathways to groundwater and surface waterbodies (Mellander *et al.*, 2016; Thomas *et al.*, 2016a, 2016b; Dupas *et al.*, 2017) or for identification of critical source areas (CSAs) (Thomas *et al.*, 2017).

Nutrient management planning

The multiple benefits of good soil NMP were the initial and most significant factor that encouraged farmer engagement with the programme. Results from the repeated soil analysis were used by the advisors to provide advice to farmers on baseline soil fertility and trends resulting from farm practice. When the programme started, tillage farmers showed greater interest in soil analysis results. However, the trends in soil fertility following subsequent soil sampling campaigns have improved nutrient management practice also for grasslandbased sheep, beef and dairy farmers.

Schulte et al. (2010) and Wall et al. (2013) examined the predicted soil P decline expected from the implementation of a specific Water Framework Directive (WFD) measure on farms. In fields with historically high soil P concentrations and for worst case scenarios of high Total P and STP starting points, the average time to the boundary (index 3) was estimated at 7-15 yr, depending on the field P balance (Schulte et al., 2010). Using P-balance scenario deficits of -30, -15 and -7 kg P/ha, for two predominantly arable and two grassland catchments with excessive STP, Wall et al. (2013) estimated an average of 5-20 yr for agronomical optimum levels to be reached. Under the largest P deficit scenario (-30 kg P/ha), it was forecast to take between 2 and 10 yr. These studies highlight the likely time lag that exists between implementation of soil P mitigation regulations and the desired outcome of few or no fields with excessive soil P. Murphy et al. (2015) focused on the P transfer continuum in a dairy-dominated and highly stocked (catchment average of 1.94 livestock units/ha) grassland catchment with free-draining soils. Over a 3-yr period the area in P index 4 decreased by 25% and this reduction in P source pressure was made while maintaining farm productivity and with financial returns comparable to the top 10% of dairy farms nationally. This indicated that nutrient source pressure can be reduced while maintaining or improving production and profitability. In an arable catchment it was found that the actual field-scale P balances, in addition to farm-gate P balances, are required to identify pressures of P, since enhanced or maintained legacies may occur within the agricultural landscape (McDonald et al., 2019). The distribution of P across the fields was sometimes poor within farms, especially where livestock manure was the source of nutrient. There was often a mismatch between the distribution of imported manures and the crops and soil P requirements at the field scale. There is an ongoing need for improved support that can deliver better farm- and soil-specific P NMP strategies for farmers.

The ACP produced colour-coded farm maps of soil fertility levels using a geographical information system (GIS). This was the initial stage in the development of the Teagasc NMP Online (https://www.teagasc.ie/about/our-organisation/ connected/online-tools/teagasc-nmp-online/). which was supported by feedback from a workshop of catchment farmers trialling the system. NMP Online has since been developed to handle a complex legislative and compliance framework that governs the management of nutrients and protection of waters. The system has grown due to increased demand from farmers and agri-consultants. There are currently more than 800 farm advisors nationwide, with over 230,000 plans on the system. The demand is further driven by policy changes from DAFM. Farmers value the benefits of optimum soil fertility and policy stakeholders have recognised the positive impacts that NMP can have on water quality. Currently 70% of the 300 ACP farmers have an "NMP Online" plan for their farm, and while a significant portion still use it for regulatory compliance reasons, the number using these plans for agronomic purposes has increased from one-third to over half. While tillage farmers are still more likely to use NMP Online for agronomic reasons, the greatest increase in this practice has taken place on grassland farms following the establishment of soil fertility trends on farms within the catchments.

Water quality

The hydrological flow paths that transfer nutrients are largely controlled by the physical settings of the agricultural landscape (Bieroza et al., 2020). The physical controls are topography, land use, soil and bedrock permeability and will influence the transfer pathways, transit times, storage and connectivity. There are also chemical and biological controls that all together influence the timing and location of nutrient delivery. The chemical controls are those affecting sorption, speciation and transformations, and the biological controls are those affecting the fixation and uptake of nutrients. Changes in drivers such as weather and agronomic pressures will further influence the dynamics and trends of nutrient loss to water and the influence of both point sources and diffuse sources of nutrients (Mellander & Jordan, 2021). There were both different magnitudes and seasonality in N and P concentrations and river discharge as monitored in the catchment outlets (Figure 2).

In a homogenous landscape, the nutrient losses would hypothetically be directly reflected by the source loading.

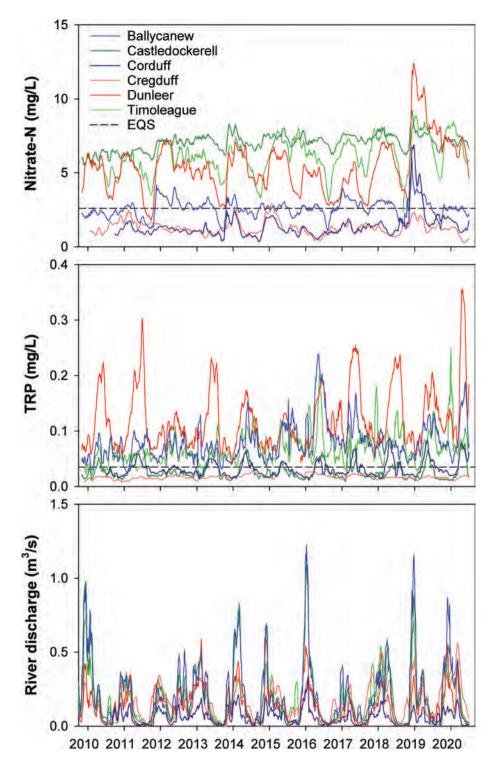


Figure 2. Time series of nitrate-N (NO₃-N) concentration, total reactive phosphorous (TRP) concentration and river discharge monitored on a 10-min time step in the catchment river outlets for the period October 2009–September 2020. The values are expressed in monthly antecedent simple-moving averages on a daily time step. EQS = environmental quality standard, 2.60 mg/L for nitrate-N and 0.035 mg/L for TRP. Stream water total oxidized N (TON) concentration was monitored using Hach–Lange Nitratax SC-Plus UV instruments, assuming TON was equivalent to nitrate-N (Melland *et al.*, 2012). The TRP concentration of the stream water was monitored using Dr Lange Phosphax–Sigmatax suite of instruments and the river discharge was calculated from established rating curves from water level recorded via OTT Orpheus Mini vented-pressure instruments as described in Jordan *et al.* (2012a).

However, for the same amount of rainfall and surface area (mm and hectare), the losses of nitrate-N and TP to water over 10 yr varied highly between the six catchments. There was no clear link between nutrient source loading and nutrient mass loads leaving the catchments when normalising the mass load to both catchment area and the amount of rainfall (Figure 3). The physical setting can override the source pressure (Jordan et al., 2012b; Mellander et al., 2012a; Shore et al., 2014, 2016). There was a large difference in loss of nutrients to water due to soil drainage (Jordan et al... 2012a). A catchment with mostly poorly drained soils had three times higher total P loss, for the same stream flow, than a catchment with mostly well-drained soils, despite similar soil nutrient sources (Mellander et al., 2015). Information on land use and management may also be required to predict relative differences in particulate P concentrations during flow events (Melland et al., 2012; Shore et al., 2014). Examples of chemical controls associated with the soil chemistry as a controlling factor for P solubility and retention were also found within the ACP catchments. For example, in two mostly groundwater-fed catchments, a catchment with iron-rich soils had three times higher loss of reactive P to the stream, via leaching to shallow groundwater, than the other catchment with aluminium-rich soils (Mellander et al., 2016). The ironrich soils encouraged P loss via a soluble form. Mobilisation processes may drive both N and P exports in groundwaterfed catchments (Dupas et al., 2017). Iron-rich soils have also been found to enhance the loss of medium-sized colloidal P (Fresne et al., 2020). In a karst spring zone catchment, with calcium- and aluminium-rich soils, P was instead largely retained and despite thin soils and numerous karst features the P loss was low and reactive P concentrations remained below the environmental quality standards (EQS) (Mellander et al., 2012b, 2013).

