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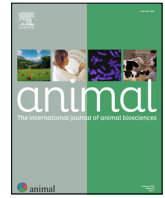
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Animal board invited review: Genomic-based improvement of cattle in response to climate change



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ABSTRACT

Climate change brings challenges to cattle production, such as the need to adapt to new climates and pressure to reduce greenhouse emissions (GHG). In general, the improvement of traits in current breeding goals is favourably correlated with the reduction of GHG. Current breeding goals and tools for increasing cattle production efficiency have reduced GHG. The same amount of production can be achieved by a much smaller number of animals. Genomic selection (GS) may offer a cost-effective way of using an efficient breeding approach, even in low- and middle-income countries. As climate change increases the intensity of heatwaves, adaptation to heat stress leads to lower efficiency of production and, thus, is unfavourable to the goal of reducing GHG. Furthermore, there is evidence that heat stress during cow pregnancy can have many generation-long lowering effects on milk production. Both adaptation and reduction of GHG are among the difficult-to-measure traits for which GS is more efficient and suitable than the traditional non-genomic breeding evaluation approach. Nevertheless, the commonly used within-breed selection may be insufficient to meet the new challenges; thus, cross-breeding based on selecting highly efficient and highly adaptive breeds may be needed. Genomic introgression offers an efficient approach for cross-breeding that is expected to provide high genetic progress with a low rate of inbreeding. However, well-adapted breeds may have a small number of animals, which is a source of concern from a genetic biodiversity point of view. Furthermore, low animal numbers also limit the efficiency of genomic introgression. Sustainable cattle production in countries that have already intensified production is likely to emphasise better health, reproduction, feed efficiency, heat stress and other adaptation traits instead of higher production. This may require the application of innovative technologies for phenotyping and further use of new big data techniques to extract information for breeding.

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Implications

Climate change increases the importance of adaptation to the changing environment and efficiency traits to reduce greenhouse gas emissions in cattle breeding. Increased production has already reduced greenhouse gas emissions in many global cattle populations. Genomic selection would allow cattle breeding in developing countries to intensify their production and adapt to the changing environment. To reach sustainable and resilient production in already intensified populations, adaptation, feed efficiency, fertility and health may be more important traits than increasing production. More studies are needed to ascertain the relationships between these traits and greenhouse gas emissions.

Introduction

The Intergovernmental Panel on Climate Change (IPCC) concluded that there is a clear link between rising greenhouse gas (GHG) concentrations in the atmosphere and the increasing frequency and intensity of extreme weather events (IPCC, 2021). Climate parameters important in cattle production include temperature, humidity, solar radiation, cloudiness and precipitation. Climate has a direct effect on the living environment, but weather also affects the quality of livestock feed. The changing climate increases the pressure on cattle to adapt to the changing environment.

Global food production is experiencing challenges due to climate change and a predicted increase in the human population (Food and Agriculture Organisation [FAO], 2013). At the same time, global living standards are increasing, which has led to increased use of animal products (FAO, 2013). As the IPCC (2021) stated in its report, “the influence of human activity on the warming of

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the climate system has evolved from theory to established fact". Livestock production produces GHGs such as methane. Global livestock methane emissions increased by approximately 25% from the period 1990–1999 to 2008–2017, mostly due to the increase in animal numbers (IPCC, 2021). Thus, the demands on livestock production seem contradictory: increased production and lower GHG emissions in a challenging environment.

The global cattle population both contributes to and suffers from the effects of global warming. Research into reducing the global footprint of cattle is important as a medium- to long-term strategy (Pryce and Haile-Mariam, 2019). The traits to be considered in mitigating the impacts of cattle production and adaptation to climate change are typically complex and polygenic. These include feed efficiency, fertility, resistance and tolerance to diseases and pathogens, tolerance to heat and other extreme weather conditions, general robustness and levels of methane production (Mirkena et al., 2010; FAO, 2015; Kantanen et al., 2015). Thus, the reduction of GHG emissions from cattle and adaptation of cattle to the changing climate may need to be included in breeding objectives.

Currently, the most accurate breeding value estimation is based on genomic selection (GS) (Meuwissen et al., 2001). However, the initial cost of GS is high due to the need to genotype many reference animals such that an accurate genomic prediction model can be calculated to be used in the estimation of breeding values for the genotyped candidate animals. Among the 33 member countries of the International Bull Evaluation Service (Interbull, Interbull.org) for dairy cattle, only 23 countries have so far provided national genomic evaluation forms. Because GS allows the selection of animals after birth using DNA information, genetic progress can be faster than with traditional approaches such that the initial costs of GS can be justified. In practice, GS can offer an efficient approach for evaluating hard-to-measure traits, such as GHG emissions and adaptation (Hayes et al., 2013; Pryce and Haile-Mariam, 2019).