The N removal capacity also varied highly between and within two groundwater-fed catchments (McAleer et al., 2017). At the catchment scale, there was a poor link with the surplus nitrate-N leached to the groundwater and the concentrations of nitrate-N monitored in the river outlet. For example, in one of the sites the nitrate-N concentration in the shallow aroundwater was locally and temporarily elevated to 23.9 mg/L due to a ploughing and pasture reseeding event. This pulse of nitrate was not detected in the stream, likely due to the locally high N removal capacity in the near-stream zone of that catchment and due to mixing of deeper groundwater (Mellander et al., 2014). Based on the dominating controls, catchments were classified into "source risky", "mobilisation risky" or "transfer risky" in order to interpret the response to changing climate (Mellander et al., 2018). Three broad scenarios of P controls in river networks were further identified by Vero et al. (2019): i) a diffuse/groundwater pathway control with a similar P concentration across the river network, ii) an instream and persistent point-source control with discrepancies in water and sediment chemistry at specific locations within the river network, and iii) a mixed-control scenario.

Critical source areas

The problem of diffuse pollution can be conceptualised with a source-mobilisation-pathway-delivery model (Haygart *et al.*, 2005), whereby the combination of high source risk areas and strong connected pathways leads to CSAs. However, identifying the locations of these areas is a key problem across different spatial scales within catchments. Defining CSAs of diffuse pollution in agricultural catchments depends upon the accurate delineation of hydrologically sensitive areas (HSAs) at highest risk of generating surface runoff pathways. An important factor is also the hydrological connectivity, and in particular at scales where CSAs can be managed (Shore

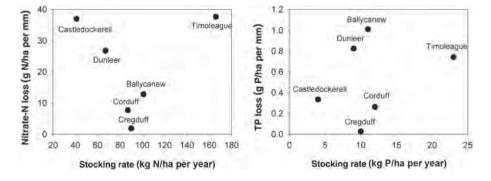


Figure 3. The annual average mass loss of nitrate-N (left panel) and total phosphorus (TP; right panel) in the catchment river outlets (2010–2019), normalised against the amount of rainfall and catchment area, plotted against the annual average stocking rate (2010–2018). The nitrate-N and TP mass loads were calculated from the concentrations and river discharge monitored on a 10-min time step in the catchment river outlets (Jordan *et al.*, 2012a; Mellander *et al.*, 2012a). Rainfall was monitored in the central lowland of each catchment (Mellander *et al.*, 2012a). Stocking rates were supplied by the Department of Agriculture Food and the Marine (DAFM).

et al., 2013). While ditches and drains enhance the hydrological connectivity, an understanding of their physical characteristics, spatial distribution and effect on fine sediment retention/ transfer was used to develop management strategies for the reduction of downstream P transfers (Shore et al., 2015). For example, over-engineered ditches slow down water flow allowing sediments to settle. Periodic removal of fine sediment and maintenance of channel bank vegetation would then help to minimise P transfers from these catchments (Shore et al., 2015). Another approach developed within the ACP used GIS, combining digital elevation maps with information on hydrological and chemical controls. This approach could identify sub-field-scale CSAs and surface pathways of P losses and stream channels at highest risk (Thomas et al., 2016a, 2016b, 2017). Such information combined with insights into nutrient mobilisation and transfer pathways gained from methods using high-frequency hydrochemistry data could complement environmental schemes and NMP. The model has been further developed by the Environmental Protection Agency (EPA) into national CSA maps of diffuse soil P losses that quantify P loads in surface runoff (https://gis.epa.ie/EPAMaps/Water).

Critical transfer times

While targeted mitigation strategies require consideration of the spatial heterogeneity in the controls, targeted mitigation should also consider the seasonality in nutrient loss to water (Jordan et al., 2012a). A closed period for nutrient application was introduced across the Republic of Ireland in 2006 by regulation referred to as GAP. The closed period represents a 3-mo winter period critical for nutrient loss to water, as nutrient uptake by plants is low and there is a high potential for runoff due to low evapotranspiration, saturated soils and frequent rainfall. Critical times for nutrient mobilisation and transfer in runoff to streams were evaluated by Shore et al. (2016). While there was no evident pulse of increased P losses at the start of the open period, there were high P concentration events related to incidental losses from storms. Regulations were suggested to be augmented with advice on antecedent soil moisture conditions for farmers to make better decisions on the time and place to spread slurry. Nutrient concentrations in streams can also increase during low-flow periods, typically in summer when baseflow is low. This indicates point-source influences that may become disproportionate and elevate nutrient concentrations well above the EQS during a critical time for the aquatic ecology (Shore et al., 2017). A reduction in point sources is required to improve river ecological quality, and both farm and non-farm point sources should be targeted (Melland et al., 2012).

Time lags and catchments scales

Both hydrological and biogeochemical time lags occur along the nutrient transfer continuum following a change to the source of N or P. It is important to be cognisant of these delays when monitoring and assessing water quality (Vero et al., 2017, 2018). In a small karst spring zone, the hydrological time lags were months to years and the biogeochemical time lags were decades (Fenton et al., 2017). At the catchment scale of the ACP catchments, time lags generally range between 1 and 10 yr (Melland et al., 2018). The length and nature of a transport pathway are important as the residence time and biogeochemical environment will determine whether dissolved solutes, such as N and P, will be retained, transformed and/ or attenuated by biogeochemical processes (Vero et al., 2019). At the catchment scale, permeability of the catchment was found to be one of the most important characteristics in understanding the time lags present. However, on smaller scales such as the meso-scale or field-scale the influence of soil type, biogeochemical processes and local weather events can dominate the impact of geology. Knowledge of the biogeochemical and meteorological processes is necessary to understand the time lags present (Mellander et al., 2018).

Climate change

Variations in weather conditions may influence how successful mitigation measures are. In the ACP catchments, there were both changes to temperature and rainfall intensity, and these are both important drivers of nutrient mobility and transfer in soils (Mellander et al., 2018; Mellander & Jordan, 2021). Also, a number of extreme weather events were observed, such as floods and droughts (Mellander & Jordan, 2021) and snow events (Vero et al., 2020). The number of extreme weather events are increasing and should be considered in nutrient mitigation strategies. An increased winter rainfall and/or reduced periodicity may provide conditions when more of the landscape and more of the nutrient sources are hydrologically connected to rivers and cause rain-induced nutrient flux. The occurrence of droughts can cause a build-up of a large soil nutrient pool due to poor plant growth and enhanced soil mineralisation. The nutrient pool can then be transferred to a river when the rain comes. Such a situation was observed in all six ACP catchments when a large pulse of nitrate-N occurred after the summer drought during the November rains in 2018 (Figure 2). The reduced stream flow during droughts can also enhance the negative influence of point-source pollution (Mellander & Jordan, 2021).

There are also long-term shifts in weather patterns, as expressed by the North Atlantic Oscillation (NAO) index, influencing both N and P concentrations in northwest (NW) Europe (Mellander *et al.*, 2018). This can result in either exacerbating or diluting the nutrient loss to water. A clearer understanding of the combined effect of climate drivers, source management and hydrological and chemical controls in the landscape was recommended. Simplified integrated climate–hydrochemical indicators are useful for shaping future policy in managing and mitigating nutrient loss to water and can be considered at the field scale and up to the functional landscape scale (Mellander *et al.*, 2018).

While large-scale changes by weather systems such as the NAO influence the decadal trends in nutrient concentrations in terrestrial waters (Mellander *et al.*, 2018), short-term weather extremes may offset baseline nutrient concentrations, enhance nutrient loads and alter the type of nutrient loss risk. Strategies to mitigate nutrient loss need to consider the effects of both long-term climate changes and the more frequently occurring short-term weather impacts (Mellander & Jordan, 2021).

There were both inter-annual and inter-seasonal trends in weather parameters over a 10-yr period. The nitrate-N and P concentrations in three of the catchments were either without trend, were stable or increased, with differences between the catchments that matched the conceptual understanding. The inter-annual trends were in some cases not reflected by inter-seasonal trends and were in other cases influenced by changes in only some months of the year. Specific months may influence or even counteract the inter-annual trends (Mellander & Jordan, 2021).

Sediment loss and aquatic ecology

The key controls for suspended sediment transport are soil type and land use. For example, arable farming on low permeability soils was particularly prone to sediment loss (Sherriff et al., 2019). The pathway for this transport was primarily through surface runoff driven by rainfall events, and thus catchment soil erosion risk can be classified according to soil drainage characteristics and land-use type (Sherriff et al., 2019). Suspended sediment export from five of the six ACP catchments was low in comparison to values for the UK and mainland Europe. This is likely due to greater density of landscape features such as hedgerows and drainage ditches which reduced field sizes and act as natural mitigation measures reducing the velocity of surface flow and thus the kinetic energy available to mobilise and transport suspended sediments (Sherriff et al., 2015). Assessment of the origins of suspended sediments found that field top soils, channel banks and roads were particularly vulnerable to sediment erosion in ACP catchments (Sherriff et al., 2018).

Deposited fine sediment was found to be the most pervasive stressor in the ACP catchments, confirming a growing number of studies in Ireland which have highlighted suspended sediment as posing a significant risk to macroinvertebrate communities in agricultural streams (Davis *et al.* 2018, 2019). Suspended sediment loads were associated with greater stress to macroinvertebrates than either N or P concentrations, although the negative influences of suspended sediment loads were exacerbated by the presence of elevated N and P concentrations (Davis *et al.*, 2019).

Emerging contaminants

Modern agricultural practices include the use of agrochemicals such as pesticides and pharmaceuticals. In Ireland, the phenoxy herbicide MCPA (2-methyl-4-chlorophenoxyacetic acid) is frequently used to reduce and inhibit rush (Juncus spp.) cover on grasslands and certain broadleaf weed species (Morton et al., 2020). The compound is highly susceptible to contaminate both surface and groundwater due to its high water solubility and low soil adsorption. While legislative steps have been taken to govern the control and use of pesticides, the national monitoring of drinking water resources has shown an increase in the number of public water supplies that are failing to meet the legislative standards (EPA, 2017). In Irish groundwater bodies, there were more pesticide metabolites present than the parent active ingredients themselves (McManus et al., 2017). Morton et al. (2020) identified a need for more knowledge on mobilisation and transfer processes of MCPA to be able to identify mitigation and treatment measures. Acid herbicides were detected in private drinking water wells (some exceeded recommendations) and were present in the rivers all year in two hydrologically contrasting catchments within the ACP, even though these areas are not associated with herbicide pollution in water. While the concentrations peaked in summer, associated with land application and low river flow, the mass loads were higher in winter suggesting restricted degradation and persistence of the herbicides in the soil, sub-surface and sediments (Khan et al., 2020). McGrath et al. (2019) recognised that for better management of surface and groundwater, it is useful to be able to forecast pesticide residues in soils in real time and developed a new stochastic model developed to account for rainfall variability after application.

For the first time, a newly developed and comprehensive analytical procedure (Mooney *et al.*, 2019, 2020a) allowed for an extensive assessment of pharmaceuticals and transformation products in Irish groundwater (Mooney *et al.*, 2020b, 2021). The occurrence of anti-coccidial veterinary drugs, mainly from poultry activity, was found to be the contaminant of concern for groundwater (Mooney *et al.*, 2021). Also anthelmintic, anti-parasitic veterinary drugs were frequently detected in groundwater and transformation products were more prevalent in groundwater than in surface waters. Temporal variations, likely linked to drug usage and weather, were observed in karst springs. This clearly demonstrates the requirement for a safe use also of pharmaceuticals.

Catchment economics and socioeconomy

Indicators of environmental sustainability

Data from the Teagasc NFS were used for socioeconomic research during the early stages of the ACP, while farmer engagement was being developed. A series of farm-level

sustainability indicators for Ireland were developed using data from the Teagasc NFS. Four dimensions, reflecting the multifaceted nature of sustainability, economic, environmental, and social and innovation were included. Indicators around the sustainable use of N and P at farm level were further developed and showed an average N and P use efficiency of 36.7% and 79.6%, respectively, across all farm systems (including tillage) (Buckley *et al.*, 2015a).

Further studies estimated farm-gate N balance and use efficiency across 150 dairy farms in the NFS over the period 2006–2012. The N balance declined by 25.1 kg/ha from 180.4 to 155.3 kg/ha over the study period. This was attributable to reduced chemical N fertiliser inputs of 23.1 kg/ha. Nitrogen use efficiency improved by 2.1% over the period from 20.8% to 22.9%. Nitrogen balance and use efficiency were significantly influenced by factors such as fertiliser prices, stocking rate, land-use potential, contact with extension services and climatic variables (Buckley et al., 2016a). For the same period, farmgate P balance and use efficiency were estimated across 150 dairy farms in the NFS. The P balance declined by 50% from 11.9 to 6.0 kg/ha. The decline was caused by reduced chemical P fertiliser inputs of 6.5 kg/ha. However, P use efficiency improved by 18% from 60% to 78%. The P balance and use efficiency were found to be significantly influenced by factors such as fertiliser prices, stocking rate, land-use potential, use of milk recording technology, contact with extension services and rainfall patterns (Buckley et al., 2016b).

The role of efficiency in the utilisation of N and P applications was found to have a positive effect on both environmental and economic returns to the farm. The average over-application of chemical fertilisers ranged from 22.8 to 32.8 kg N/ha and 2.9 to 3.5 kg P/ha in 2008, which were the same or greater than the losses to leaching and runoff for N and P from similar intensive agricultural land uses. Potential cost savings on chemical fertilisers across all farm systems ranged on average from €38.9/ha to €48.5/ha. Potential cost reductions on imported feeds of €65 to €84 per livestock unit were indicated for the dairy farms in the study versus efficient benchmark farms. Average excess of imported feedstuffs equated to 5.82-7.44 kg/LU of N and 0.92-1.17 kg/LU of P. Such reductions have the potential to deliver a double dividend by reducing the risk of diffuse nutrient losses from agricultural land while improving economic margins at farm level (Buckley & Carney, 2013).

In the current phase of the ACP, two data recorders are using NFS protocols to collect socioeconomic data from catchment farms. This will enable comparisons with the national data set, and substantiate the sustainability indicators against the biophysical environmental monitoring in the programme.

Farmers attitude and behaviour

To investigate farmer subjective opinions on the implementation of the EU ND, a Q methodology was used. Results indicated

four main opinion groups, and while farmers were sceptical of the validity of certain NAP measures, there was a growing acceptance among some farmers of environmental benefits accruing from the regulation (Buckley, 2012). Research has also shown that farmer motivations play a role in the adoption of nutrient management best practice. Specifically, farmers classified by "farm stewardship", "ecocentric" and "productivist" considerations were more likely to adopt a greater number of the nutrient management best practices. Demographic and structural variables such as age, off-farm employment status and contact with extension services were found to be significantly related to the probability of adoption of nutrient management practices examined (Buckley *et al.*, 2015b).

Public preference for good water quality (WFD objectives) was evaluated by asking 650 adults how much of a tax increase would they be willing to pay (WTP) to get all rivers in Ireland up to the standard required for the WFD, having been previously given a background to the WFD and water quality in Ireland. Mean WTP was €19 per respondent per annum and was influenced by their social class, perception of household financial status, education, amount of water way recreational use, personal environmental values/apathy and which river basin district they lived in (Buckley *et al.*, 2016c).

Uptake of mitigation measures

In a survey of all catchments, 53% of the farmers indicated a negative preference for provision of a fenced 10-m riparian buffer zone under a 5 yr scheme. Willingness to adopt the proposed buffer zone was influenced by the economic, attitudinal and farm structural factors. The mean payment required by those willing to adopt the measure was estimated at $\leq 1.51/m$ of linear stream reach (Buckley *et al.*, 2012). National survey data showed that 9–15% of farmers nationally would be WTP for poultry and pig manures and a further 17–28% would import manure if offered it on a free-of-charge basis. The demand for these manures is strongest among arable farmers, younger farmer cohorts and those of larger farm size with greater expenditure on chemical fertilisers (Buckley & Fealy, 2012).