In the following sections, we outline a global perspective on cattle production and climate change, briefly explain GS and consider its role in breeding cattle in response to climate change. Breeding cattle to mitigate GHG emissions and adapt to climate change is considered in three sections: breeding towards lower greenhouse emissions, improving feed efficiency, and breeding functional and adaptive traits. Selective breeding can lead to reduced genetic diversity, which can threaten and limit future breeding options. We review concerns on global genetic variation and genomic introgression as an approach to improve adaptation. Finally, we discuss future opportunities.

Global challenges

In the last two decades, climate variability and extreme weather events have increased. Together with global economic recessions, now deteriorated by COVID-19, hunger has increased and programmes to reduce malnutrition have diluted, particularly in low- and middle-income countries (FAO, 2021). Nevertheless, the population and income increases have increased the demand for livestock products (FAO, 2013; Komarek et al., 2021). The world population is predicted to increase from 7.2 billion to between 9 and 10 billion people by 2050. Worldwide, the FAO (2013) estimates that dairy and meat consumption will increase by 58% and 73%, respectively, over 2010 levels by 2050. Komarek et al. (2021) predict an increase in the use of livestock-derived protein by 38% over 2020 levels by 2050.

The global share of anthropogenic emissions attributed to livestock is about 14.5% (FAO, 2013). Beef cattle and dairy cattle have a share of about 35% and 30% of total livestock emissions, respec-

tively, while beef and cattle milk as commodities have a share of 41% and 20%, respectively. The three main GHGs emitted by livestock are methane (CH₄), nitrous oxide (N₂O) and carbon dioxide (CO₂). According to the Global Livestock Environmental Assessment Model (FAO, 2013), emissions (in CO₂-eq) from the livestock sector consist of 44% CH₄, 29% N₂O and 27% CO₂.

Livestock may also play a positive role. For instance, improvements in manure management and more emission-efficient feed production can allow a reduction in the use of N fertiliser and improve land carbon sequestration. Furthermore, new technologies can be used to reduce GHG emissions. According to an FAO report, "intensification—in terms of increased productivity both in food animal production and in feed crop agriculture—can reduce greenhouse gas emissions from deforestation and pasture degradation" (Steinfeld et al., 2006). Productivity has increased and GHG emissions have already decreased in some cattle populations. The main reason for this is that as productivity (milk yield, meat yield or growth rate) increases, the proportion of daily energy allocated to maintenance decreases and the maintenance requirement of the total animal population decreases. Increased production thus dilutes out the fixed cost (maintenance) over more units of production, reducing the total energy requirement per kg or per unit of milk yield, meat yield or growth and hence lower emission per unit of a product. For example, in the US dairy sector, feed, land and water use have been reduced by 77%, 90% and 65%, respectively, and emissions (CO₂-eq) per kg of milk have been reduced by 63% in 63 years, from 1944 to 2007 (Capper et al., 2009). In the US beef sector, the intensification has reduced emissions (CO₂-eq) per kg of beef by 16% in 30 years, from 1977 to 2007 (Capper, 2011).

Modern animal breeding tools have been developed and are in use in only a fraction of the world. The use of these tools in national dairy cattle evaluations is a requirement for membership of a country in Interbull. Currently, Interbull has 33 member countries: one is in Africa, three in the Americas, three in Asia, 24 in Europe, and two in Oceania. Climate change is a global challenge that needs global solutions. Modern breeding tools can either be put into use globally, or the new enhanced genetics can be imported. GS allows the use of an effective breeding approach at a lower cost than traditional breeding schemes (Schaeffer, 2006). However, the change in the breeding approach has changed the cost structure as well. While GS has reduced the costs for a breeding company to keep bull service stations, the genotyping costs can burden the farmer if not compensated by a breeding company. The cost distribution and the high initial cost of GS are important factors to be acknowledged when advocating GS for low- and middle-income countries. Animal breeding can be used to change cattle to meet the new external demands by using the latest advances in genetic technologies, such as GS.

Genomic selection and cattle breeding

The breeding of animals and plants is in the middle of a genomic revolution, in which genomic information is used through GS (Meuwissen et al., 2001). Genomic information implies the use of many DNA markers along the genome. These DNA markers are often single nucleotide polymorphisms (SNPs) and are used in the prediction of breeding values. In dairy cattle breeding, investments in genotyping began after the publication of theoretical ideas on transforming the breeding programme to be more efficient using GS (Schaeffer, 2006).

GS has been made possible by accurate and inexpensive genotyping (VanRaden, 2020). Genomic breeding values depend on the high quality of DNA samples, similar to the need for reliable pedigree information by traditional evaluations. In practice, it has been observed that approximately 50 000 SNP markers are enough

for genomic-based breeding value estimation, because livestock are selected within the population with many common ancestors, which allows DNA segments to be traced with only a few markers (VanRaden, 2020).