A technology acceptance model (TAM) was used to investigate the key factors which influence farmer adoption of an online NMP. The TAM identifies two psychological constructs, perceived usefulness (PU) and perceived ease of use (PEOU), which are believed to be key factors in technology adoption. Results indicate that PU and PEOU of an NMP are positively and significantly related to a farmer's intention to adopt and use the technology in the future. However, PU, which captures the perceived benefits in terms of usefulness, is the main driver of technology adoption (McCormack & Buckley, 2018). There were difficulties involved in the implementation of agri-environmental policies due the variety of actors involved. A participatory approach, including stakeholders with conflicting interests, was used to select P transfer mitigation policies. Stakeholders were found to be diverse, and perceived effectiveness is based on groupspecific operational and social factors. There was also a need for integration of conflicting opinions in policy design, and a bottom-up approach to decision making. Improved KT is also required between interested actors (Micha *et al.*, 2018).

Knowledge exchange and stakeholder engagement

The ACP advisors provide a service to all farmers with land in the catchment, regardless of enterprise type. Most of the advisors' contact with clients is one-to-one, through on-farm visits, consultations and phone calls concerning all aspects of the farm business and not just water quality and soil fertility issues. Advice is provided on farm husbandry, production, schemes, regulatory compliance and financial performance. In addition to one-to-one advice, the ACP advisors also facilitate discussion groups attended by farmers from the catchments. This can be a very effective and efficient method of KT, but it is important to be aware that many farmers are not members of such groups. Farmer engagement in the ACP would not be at the level it is if the advisory services were limited to catchment science and water quality issues alone. The good advisor-client relationship is evident in the number of ACP farms that have facilitated research through siting of monitoring and experimental sites, and even suggesting research topics applicable to the NAP review. In addition, the broad focus of the advisory service facilitates the collection of environmental, economic and production data from the farms.

The meteorological data collected for research from the seven automated weather stations within the catchments generate interest from farmers local to the catchment areas. Current weather information for each of the catchments, updated every hour, is now publicly available online (www. acpmet.ie). These data support decision making on timing of nutrient application, improving agronomic response and reducing the risk of loss. Avoiding early nitrogen applications when soil temperatures are below that required for appreciable grass growth (6°C) is an example. Localised weather forecast provided by Met Éireann has been added to the web site, further aiding farming decisions. There are typically between 200 and 400 page views per wk, but during the month of February decisions are being made on when to first apply N, and page views increase to between 400 and 500.

The role of catchment advisors is also to disseminate research generated by the programme to the wider farmer audience

and other stakeholders. Visiting farmer discussion groups are regularly hosted by the ACP across all six catchments. Ideally, the group will visit a catchment with similar farming systems and/or water quality issues to their own farms. This ensures a focused and topical discussion. Other KT activities include presentations to visiting third-level college courses, agricultural students, farmer courses, policy agencies and researchers. Findings from the ACP are also disseminated through scientific journals, popular press, radio interviews, Twitter and YouTube.

Extended baseline monitoring and catchment modelling

The baseline data collection in the ACP has in its current phase been extended to align with the WFD and include measurements of greenhouse gas (GHG), ammonia emissions and soil carbon sequestration across the catchments.

Eddy covariance towers (ECTs) will be deployed in the catchments to provide *in situ*, high-resolution (10 Hz) measurement of carbon dioxide (CO₂), water vapour (H₂O) and methane (CH₄) in air. The main objectives will be to examine long-term (>4 yrs) GHG fluxes for different land uses (arable and grassland) as well as examine how soil drainage, management practices, land-use change and climatic drivers impact on the magnitude of GHG fluxes.

Monitoring of ammonia (NH_3) will be conducted using ALPHA (Adapted Low-cost Passive High Absorption) and DELTA (DEnuder for Long-Term Atmospheric sampling) methods. The monitoring will be conducted at the ACP catchment scale and samplers will be spatially distributed to provide a representative concentration of NH₃ within a specific catchment. For a better understanding of the impact of farm management practices on NH₃ loss, the emissions of NH₃ will be modelled.

Measurement of soil organic carbon (SOC) will be quantified in chronosequences at each ECT site: ≥ 0.5 m depth at various incremental depths (e.g. every 10 cm) and corrected to the equivalent soil mass. This combined soil-core analysis with ECT flux measurements approach will help to quantify how much carbon is transferred from plants (root and shoot litter) to soil organic matter and elucidate the mechanisms responsible for C stabilisation in agricultural soils.

To advance the research priorities of the ACP, a comprehensive set of modelling objectives have been established. These objectives include the selection, development and adaptation of catchment models to simulate fluxes from both higherstocking-rate and lower-stocking-rate farms. Once baseline models have been developed, models will be up-scaled to larger catchments, river basin districts and the national level. Finally, the models will be utilised to test environmental impacts of future agricultural, regulatory and climate scenarios, to facilitate sustainable farming practices.

A two-track modelling strategy is being developed. In the first track, hydrologic modelling frameworks are being explored. as a means of adopting a flexible methodology to modelling. This will allow models to be constructed in a modular way, where the model complexity can be increased (or decreased) as required to simulate the target catchment. This allows us to tailor the models at each catchment to represent the different dominant hydrologic processes, and to better control and quantify model uncertainty at each step of increasing complexity. Over the last decade, a range of different modelling frameworks have been developed, such as Catchment Modelling Framework (CMF) (Kraft et al., 2011), Structure for Unifying Multiple Modelling Alternatives (SUMMA) (Clark et al., 2015), Raven (Craig et al., 2020) and Mobius (Norling et al., 2021). These frameworks all have similar conceptual underpinnings, but vary in their relative strengths and weakness, which are currently being reviewed with respect to suitability to the ACP modelling programme. The second track is focused on the use of established "stand alone" models, where models capable of simulating fluxes across the soil-water-atmosphere system at the catchment scale will be tested and applied. The advantage of this approach is that models can be applied relatively quickly at the larger catchment/basin scale for purposes such as scenario testing (e.g. climate scenarios, BMP implementation). A wide range of established hydrologic models will be explored, which may provide a good representation of catchment processes.

Conclusions

Using a holistic approach of agro-environmental studies in six *ca*. 10 km² river catchments, the ACP has provided research for an improved process-based understanding of nutrient loss to water in heterogeneous agricultural landscapes, under changing weather patterns and intensified agriculture. The research provided ongoing support for environmental schemes and NMP. In its current phase the ACP combines monitoring of water quality, GHGs, ammonia, soil C sequestration and socioeconomy all in one programme, in order to facilitate sustainable farming practices. Some key findings are listed below:

- (1) Catchment controls can override nutrient source pressures. There was no clear link between stream N and P concentrations and nutrient loading at small catchments scale. Targeted and efficient mitigation measures are required.
- (2) In some catchments, long-term weather shifts, as expressed by the NAO, influence both N and P concentrations in the catchment rivers. The catchments

respond differently to these changes depending on their physical and chemical settings.

- (3) Weather changes can override trends of source pressures. Both long-term weather shifts and short-term weather shocks need consideration and may require different mitigation strategies.
- (4) There are time lags between agricultural pressures and water quality state. The response time mostly increases with catchment size. Time lags need consideration when linking agricultural pressure to water quality state.
- (5) Spatiotemporal information on pathways and delivery sites can facilitate targeted and efficient mitigation measures to encompass the impact of climate change. Results from the ACP can provide transferable information to scale up to larger areas.
- (6) Following heavy rainfall, stream P concentrations were gradually reduced during the "closed period" for spreading organic manures. Storm P concentrations did not increase in the 4-wk period after the end of the "closed period". Advice on soil moisture conditions can facilitate better decisions on time and location for slurry spreading.
- (7) Most of the sediment losses came from stream bank/bed erosion and road losses on the more common land uses. Soil permeability largely influenced the sediment loss.
- (8) Sediment was the most pervasive stressor on stream macroinvertebrate communities. Improving river ecological quality requires improved management of sediment inputs and influence of point sources in low flow.
- (9) Safe use of pesticides and pharmaceuticals is required. Herbicides were detected in private drinking water wells and were present in the rivers all year: concentrations peaked in summer and mass loads in winter. Anticoccidial veterinary drugs and anthelmintic residues were detected in groundwater. There is a need to identify mitigation measures and/or alternative treatments.
- (10) There is room for improvement in reaching agronomical/ environmental goals. The distribution of P sources can be improved. At the field scale, there was often a mismatch between P inputs and the crop/soil P requirements. There is a need for improved support to knowledge exchange mechanisms that can deliver better farm- and soil-specific NMP strategies.
- (11) The role of efficiency in the utilisation of N and P applications has a positive effect on both environmental and economic returns to a farm.
- (12) A growing acceptance of environmental benefits from regulation was found. The likelihood of adopting certain nutrient management practice is related to demographic and farm structural factors.
- (13) Economic, attitudinal and farm structural factors influence the willingness to adopt a mitigation measure such as a buffer zone.

(14) Knowledge exchange is required for effective NMP. Farmers prefer a flexible NMP approach combining a durable map with a table. Factors such as fertiliser prices, stocking rates, land-use potential, use of milk recording technology, contact with extension services and rainfall patterns influence the P balance and use efficiency. Advisory support is required.

Acknowledgements

This study was made within the Agricultural Catchments Programme (ACP) funded by the Irish Department of Agriculture, Food and the Marine (DAFM). We thank the farmers for their cooperation and access to their land. We thank Dr. Karl Richards and current members of the Agricultural Catchments team: Maria Merriman, Una Cullen, Simon Leach, David Ryan, Eamonn Harty, Eilish O'Sullivan, John Kennedy, Kevin Madden, Mark Boland, Meadhbh Murphy, Oisin Coakley, Sean Hegarty, Suzanne Neary, Syed Faizul Islam and Tom O'Connell. We also thank all previous members of the team, Walsh Fellow students linked to the programme and staff of the Teagasc Johnstown Castle Environmental Research Centre.

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Special Issue Article • DOI: 10.15212/ijafr-2020-0143 IJAFR • 61(1) • 2022 • 218-228



Irish Journal of Agricultural and Food Research

An outline of achievements in selected areas of forest research in Ireland 1960–2021

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Abstract

In this paper, we provide an overview of achievements in forest research in Ireland carried out by various agencies over the past 60 yr. Many of the outcomes of the research have ensured that policy and practice are well-founded, and many of the research results form the basis of current forest standards and practice. Forest research has, and will continue to have, a significant role in national policy development and international reporting commitments. The achievement of future goals and targets is increasingly dependent on the maintenance of the goods and services that forests provide; these can be enhanced through the establishment of new forests and by appropriate management of the resource (e.g. The EU Green Deal and EU Forest Strategy). We outline the current state of knowledge which can be used to inform afforestation goals and the importance of tree improvement, forest management and forest protection to improve competitiveness and sustainability. Research into forestry and carbon provides a focus on the opportunities and challenges of climate change to Irish forestry. Future efforts will involve longer-term monitoring of environmental change commensurate with the forest rotation to reduce the uncertainties associated with climate change. Research into forestry goals. Reducing the impacts of biotic attack through efficient surveying, disease monitoring and assessing future risk is likely to be the focus of future research effort.

Keywords

Climate change • forest policy and practice • forest research • Irish forestry

Background to forest research in Ireland

Since the early 20th century, Irish forest policy has focussed on the restoration of forest cover and considerable progress has been achieved; forest cover has increased from 1.5% of the land area in 1900 to 11% of the land area in 2020. Early forestry establishment practice was informed by trial plantings, learned experiences and shared knowledge from Britain and Europe, the former whose programme shared many similarities with the Irish programme. The 1950s saw a rapid expansion in state planting, with national policy targets of 10,000 ha/yr. The demand for eligible land to support the new programme (land deemed unsuitable for productive agriculture) resulted in crops being planted on previously avoided areas (O'Carroll, 1962). In 1957, a research branch was established in the Department of Lands to provide technical information to assist the expanding state afforestation programme. The research branch had a mandate to conduct a forest inventory of state and private forests and included a soils and nutrition section whose work focussed on species selection, innovations in soil cultivation techniques and fertiliser application. Research into thinning and spacing of forest crops, forest genetics, forest pathology and vegetation control was added as the research branch became more established (Gallagher, 2021). Research into wood resource utilisation was conducted by the Forest Products Department of IIRS/Eolas/Forbairt based in Glasnevin in 1963. From this basis, the concept of career forest researchers working in specified areas was established and researchers became recognised national experts. From the mid-1970s to the mid-1980s, the research branch had

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42 permanent staff. 14 of whom were permanent researchers. 20 field foresters, 3 lab technicians and 5 support staff. In 1989, the forest enterprise and the research branch were vested in a newly established state forestry company. Coillte Teoranta. It focussed on operational research and tree improvement. In the 1990s, Coillte rearranged its research effort into five key areas: genetics and tree improvement; crop structure; silviculture; site studies; and forest protection. However, forest research effort was gradually phased out with tree improvement research and development continuing up until 2015. Early research was also conducted by An Foras Taluntais (now Teagasc) as part of the National Soil Survey (1958–1990) focussing on the capacity of Irish soils to grow various forest crops (Bulfin et al., 1973) and latterly research on the potential of farm forestry as a viable farming enterprise (Frawley & Leavy, 2001).

In 1992, the National Council for Forest Research and Development (COFORD) was set up to coordinate national forest research and fund competitive research projects; this role was subsequently taken up by Department of Agriculture Food and the Marine (DAFM) in 2009 and remains part of the Firm/Stimulus/COFORD call for competitive research. The competitive call for proposals from COFORD has resulted in the emergence of forest research providing organisations (RPOs) at the third level (e.g. University College Dublin (UCD), National University of Ireland-Galway (NUIG), Waterford Institute of Technology (WIT), University College Cork (UCC), Trinity College Dublin (TCD), University of Limerick (UL)) and encouraged the increased involvement of Teagasc in contract forest research (Hendrick, 2017). Many of the outcomes of forestry research programmes have been incorporated into policy and practice (e.g. codes of forest practice, national forestry standard). In more recent years, research is reflecting the increasing awareness of the services provided by forests and there has been a growing awareness of the environmental role and impact of forests (Hendrick, 2010). The requirements to meet national and international commitments on climate change, biodiversity, water quality and forest health are becoming increasingly important drivers of forest policy (e.g. the Kyoto Protocol and the Paris Agreement). The European Green Deal (European Commission, 2019) also puts a focus on ensuring healthy and resilient forests so that they can contribute significantly to biodiversity and climate goals, reduce and mitigate natural disasters, while securing livelihoods and supporting a circular bioeconomy and rural communities. The role of research to address the potential negative impacts of climate change, increase sustainability and the circular bioeconomy is becoming increasingly important.

The objective of this paper is to provide the reader with an overview of forest research achievements across areas relating to forestry practice and policy covering the last 60 yr. The review is intended to provide the reader with a

perspective on how the outcomes of research have informed policy and practice and the potential role of this and future research to assist in the achievement of sectoral targets and wider national and international goals.

Establishing new forests

Increasing forest cover is at the heart of current government policy to develop a competitive and sustainable forest sector and is central to the government's Climate Action Plan (DAFM, 2014; Anon, 2019a). Here, we look at research which may assist policy development in this area.

To achieve planting targets of 8,000 ha/yr, additional land will be required to be planted; is this feasible? Farrelly & Gallagher (2015a) identified an area of 3.75 million ha of land suitable for afforestation in Ireland, of which 1.3 million ha was classified as marginal agricultural land. In the 1980s, Bulfin (1987) performed a similar analysis and concluded that much of the marginal agricultural land had the potential for forestry to provide good yields over relatively short rotations, providing alternative sources of incomes for farmers. As a result, many farmers on marginal land availed of forestry grants and premiums to plant, particularly in the 1990s and 2000s, and many owners' forests have reached the final harvest age. The technical feasibility of planting land is well established and forms current operational practice (Forest Service, 2015). The outcomes of early research succeeded in providing guidelines to enable tree growth on a range of soils, with a limited history of agricultural usage (e.g. O'Carroll, 1962, 1975). However, as better land has been planted, opportunities to diversify species and plant broadleaves will require prior knowledge of the species site requirements. Much of the current knowledge base for species selection comes from practical research and development and uptake by state foresters, supplemented by knowledge of similar species and soils in the UK and wider afield. While disseminated within the state sector, many research outcomes were not formally published in peer-reviewed journals. Some of the results were synthesised in the COFORD book "A Guide to Species Selection" published in 2003 (Horgan et al., 2003).