Meuwissen et al. (2001) described GS as the use of estimated genome-wide SNP marker effects in a reference population to predict the breeding values of selection candidates. A typical dairy cattle population has many non-genotyped but phenotyped individuals and pedigree information. Alternative approaches to genomic evaluation for GS exist, but single-step genomic BLUP is considered to be the best due to its theoretical properties (Aguilar et al., 2010; Christensen and Lund, 2010). In the single-step method, all phenotype, pedigree and genomic information are considered simultaneously, which supports unbiased predictions. In practice, a single-step model is like a traditional breeding value estimation approach augmented with genomic information. Because of the large additional computational requirements for genomic information, many computational approaches have been developed to ease practical implementation (Mäntysaari et al., 2020; Misztal et al., 2020).

GS has changed dairy cattle breeding schemes. The main reason for the change is that genomic information allows for estimating the breeding values of young animals more accurately than using a pedigree-based model. The reliability of genomic-based breeding values for young animals can be even higher than that of traditional evaluations for progeny-tested bulls (VanRaden, 2020). Consequently, more young sires have been selected than before and fewer elite sires are used. Thus, the generation interval has decreased, and the costs of keeping males have decreased. In future, the number of genotyped cows will increase further to support GS. This increase in the number of young genotyped animals with phenotypes can reduce the need to use old data and pedigree information in genomic prediction.

GS is a general breeding tool which has changed the genetic evaluation and the breeding scheme. The advantage of GS over traditional genetic evaluation (based on pedigree and phenotype data alone) is that genomic predictions allow a more accurate selection of animals early in life. Genotypes allow the use of phenotypes from distantly related animals in the estimation of breeding values for distantly related genotyped candidate animals in the same breeding population. Furthermore, a GS-based breeding scheme can be equally efficient with a lower number of phenotyped animals than a traditional progeny testing scheme where the daughter's phenotype increases the prediction accuracy of its sire but in GS, the whole reference population benefits through the genotyped sire. Therefore, GS is particularly suitable for predicting breeding values for traits that are difficult or too expensive to measure on a large scale such as fertility, disease resistance, feed efficiency and methane emissions (Hayes et al., 2013).

Breeding cattle in response to climate change

Breeding towards lower greenhouse gas emissions

Direct breeding goals for reduced GHG emissions need to consider the origin of enteric CH₄ emissions in ruminants. The rumen is a complex bioreactor, and CH₄ production is necessary to maintain rumen homeostasis (González-Recio et al., 2020). Because the biological limit of CH₄ reduction is still unknown, it is necessary to ascertain that selection against methane emissions does not harm feed digestion or animal welfare. The sizeable contribution of enteric fermentation to total agriculturally derived GHG emissions has led to extensive research efforts to develop approaches to reduce these emissions from ruminants (e.g. Fitzsimons et al., 2013).

One viable strategy to reduce CH₄ emissions is animal breeding. It allows a permanent and cumulative reduction of these emissions in a population (Negussie et al., 2017a; Pryce and Haile-Mariam, 2019). Breeding has been used to increase production which has reduced emissions per kg of milk produced (e.g. Capper and Cady, 2020). However, emissions may be reduced even faster by using GS to select traits that have a higher correlation with methane emissions than with production (Hayes et al., 2013; González-Recio et al., 2020). For this, Wall et al. (2010) and Negussie et al. (2017b) proposed three paths that could help reduce CH₄ via genetic selection: (1) improving productivity and efficiency (e.g. residual feed intake, longevity); (2) reducing wastage in the farming system; and (3) directly selecting on emissions, either on CH₄ or on a related proxy.

Whatever mitigation path is chosen, the correct knowledge of available genetic variation and the relationships between emission traits and production and functional traits is needed. Tables 1 and 2 provide summaries of the currently available literature on heritability estimates of emission traits and their genetic correlations with production, BW, fertility and health traits. A major challenge in calculating accurate parameter estimates is, in part, due to the inability to assemble large enough emission trait data. This is because, thus far, routine individual measurements of emission traits have been expensive (Negussie et al., 2017b). Although genomic prediction models allow equally accurate estimation with fewer phenotypes than non-genomic models, GS needs several thousand animals to be phenotyped (de Haas et al., 2017). International collaboration is essential not only for sharing phenotypes and genotypes but also for sharing ideas and experiences.

Methane is not yet part of the breeding goals of any dairy cattle breeding programme (de Haas et al., 2017). However, it is necessary to evaluate the consequences of different incentivisation or penalisation policies that might be implemented. Recently González-Recio et al. (2020), working on data from Spain, concluded that whether methane emission is considered a tax or a net energy loss for an animal, its effect on production and functional traits is expected to be minor if methane is incorporated into the breeding goal. Furthermore, including methane in the breeding goal as an economic loss for an animal or with the current carbon tax would slow this increment but would still lead to larger methane emissions per cow/year. This is because the genetic correlation between methane and production traits is positive (Table 2), and most income in the dairy industry comes from milk sales. When milk production per cow increases, fewer cows are needed to produce the same amount of milk. Consequently, total CH₄ emission is expected to decrease by 4–6% in 10 years, although the CH₄ emission per cow will increase (González-Recio et al., 2020). However, reducing the number of dairy cows reduces meat production in the dairy sector which may require increasing the number of beef cows to keep the same level of meat production. On the other hand, if the weight for fertility and health increases in the breeding goal but the weight for milk production decreases, GHG emissions can decrease and the number of cows will decrease at a lower rate than with a higher weight on milk production.

Current estimates of correlations between methane emission and other traits suggest that reducing methane emissions by breeding is likely to have only minimal effects on such traits as reproduction and health (Zetouni et al., 2018; Pszczola et al., 2019). However, CH₄ and milk production (e.g. López-Paredes et al., 2020), as well as DM intake (DMI) (Difford et al., 2019), are correlated. Selection against methane production can give healthy, fertile and long-living cows that emit less CH₄ (de Haas et al., 2021). More analyses on larger data sets are needed to confirm the correlations with other traits. Accurate estimates of these correlation structures allow applying an appropriate weight to

Table 1
Estimates of heritability and repeatability for methane emission in different livestock species and from different methane measurement methods.

Reference	Methane Phenotype	Measurement method	Unit	Species	Heritability	Repeatability
de Haas et al. (2011)	Predicted	-	g/day	Dairy cattle	0.35-0.44	-
Donoghue et al. (2016)	Measured	Respiration chamber	g/day	Beef cattle	0.27	-
Pickering et al. (2015)	Measured	Laser methane detector	mg/kg	Dairy cattle	0.05	0.07
Lassen and Løvendahl (2016)	Measured	Gasmet/Sniffer	g/day	Dairy cattle	0.21	0.35
Pszczoła et al. (2017)	Measured	Gasmet/Sniffer	g/day	Dairy cattle	0.23-0.30	0.17-0.40
Zetouni et al. (2018)	Measured	Gasmet/Sniffer	g/day	Dairy cattle	0.25	-
Breider et al. (2019)	Measured	Sniffer	g/day	Dairy cattle	0.12	0.50-0.69
López-Paredes et al. (2020)	Measured	Sniffer	g/day	Dairy cattle	0.12	-
Manzanilla-Pech et al. (2020)	Measured	Sniffer	g/day	Dairy cattle	0.15	0.50
Manzanilla-Pech et al. (2021)	Measured	Greenfeed, SF ₆ , Sniffer	g/day	Dairy cattle	0.21	0.46
Negussie et al. (2021)	Measured	Sniffer	g/day	Dairy cattle	0.04	0.35

Table 2
Genetic correlation between methane emission and some production, fertility and health traits in different livestock species.

Trait category	Trait	Methane measurement method	Species	Genetic correlation	Reference
Production	MY	Laser methane detector	Dairy cattle	0.55	Pickering et al. (2015)
	FPCM	Sniffer	Dairy cattle	0.43	Lassen and Løvendahl (2016)
	MY	Sniffer	Dairy cattle	0.38-0.57	Breider et al. (2019)
	ECM	Sniffer	Dairy cattle	0.60	Manzanilla-Pech et al. (2020)
	MY	Sniffer	Dairy cattle	0.22	López-Paredes et al. (2020)
	FY	Sniffer	Dairy cattle	0.27	López-Paredes et al. (2020)
	PY	Sniffer	Dairy cattle	0.22	López-Paredes et al. (2020)
	MY	Greenfeed, SF ₆ , Sniffer	Dairy cattle	0.29	Manzanilla-Pech et al. (2021)
	ECM	Sniffer	Dairy cattle	0.54	Negussie et al. (2021)
	BW	BW	Respiration chamber	Beef cattle	0.36
BW		Sniffer	Dairy cattle	-0.18	Lassen and Løvendahl (2016)
BW		Sniffer	Dairy cattle	0.01-0.02	Breider et al. (2019)
BW		Greenfeed, SF ₆ , Sniffer	Dairy cattle	0.65	Manzanilla-Pech et al. (2021)
Fertility	CF	Sniffer	Dairy cattle	0.17	Zetouni et al. (2018)
	FL	Sniffer	Dairy cattle	0.28	Zetouni et al. (2018)
	NI	Sniffer	Dairy cattle	0.07	Zetouni et al. (2018)
Health	Other diseases	Sniffer	Dairy cattle	-0.32	Zetouni et al. (2018)
	Udder health	Sniffer	Dairy cattle	0.06	Zetouni et al. (2018)
	Longevity	Sniffer	Dairy cattle	-0.06	Pszczoła et al. (2019)

Abbreviations: MY = milk yield, FPCM = fat protein-corrected milk; ECM = Energy-corrected milk; FY = Fat yield; PY = Protein yield; CF = Interval from calving to first insemination; FL = Interval from first to last insemination; NI = Number of inseminations.

methane emission in a breeding goal and avoid unfavourable correlated responses in production, fertility, longevity or health traits.