Research into species selection can provide a deeper understanding of the cause-and-effect mechanisms that affect forest tree growth and yield, the aim being to predict the forest growth for investment decisions or to quantify the impact of climate change on the species growth (Farrelly *et al.*, 2011). Vegetation and indicator species have been used to provide an indication of the inherent wetness and nutritional status of soils and their suitability for various tree species (Anderson, 1950). More recently, vegetation criteria have been used to provide an assessment of the eligibility of land for afforestation grant aid (Farrelly & Gallagher, 2015b).

To assess national and regional opportunities for afforestation. soil maps, such as those completed by the National Soil Survey (An Foras Taluntais 1958–1990; now Teagasc), can be used to assess the potential of forest tree species based on the occurrence of certain soil types (e.g. Conry & Clinch, 1989). Advancements in geographic information systems (GIS) have used these principles to assess the suitability of Irish soils for forestry (Loftus et al., 2002). In recent years, more complex GIS modelling techniques incorporate multiple competing land use objectives to provide a more realistic assessment of the amount of land available for afforestation (Farrelly & Gallagher, 2015a). The advent of climate change creates uncertainty in the current state of knowledge surrounding tree species selection and new research into the adaptive potential of key forest tree species to climate change in Ireland is necessary (Farrelly, 2021).

Forest genetics and tree improvement

Tree improvement is at the heart of increasing the competitiveness of the forest sector and offers the potential to increase carbon sequestration and harvest output. Here, we consider the advancements in tree breeding over the last 60 yr.

Tree improvement has been conducted in Ireland since the 1950s, with most of the early work focussing on provenance testing (Fennessy et al., 2012). Early provenance testing focussed on lodgepole pine (Pinus contorta Douglas), assessing provenances that offered a combination of acceptable yield and acceptable stem form (Pfeifer, 1993). In the 1960s and 1970s, an extensive provenance testing of Sitka spruce (Picea sitchensis (Bong.) Carr) took place. Results of the trials confirmed that selecting Sitka spruce origins from the southern part of its native range (Washington and Oregon) provided significant increases in productivity of up to one yield-class (2 m3/ha per year) over conventional Queen Charlotte Island sources (Pfeifer, 1984). Based on these results, Coillte, the Irish Forestry Board, recommends the planting of Washington and north Oregon seed origins for all sites except those above 300 m and those that are susceptible to autumn frosts (Thompson et al., 2005). For some species, provenance selection may be the final step in the tree improvement process, mainly because further returns on any investment on breeding are likely to be low (or even negative) (O'Reilly et al., 2014). For Sitka spruce, an improvement programme has been in place since the 1970s and individuals (parents) have been selected for breeding based on their progeny achieving a 15% increase in height gain over an untested control (Thompson, 2013). Typically, parent trees are grafted and put into seed orchards to produce improved seed, and Coillte currently has seed orchards of Sitka spruce

and Lodgepole pine, for use in its reforestation programme. Research as part of the DAFM FORM project focussed on developing methods for early selection of improved parents and assessment of the performance of full-sib families under drought conditions (Grant *et al.*, 2016). More recently, the GeneSIS project hopes to evaluate the potential of using genomics and genomic selection tools to accelerate the Sitka spruce tree improvement programme (Farrelly *et al.*, 2020). The research hopes to identify good parental combiners using genomic and progeny test data to develop a genomic prediction model; the aim is to reduce the time associated with progeny testing (often 15+ yr). The impacts of the Sitka spruce improvement programme are estimated to generate a potential annual benefit of \in 5.7 million, assuming an annual planting programme of 9,000 ha/yr (O'Reilly *et al.*, 2014).

Research into broadleaved tree improvement has been conducted by Teagasc since the late 1990s and is focussed on the development of a sustainable supply of improved, adapted and healthy seed and plant material to satisfy the European Union (EU) Forest Reproductive Material (FRM) regulations. The research to date has brought about the commercial supply of improved birch (Betula spp.) and alder (Alnus glutinosa L. Gaertn.) seed which is available to farmers and landowners wishing to plant broadleaves (Sheridan, 2021). Other research carried out as part of the DAFM FORM project seeks to select ash (Fraxinus excelsior L.) genotypes which show tolerance to the ash dieback disease (Hymenoscyphus fraxineus (T. Kowalski) Baral, Queloz & Hosoya) and identify the primary method of infection of ash plants (Nemesio-Gorriz et al., 2019). The research is focussed on identifying genotypes which show tolerance to the disease. Tolerant genotypes have been sourced after screening under high disease pressure in Lithuania, and others have been obtained by sourcing tolerant genotypes from European institutions. A gene bank of selected material has been established in Co. Kilkenny, and further research will continue to monitor which genotypes continue to show tolerance to the disease.

Forest management

The EU Green Deal (EC COM [2019] 640) and the New EU Forest Strategy for 2030 (European Commission, 2021) promotes the sustainable production of timber from wellmanaged forests. In the following section, we consider research in broadleaved management and timber forecasting.

Broadleaved management

The production of high-quality sawlog is dependent on timely management. A management intervention carried out decades prior to felling can have a large impact on whether the timber is high grade and suitable for sawlog, or low grade and suitable for firewood. Considerable loss of expertise in broadleaved management exists in Ireland; this can be traced back to the Industrial Revolution, when the importance of growing highquality stems for industrial needs was less important as iron and steel displaced many timber products (Bulfin & Radford, 2001). Thus, the decline in management of broadleaves required research commensurate with the renewed interest in planting broadleaves. Early work in broadleaved management focussed on the establishment and management of broadleaf species to replace those cleared for fuel and food production during the Second World War for use as shelterbelts (Petrie, 1943). The growing of ash for hurley production was a subject of much research. Fitzsimons & Luddy (1986) provided the silviculture prescriptions for growing of ash for hurley production, incorporating planting rate, fertiliser, protection from browsing and thinning. Other options for growing ash included the planting of ash in mixtures with silver fir (Abies alba Mill.), Norway spruce (Picea abies (L.) H. Karst.) or noble fir (Abies procera Rehder). The use of the mixture provided protection from frost and exposure and served to suppress ground vegetation and provided much-needed revenue in the early years through the sale of Christmas trees (Fitzsimons & Luddy, 1986). Further research by Culleton & Bulfin (1992) and Culleton et al. (1995) examined the impact of vegetation control on the early height growth of ash concluding that it was vital for rapid and consistent establishment. Research into the management of young broadleaved crops concluded the benefits of formative shaping - the pruning of young trees - with the objective of producing a single straight stem of at least 5 m in length with small branches that will guickly die at the onset of canopy closure leaving the bole virtually defect free (Kerr, 1992). Research conducted by Bulfin & Radford (1998a, 1998b) on formative shaping on eight broadleaf species concluded that formative shaping improved stem form over that period and should commence ideally when the trees are 1.0 - 1.6 m in height. As better land was beginning to be planted by farmers in the early 1990s, COFORD published a book, "Growing Broadleaves" (Joyce et al., 1996), to assist practice development and an updated publication, "Broadleaf Forestry in Ireland" (Huss et al., 2016), which integrates forest research across soils, forest genetics, silviculture, forest growth and yield. More recent research has focussed on early tending and thinning of broadleaved crops and developing methods for rehabilitating poorly performing broadleaved stands where research is used to inform management practice (Short & Hawe, 2012, 2018).