Improving feed efficiency

Genetic improvement of production and functional traits in dairy cattle reduces GHG emissions from milk production. This is because the share of the feed in a cow that is allocated for production is increasing while the share of the feed that is allocated for maintenance is only slightly or not increasing or even decreasing. This phenomenon is called dilution of the feed requirement for maintenance. Consequently, the amount of feed needed and the amount of GHG emitted for producing one unit of milk decreases. Although the dilution effect has diminished for modern high-producing dairy cows (VandeHaar et al., 2016), it will remain important. According to Huhtanen et al. (2022) for the Finnish dairy cattle population, it can be expected that the additional reduction in GHG emissions due to the dilution effect will continue in the next decade at an annual rate of 0.5%.

In addition to the dilution effect, significantly higher genetic progress in feed utilisation can be achieved by the direct inclusion of efficiency traits into the breeding goal (i.e. the total merit selection index). The importance of different feed efficiency traits can be quantified by relating the estimated additive genetic variances to the mean feed intake. Improving a particular trait by one genetic SD equals an improvement of dairy cows' feed utilisation by about 6% for ratio traits (Van Arendonk et al., 1991; Vallimont et al., 2011), by about 3.5% for metabolic efficiency traits (Pryce et al.,

2015; Tempelman et al., 2015), by about 1.5% for maintenance traits (Manzanilla-Pech et al., 2016; Lidauer et al., 2019) and by about 1% for digestibility traits (Berry et al., 2007; Mehtiö et al., 2019).

Ratio traits like feed conversion efficiency, which is milk energy output over feed intake, are easy to define and understand. However, ratio traits have received little attention in dairy cattle feed efficiency studies, because selection based on a ratio trait may add selection pressure to the component traits in a non-linear fashion, depending on the correlations between the traits and their heritability (Gunsett, 1984). Alternatively, most of the genetic variation described by a ratio trait, such as feed conversion efficiency, can be captured by including two traits in the selection index (Pryce et al., 2015): one from the metabolic efficiency trait group and one from the maintenance trait group. This is because feed conversion efficiency captures both the metabolic efficiency that describes the ability of a cow to use feed efficiently for the various energy pathways and the feed requirement due to the maintenance of body functions.

For maintenance traits, developing a reliable genomic prediction is feasible for many dairy cattle populations because metabolic BW (the target trait) has an intermediate to high correlation with slaughter weight and highly heritable conformation traits (Mehtiö et al., 2021). At least the correlated traits are often recorded routinely. For instance, Kempe et al. (2022) reported a cross-validation reliability of 0.86 when using single-step genomic breeding values for metabolic BW in Nordic Red dairy cattle. In practice, reliable genomic predictions for metabolic

efficiency traits would allow for increasing genetic progress in feed utilisation.

The use of residual feed intake (RFI; Koch et al., 1963) to describe metabolic efficiency in dairy cows has been studied intensively, but its modelling is not trivial. In earlier studies, DMI was regressed on energy sink traits to obtain RFI observations, which were then used for genetic evaluations. Recently, regressions on energy sink traits have been directly included in the genetic evaluation model (Tempelman et al., 2015). Kennedy et al. (1993) showed that RFI can be described as a linear function of feed intake and energy sink traits using a multi-trait model. The multi-trait RFI model includes feed intake and energy sink traits, which commonly include DMI, energy-corrected milk, metabolic BW and BW change as distinct traits. The multi-trait approach allows for the modelling of the environmental effects specific to each trait and for deriving an RFI selection index that is genetically uncorrelated with the energy sink traits and where a multi-trait random regression model can be used (Islam et al., 2020).

Lu et al. (2015) showed that the multi-trait variance components from the multi-trait RFI approach can be decomposed by a square root-free Cholesky decomposition to obtain autoregressive parameters that are partial efficiencies of feed intake on the energy sink traits. They also showed, given that the partial efficiencies are the same at the genetic and residual levels, that the partial efficiencies correspond to the partial regression coefficients estimated by a classical RFI model that regresses feed intake on the energy sink traits. However, the partial regression coefficient estimates from the classical RFI model may depart significantly from the feed requirement regression coefficients developed in animal nutritional studies (e.g. Agnew et al., 2003). This discrepancy should be investigated through research efforts involving both geneticists and animal nutritionists. Because partial regression coefficient estimates may depart significantly from the feed requirement regression coefficients, Lidauer et al. (2022) suggested an approach in which DMI is regressed on expected DMI calculated from energy requirements and production. This approach models the additive genetic effect of an animal by one random regression coefficient, which is the deviation from the fixed regression of DMI on expected DMI, which has an expectation of unity. Therefore, the estimate for the additive genetic effect will be equivalent to differences in efficiency on a percentage scale. The fixed regression on expected DMI replaces the partial regression coefficients of the classical RFI model, which enhances the modelling of differences in the energy density of the feed. This is because, instead of all partial regression coefficients, only one regression coefficient needs to be fitted for a feed stratum.

Difficulties in measuring feed intake are the greatest challenge in the development of reliable genomic predictions. So far, only a few dairy cattle populations (Pryce et al., 2015; Li et al., 2020; Stephansen et al., 2021) routinely calculate genomic predictions for RFI, but their reliability is low (Li et al., 2020). In a simulation study by Negussie et al. (2019), the reliability of cows' RFI breeding values was as low as 0.13 when feed intake was measured monthly. The validation reliability of bull candidates' genomic breeding values for RFI was 0.41 with a genomic reference population of 5 000 genotyped cows, corresponding to about 400–500 new cows entering feed efficiency recording schemes every year.

Breeding functional and adaptive traits

Breeding for better fitness (lifespan, health, fertility) helps reduce GHG emissions. Increasing the lifespan of dairy cows reduces the number of replacements to be kept. For example, methane emissions are reduced by 3% when the lifespan of dairy cows is increased from 3.0 to 3.5 lactations (Wall et al., 2012). Further decrease in emissions can be achieved by improving health

and fertility which will reduce involuntary culling rates and the number of required replacements. Improving fertility shortens dry and unproductive periods. Improving health reduces health problems and diseases that reduce emissions by supporting the animals' productivity levels. In the UK, methane production from the dairy sector would decrease by 10–15%, if cow fertility was improved from the year 2003 levels to 1995 levels (Garnsworthy, 2004).

Little attention has been given to the specific design of breeding programmes for reducing environmental impact, especially the choice of indicator traits and recording schemes. In a simulation study, Axelsson et al. (2013) tested GS for specific indicator traits (mainly functional traits such as fertility, longevity, etc.) recorded in a small number of contractor herds. By using indicator traits to environmental impact (EI), e.g. GHG emissions, in the predictions, the genetic gain in EI was enhanced by 20–34%. This was due to favourable and moderate correlations between EI and milk production and between EI and functional traits.

In some countries, GHG mitigation plans by breeding are affected by the increasingly warmer climate. As Hayes et al. (2013) stated, milk production decreased when temperature and humidity levels increased above a certain threshold, such that there will be more GHG emissions for the milk produced. Furthermore, increased heat stress reduces fertility. Thus, although selection on production and many other traits common in the total merit index reduces GHG emissions, heat stress tolerance can limit breeding response. Because milk production and heat tolerance have an unfavourable correlation (Nguyen et al., 2016), a high milk yield may not always be desirable (Pryce and Haile-Mariam, 2019). Therefore, because any changes in a cattle breeding programme will take some time to take effect, correct breeding weights in the total merit index and knowledge of the genetic correlations between GHG emissions, heat tolerance and traits under selection are important (de Haas et al., 2017).

GS has decreased GHG emissions from dairy cattle in at least three ways. First, higher genetic progress leads to increased production efficiency, whereby the same amount of milk can be produced with a smaller number of animals. Second, a lower number of heifers and bulls for beef production are raised; thus, a lower number of cattle are needed to consume feed and produce GHG. Third, GS can improve health, leading to lower levels of involuntary culling and increased fertility. For example, current breeding goals have led to only a marginal increase of 1% in GHG emissions in the US, although energy-corrected milk increased by 17% between 2007 and 2017 (Capper and Cady, 2020). With the export of the US dairy genetics across different countries, these changes are not limited to the US but affect breeding schemes that may or may not use GS. In future, this trend may be harder to continue in some regions because of changes in the production environment due to climate change (e.g. increased heat stress). When heat stress occurs during a cow's pregnancy, performance may be affected for at least three generations (Weller et al., 2021). Thus, heat stress and adaptation to climate change are likely to become important in breeding goals.

Contrasting environments

Countries exhibit differences in animal agricultural practices and needs. For instance, overconsumption and high GHG emissions are prominent issues in the US and the EU, while low- and middle-income countries are mainly concerned with public health issues, food security, malnutrition and adaptation to climate change. High-income countries have high emissions but significantly lower emission intensities than low- and middle-income countries due to better livestock genetics, diets, health and management practices

(Thornton, 2010). Methane emissions from domesticated ruminants have been estimated by Herrero et al. (2008) to increase by 40% between 2000 and 2030 in sub-Saharan Africa largely because of increased animal numbers. Consequently, increased production in low- and middle-income countries could increase significantly GHG emissions, deforestation, loss of biodiversity and other negative environmental impacts (Herrero et al., 2016).

An example of the large difference in average milk production per cow between low- and high-income countries is that between Ethiopia and the US. Ethiopia's livestock resources are the largest in Africa and 10th in the world. Ethiopia has approximately 12 million dairy cows, and the annual milk yield per cow ranges from about 270 kg to 3 600 kg (FAO and New Zealand Agricultural Greenhouse Gas Research Centre, 2017). Compared with the US Holstein average of about 13 000 kg of milk per cow per year, this illustrates the milk production differences and the potential for improving milk production in Ethiopia. Livestock is raised in high numbers due to low productivity in most parts of Africa and Latin America. In these regions, the genetic potential of production animals needs to be improved to reduce GHG emissions per unit of product (Gill et al., 2010).