Timber forecasting

Efficient forest management requires estimates of stand development and productivity to enable forest managers to plan operations and arrange timber sales and for financial managers to forecast costs and revenue. The British Forestry Commission

vield tables have traditionally been used for forecasting production in Irish stands since the first table was produced in 1953 (Hummel & Christie, 1953). The yield tables are based on the vield class system (the maximum mean annual increment of a stand) and allow growth projections to be made following a prescribed management regime (Edwards & Christie, 1981). While the range of yield classes available covered yield class 6-24 m³/ha per year, early indications from assessments of the growth of Irish stands suggested that the yield classes in Ireland were often more than this range, owing to differences in growth rate, tree form and provenances grown in Ireland (Joyce & O'Carroll, 2002). This precipitated the development of yield tables for lodgepole pine in 1966 (Gallagher et al., 1987). The increased use of mathematical models and, later, computers assisted developments in yield research as it allowed complex functions to be fitted to large datasets and provided flexibility to incorporate diverse management objectives which were not dependent on a defined course of management. As a result, dynamic yield models were developed for Sitka spruce, Norway spruce and Douglas fir (Pseudotsuga menziesii (Mirbel) Franco) (Broad & Lynch, 2006), followed by the development of yield models for ash and Japanese larch (Larix kaempferi (Lamb.) Carr.) (McCullagh, 2013). The Irish dynamic yield models are available from COFORD as a software program called Growfor and are used primarily to assist the management of forest stands and produce forecasts for even-aged monospecies stands. Another yield model called Carbware has been developed for use in Irish forestry and has been used to assess carbon stocks in Irish forests (Hawkins & Black, 2012). The Carbware model is a single-tree growth model that simulates carbon dynamics in the forest, is useful at the individual tree level and can be used for uneven-aged and mixed stands. Single-tree modelling is data intensive, requiring that each tree is measured, and data costs and computing time can be significantly greater than those of stand model approaches. Future research may require re-development of models to incorporate the impact of genetic improvement and climate change and their impact on the growth and yield of forest crops.

Forest protection

Ensuring healthy and resilient forests is central to the new EU forest strategy for 2030 (European Commission, 2021); in this section, we consider two areas where research can assist with these objectives, notably windblow and insect pests and diseases.

Windblow

Given the climate and historical trends in planting, it is not surprising that the most significant abiotic factor causing damage to forests in Ireland is wind. Climate change is expected to bring about an increase in the frequency and intensity of winter storms in Ireland (Ní Dhubháin & Farrelly, 2018). Wind causes trees to be uprooted (windthrow) or break (windsnap), leading to significant financial losses for forest owners (Nieuwenhuis & Fitzpatrick, 2002). The impact of these storms can also result in the provision of ideal breeding grounds for insects and fungi (Peltola, 2006). Research has shown that management of forests, particularly on poorly drained soils, can result in the onset of windblow. In a survey of research plots by Gallagher (1974), those which had been unthinned suffered less damage than thinned plots. In a study of forests in Northern Ireland, the effect of altitude, soil type, and aspect were factors linked to increased windblow with high elevation sites, planted on gleyed soils on windward slopes, being more vulnerable to windblow (O'Cinneide, 1974). Hendrick (1989) and Rodgers et al. (2006) investigated the impact of site cultivation methods on tree stability and concluded that the force required to overturn trees planted on mole drains was greater than those planted where furrow ploughing had been used.

Useful tools have been developed to assist forest managers to quantify the risk of windblow. Ní Dhubháin *et al.* (2001, 2009) produced a model to predict the probability of windthrow risk in Sitka spruce stands based on site and crop factors. The model requires the height of the forest (risk increases as height increases), thinning status (thinning increases risk), soil type (risk is higher on poorly drained soils) and site elevation (risk increases with increasing elevation). Future research should build on established research and focus on methods for mitigating risk, especially as the frequency of winter storms is expected to increase. Forest management operations and those which predispose forest stands to windblow need further study (Ní Dhubháin & Farrelly, 2018).

Insect pests and diseases

In the 1950s, a strategic forest protection research programme was set up by the research branch of the Forest Service. Early work included an investigation into pine shoot dieback (putatively linked to Pullularia pullulans (de Bary) G. Arnaud) (de Brit, 1967) and group dieback (causal agent Rhizina undulata Fr.) of conifers (McKay & Clear, 1955). Research into the ongoing threat of fungal pathogens such as Heterobasidion annosum (Fr.) Bref. which caused heart rot of many forest species was conducted by McAree (1975) and subsequent control resulted in the use of urea on tree stumps to promote the growth of saprophytic fungi and limit the opportunities for the spread of the pathogen. Often collaborative work with the UK facilitated the quick discovery of pathogens and surveys for Dutch elm disease (Ophiostoma ulmi (Buisman) Melin & Nannf.) in Ireland (Mangan & Walsh, 1980) were conducted after it had been discovered on elm

(Ulmus glabra Huds.) several years earlier in Britain. It is likely that the increase in the numbers of threatening nonnative pests and pathogens being detected in Ireland can be linked to imports of lumber and wood packaging material as far back as the 1970s (e.g. O'Connor & Nash, 1979). In 1977, the first species-specific horizon scans for current and future pest threats were carried out for Sitka spruce (de Brit & McAree, 1977). Extensive work has also been done on control methods for the large pine weevil (Hylobius abietis L.) (e.g. Dillon et al., 2006); however, the pest remains a serious issue on reafforestation sites and control measures are becoming more difficult as pesticide options are becoming more limited. The outbreak of Phytophthora ramorum Werres, De Cock & Man in 't Veld. in Japanese larch provided insights into the pathogen behaviour and efficient controls (O'Hanlon et al., 2017). The ash dieback epidemic has resulted in research to understand the epidemiology of the pathogen (Burns et al., 2017) and more latterly to understand optimal ways to control the disease and in the selection of tolerant genotypes (DAFM funded FORM and NEXCELSIOR projects).

The FORM project provided additional horizon scanning and pest risk assessment research findings for the benefit of Irish forestry (Truffen & Grogan, 2018). Preventative research through EU and the European and Mediterranean Plant Protection Organisation Pest Risk Assessments has succeeded in identifying over 200 EU-regulated pests and pathogens and protected zones to exclude pests indigenous to Europe from areas they are not already present. Routine surveys and protective measures are being implemented to prevent establishment of such pests in Ireland (Anon, 2019b) and updates to the regulated lists are recommended as research progresses (Anon, 2019c).

Forestry and carbon

Ireland's commitment to emission reduction under the Kyoto Protocol (UNFCC, 1997) and Paris Agreements (United Nations, 2015) has resulted in significant research effort to provide increased knowledge about the carbon balance in forest ecosystems.

Research into forest carbon sequestration of Irish forests began to be funded by COFORD in the early 2000s, beginning with the CARBiFOR project (Black & Farrell, 2006). Research focussed on improving inventory-based estimates of forest carbon sequestration in the most commonly occurring Sitka spruce dominated forest type in Ireland. An ecosystem approach was used to examine stocks and fluxes between the soil, tree and ground debris/vegetation pools. Biometric inventories of chronosequence sites were used with biomass models to estimate tree biomass and carbon accumulation

(Tobin & Nieuwenhuis, 2007), Deadwood (Tobin et al., 2007) stocks were also examined, as were soil (Saiz et al., 2007) and tree respiration. Eddy covariance measurements from a core research site (Dooary, Co. Laois) were used to estimate the net ecosystem exchange, which was used to validate estimates made based on inventory-based measurements (Black et al., 2009). The research was instrumental in determining that over the first Kyoto commitment period from 2008 to 2012, annual sequestration rates were higher than previously reported (4-8 t C/ha per year compared to 3.36 t C/ha per year as reported by Kilbride et al. (1999). Research included the development of a national accounting software system for forestry called CARBWARE (Hawkins & Black, 2012) which estimated that Irish forests sequestered 17 Mt CO₂ eq. during the period 2008–2012, representing 20% of Ireland's national greenhouse gas emissions reduction target for the period (Black et al., 2012).