In most regions of low- and middle-income countries, informal markets and subsistence farming systems dominate. The dairy cattle breeding infrastructure in these countries has much scope for improvement. GS can offer some shortcuts to achieve an efficient breeding programme (Mrode et al., 2021) when the pedigree data needed for traditional non-genomic-based breeding evaluation are scarce. Mrode et al. (2021) reported moderate to high prediction accuracy for milk yield using different genomic prediction models (0.53–0.59). They concluded that GS is feasible in smallholder dairy systems and is most likely to be the only way to a sustained genetic improvement programme with the available environmental and infrastructural resources.

Genetic diversity and adaptation

Global genetic variation

The genetic variation of domestic cattle has been influenced by multifactorial evolutionary processes, including domestication from ancestral wild species, adaptation to the local environment, genetic drift and very recent strong artificial selection (FAO, 2015; Weldenogodguad et al., 2019). These processes have shaped structural and functional genomic variations in domestic cattle and have led to the development of breeds and genetic resources for agriculture and food production. Cattle genetic resources for breeding are defined as genetic variations that have economic or other socio-cultural values and are present within and among cattle breeds (Kantanen et al., 2015). In addition, cryoconserved genetic materials (embryos and semen) are included in the available genetic resources.

From an economic point of view, the most important dairy cattle breeds are the humpless type of taurine cattle (*Bos taurus*), such as the Holstein, Jersey and Red and White Ayrshire cattle-based breeds (e.g. FAO, 2015). However, taurine cattle genetic resources can be argued to have been utilised narrowly. Few international transboundary dairy cattle breeds, particularly Holstein and Jersey, have spread to every continent. In contrast, a large proportion of local native cattle breeds have become extinct or are endangered. According to the FAO (2015), 13% of cattle breeds have become extinct, and 12% of the existing breeds are endangered (i.e. the total number of breeding females is less than 1 000). Moreover, the FAO's Domestic Animal Diversity database has no census-size records for 55% of the registered breeds, which may include many endangered breeds. All the critical genetic variation for future

breeding to promote adaptation to changing environments and production circumstances exist in the remaining cattle breeds. No bovine genes can be obtained back from nature because the ancestral species of domestic cattle, aurochs (*B. primigenius*), is extinct (Ajmone-Marsan et al., 2010). Maintaining native breeds strengthens the options available for matching breeds or their cross-breeds to various production environments.

The continuing genetic erosion in cattle is demonstrated by the declining number of native cattle breeds and the limited effective population sizes typical of cattle breeds (Taberlet et al., 2008). To determine current genetic resources, it has been recommended to characterise the phenotypic and genomic diversity of breeds and implement *in vivo* and *in vitro* conservation measures for cattle genetic resources (FAO, 2015; Kantanen et al., 2015). In practice, this knowledge can be used in animal breeding schemes to change animal genetics to reduce the negative environmental effects of cattle production and promote adaptation to the changing environment (Hoffmann, 2010; Kantanen et al., 2015; Strandén et al., 2019).

Selection signatures in the genome can be detected by many statistical methods, as reviewed by Utsunomiya et al. (2015), Horscroft et al. (2019), Saravanan et al. (2020) and Passamonti et al. (2021). In addition, landscape genomics methods may reveal associations between genomic data and environmental variables and thereby environmental adaptive signatures (Passamonti et al., 2021). Using genome-wide selection-mapping scans, some research teams have detected important genomic variations for production traits, immune systems and several physiological traits in international transboundary cattle breeds and local native breeds (Gutiérrez-Gil et al., 2015). For example, using whole-genome re-sequenced data, Weldenogodguad et al. (2019) identified positively selected candidate genes underlying adaptation, disease resistance, sensory perception and meat quality in northern Eurasian native cattle breeds in Finland and Sakha, Russia. Bhati et al. (2020) sequenced the whole genomes of 49 original Braunvieh cattle from Switzerland and detected selection signatures in genomic regions associated with milk production and feed efficiency.

Gene expression regulation factors and epigenetic marks may also play an important role in the improvement of future animal production through GS. In studies on selective sweeps in domesticated animal species, signatures of selection or association signals with complex phenotypic traits have often been identified outside the annotated protein-coding regions of genomes (e.g. Librado et al., 2015; Weldenogodguad et al., 2019; Bhati et al., 2020). These findings indicate that selection occurs specifically via the regulation of gene expression, leading to phenotypic variation in important quantitative traits (Ibeagha-Awemu and Zhao, 2015). Epigenetic marks, such as the methylation of cytosine bases, may have the ability to change gene expression, leading to changes in development, phenotypes and performance in response to environmental variables, such as nutrition, pathogens and climate (Ibeagha-Awemu and Zhao, 2015). In addition to selection and management practices, epigenetic marks may have played an important role in adaptation to challenging and very variable biogeographic and climatic environments. For example, Yakutian cattle in north-eastern Siberia and tropical cattle in Central America have adapted to very different and challenging environments (e.g. Sevane et al., 2019).