Further research by Saunders et al. (2012) reported a climate-dependent impact of thinning on forest carbon uptake. Higher air temperatures and solar radiation in the growing season following the thinning were responsible for an immediate compensatory increase in photosynthesis by the remaining trees. Forest soil carbon stocks have been investigated by Wellock et al. (2011b), who found that the afforestation resulted in no significant changes in soil carbon, citing the high degree of uncertainty arising from a low sampling number. For the estimation of peat soil stocks, Wellock et al. (2011a) found peat depth and type to be significant factors. Byrne & Milne (2006) found that the afforestation of peat soils resulted in net emissions of carbon, but this finding depended heavily on a range of assumptions regarding the rate of peat carbon loss. However, Byrne & Farrell (2005) demonstrated that losses due to afforestation of blanket peat soils could be compensated by carbon taken up by tree growth. However, the difficulties presented by the drying of such large carbon stores by forests growing on peat soils, as anticipated by Farrell & Boyle (1990) and Tomlinson (2005), will continue to be a challenge for future management in light of expected changes in climate (Jovani-Sancho et al., 2021).

Forestry economics

Early economic research focused on qualitative analysis of planting policy with reference to the area planted (Attwood, 1964) and critiques of the poor quality of the land being acquired for planting by the state. Given the focus on increasing afforestation rates, it is not surprising that the comparison of agriculture and forestry in terms of land use change is a frequent point of discussion in the early literature (Clear, 1948), later analysed in detail in Frank Convery's work

(1973). Other early topics of interest included assessing the wider benefits of the forest estate in relation to its economic value (Durand, 1992) and the social impact of forestry (Convery, 1970; Clinch, 2000). Research into the economics of crop types was conducted for lodgepole pine (O'Driscoll, 1980) and Sitka spruce (O'Brien, 1986). The economics of timber production and the relative merits of management operations such as spacing and re-spacing to improve returns were studied by O'Brien (1981) and the economic merits of thinning by Gerely & Phillips (1999). The 1970s and the oil crisis saw research into the economics of wood energy (Neenan, 1977) and short rotation forestry (Neenan & Lyons, 1981). Research into the timber processing sector was also conducted to include sawmilling and the economy by Convery (1981), while Anderson et al. (1994) examined the wood processing and forest products wood chain.

The 1970s and 1980s saw early research into biodiversity (Long & Whelan, 1984), and recreation economics were examined by Murphy & Gardiner (1983). Later studies of the ecosystem services provided by forests included the "tourists" perception of the landscape (O'Leary *et al.*, 1998), forests and water quality (Kelly-Quinn *et al.*, 1997), the role of forest carbon sequestration (Hendrick & Ryan, 2001) and the amenity value of forests (Hynes *et al.*, 2007). Bullock *et al.* (2016) undertook a comprehensive review of ecosystem services and their valuation, while more recently, Duffy *et al.* (2020) examined the impact on water quality of agriculture replacing forests.

Research into the factors influencing planting accompanied the rapid uptake of forestry grants by farmers (e.g. Ní Dhubháin & Gardiner, 1994; Ní Dhubháin, 1995; McCarthy et al., 2003). However, as planting rates began to decline in the 2000s, research into the barriers to farmer planting was initiated. McDonagh et al. (2011) found that the most important barrier to afforestation was that farmers needed their land for agriculture and the permanent nature of the planting decision. The relativity of agricultural and forest incomes was investigated by Behan & McQuinn (2005), while Ryan et al. (2017) investigated the impact of taxation and benefits. Duesberg et al. (2013) undertook qualitative analyses to provide more nuanced information on farmers' attitudes to forestry that concurred with findings from a detailed farm-level quantitative analysis (Ryan et al., 2018), namely that while financial drivers are important, other factors such as nonpecuniary benefits (Howley et al., 2015) are also important drivers or barriers to land use change.

Discussion and conclusion

It is sometimes stated that research meets society's needs only when it contributes to policy aims being met. However, research also has a role in ensuring that policy goals are well founded, so research must inform policymakers, as well as practitioners, through scientific, timely and effectively communicated information. This review is intended to give a perspective on some of the outcomes of forestry research over the last 60 yr and how many have been taken up in policy and practice (e.g. Code of practice and Forestry Standards Manual [Forest Service, 2000, 2015]). Perhaps the most important goal commensurate with forest policy is to increase forest cover. Recent low planting levels suggest that there is an uncertainty as to whether goals and targets can be achieved. The outputs of research have informed afforestation scenario modelling and had a significant impact in providing input to forest policy development and public discourse on forestry in relation to economic impact of forestry. To achieve desired afforestation targets, the work of Farrelly & Gallagher (2015a) suggests that in principle sufficient land resources exist to increase forest cover, while the research of Ryan et al. (2018) suggests that considerable effort will be required to initiate future land use change, perhaps requiring a deeper understanding of the drivers of land use change. The incorporation of behavioural economics, particularly in relation to long-term decisions and attitudes associated with afforestation, is necessary. The importance of carbon as an ecosystem service is a key driver, and further research in relation to its implications for carbon policy needs to be conducted. The role of harvested wood products in carbon sequestration and the circular economy will only increase in importance.

Research in forest establishment, particularly on the nutrition of forest crops (e.g. O'Carroll, 1975), did much to enable tree growth on a range of soils associated with early state afforestation which was confined to marginal and submarginal soils to avoid competition with agriculture (Gray, 1964). This research contributed significantly to continuing wood production and harvest on these soils. Research on species selection synthesised in the book by Horgan et al. (2003) has been instrumental in informing the Forest Service, who use it to inform the list of approved species and provenances for afforestation. The benefits of various tree improvement programmes are currently being realised with the availability of improved seed for various tree species (e.g. Thompson, 2013). The outcomes of this research will play a key role to increase carbon sequestration, improving the quality of timber products from forests and increasing the competitiveness of the forest sector. The uncertainties posed by climate change are creating uncertainties in Irish forestry. Increasing the knowledge base of how tree species respond to climatic stresses will become increasingly important to evaluate tree planting decisions to promote forest health and resilience of the resource (Farrelly, 2021).

Forest management decisions have been assisted by the development of Growfor, a dynamic yield model for forest management which has been the outcome of much research into crop growth and yield (e.g. Broad & Lynch, 2006) and is widely used within the forest sector to forecast future growth and yield of stands and the likely impact of management interventions on crop development.

Methods to mitigate the risk of windblow will be necessary which may include alternative management strategies, these will require further research (Ní Dhubháin & Farrelly, 2018). To assist the development of broadleaved silviculture which was lacking, many research outcomes on soils, forest genetics, silviculture and forest growth and yield have been incorporated into two significant publications on practice – *Growing Broadleaves* (Joyce *et al.*, 1996) and *Broadleaf Forestry in Ireland* (Huss *et al.*, 2016) which serve as important reference guides for broadleaved forest management.

The significant afforestation programme in Ireland over the last two decades has resulted in the sequestration of a large quantity of atmospheric carbon. Research to quantify the carbon resource (e.g. CARBiFOR) has been instrumental in assisting the development of a national greenhouse gas accounting system to UNFCCC to Tier 2 and Tier 3 levels which is used for national reporting. However, the management of this carbon store and the forest resource has acquired a consequent responsibility. The impact of disturbances caused by management interventions such as thinning and clearfelling operations, as well as abiotic factors such as fire and wind and biotic factors, has a consequence for greenhouse gas dynamics in forests. It is essential therefore to maintain long-term forest monitoring datasets, where both biometric and flux measurements can be directly associated with climatic factors. Opportunity for the combined use of remote sensing with inventory measurements to monitor changes in forest health and aboveground carbon mass may assist the process (McInerney et al., 2011). The continued provision of ecosystem services requires that the resource is adequately protected. Some of the outcomes of forest protection research have been incorporated into advice and practice, notably in pine weevil control and the Forest Service schemes to control and replace Chalara-infected stands. New research into the basic biology of forest pests is necessary. Further research into pre-emptive methods and pest risk analysis (e.g. Truffen & Grogan, 2018) will be necessary to be better prepared for biotic challenges.

Acknowledgements

The authors would very much like to thank Dr. Gerhardt Gallagher for providing background information on the

activities of Research Branch, Department of Lands. We would also like to thank an anonymous reviewer whose suggestions have succeeded in improving the article. Thanks also to Oliver Sheridan for an update on the status of the Teagasc birch and alder improvement programme.

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