Genomic introgression for improved adaptation

Climate change affects the key conditions of cattle in diverse ways across the globe, such that the need for adaptation may lead to more differences in breeding objectives in different regions. For example, although the northern Arctic region and higher latitudes

are expected to have a larger average increase in temperature than lower latitudes, the lower latitudes are expected to suffer from extreme heatwaves, which are unlikely to occur in the north (IPCC, 2021). These weather phenomena make the differences between environments larger than before.

Various genomic and bioinformatic approaches provide useful tools to identify valuable genomic variations associated with adaptation and other important traits in terms of resilience and sustainability (e.g. Passamonti et al., 2021). Selective breeding within an adapted breed to become higher-producing or within a high-producing breed to become better adapted may be slow. Genes allowing local environmental adaptation may be present in local breeds but missing from high-producing breeds (Hoffmann, 2013). Thus, rapid genetic change may be possible by cross-breeding an adapted breed and a high-production breed (Hayes et al., 2013). Hayes et al. (2013) predicted that the introgression of desirable genes from one breed into another could be achieved efficiently by using GS and advanced reproductive technologies.

Traditional introgression assumes that a donor population has one or more alleles in genes of interest which are missing in the recipient population. Most traits in dairy cattle breeding have only a few known gene locations that could be used in traditional introgression. An alternative is to use GS in introgression or so-called genomic introgression, where the specific location(s) of the important gene(s) need not be known (Strandén et al., 2019).

Genomic introgression for dairy cattle has been studied using simulation. Strandén et al. (2019) considered different breeding strategies in a simulation study with two traits with a low negative genetic correlation. The traits mimicked adaptation having low heritability and production having moderate heritability. The breeding goal was a well-adapted and high milk-producing cow population. In their study, genomic introgression proved superior to within-breed breeding by producing a better adapted and higher-producing population within the simulation period. Furthermore, the use of genomic introgression gave the lowest rates of inbreeding (i.e. the lowest risk). Thus, their study suggests that genomic introgression can be used efficiently to improve the adaptation of a population of high-producing animals.

The genomic introgression approach requires the existence and maintenance of a population with high adaptation. Such a population is likely to have a low production capacity, which is typical for a local native breed (Hoffmann, 2013; Kantanen et al., 2015). Maintaining a local breed may be too costly in the long term. Consequently, there is a danger of losing genetic diversity, as these native breeds will become rare or even extinct. This illustrates the need for care when applying GS. For example, breeding work during the past 50 years has led to the dominance of Holstein dairy cattle and a reduction in the numbers of many formerly popular local breeds in Europe. The same may happen in Africa. Conversely, this can be considered an example of how effective traditional breeding programmes have been in finding and selecting a high-producing breed.

Future opportunities

Genotype-by-environment (G×E) interaction may assume significance as the adaptation to climate change becomes important. Thus, there will be demand for animals suitable for the environments altered by climate change (e.g. disease challenges, shorter/longer housing periods and feed quality). G×E interactions are already included in international genetic evaluations or multi-trait across-country evaluation (MACE) and genomic MACE (VanRaden, 2020). The inclusion of climate change-related traits in genomic evaluation models may lead to the need to include G×E interaction effects in some within-country evaluations.

The success of GS depends not only on accurate genomic information but also on phenotypes. Direct measures of certain traits, such as GHG emissions and adaptation, are expensive and challenging to make. An alternative is to use correlated indicator traits and other correlated traits in an index (Negussie et al., 2017b). However, advances in technology are bringing new measuring devices, sensors, robots and 3D camera systems and approaches that can be used to make new phenotypes or improve existing phenotypes (Negussie et al., 2022). This so-called phenomics means the use of technologies to collect phenotypes cheaply, easily and in large volumes (Mrode et al., 2020).

The use of modern technology is likely to increase, as it allows for decreasing costs of phenotyping and their recording. This kind of farm digitalisation may bring about phenotypes that are a result of machine learning for traits that are difficult and expensive to measure directly. For example, methane emissions of cattle by kg of milk or meat may use proxies with machine-learning tools (Negussie et al., 2022).

At least two potential approaches with feasible annual costs that may be used for a feed efficiency phenotype exist. One approach is based on using 3D images of eating cows to predict feed intake (Lassen et al., 2018). The other approach is to regress CO₂ production on energy sink traits, based on the finding that there is a high correlation between cows' heat production and CO₂ exhalation (Huhtanen et al., 2021). For the latter approach, CO₂ production is measured instead of feed intake. This approach does not need to model differences in the energy density of the feed, but cannot capture genetic variation in digestibility, and its own recording for digestibility is not readily available.

Climate change puts our food production systems to the test of resilience. Resilience may be challenged through a combination of simultaneous disruptive weather events or other catastrophes that may reduce global agricultural production and increase feed prices. Cattle can turn feed that is unsuitable for human consumption, such as grass, into milk and meat. In future, increasing grain prices may lead to requiring the use of lower-quality or more grass-based feed for livestock (Hayes et al., 2013), which may require changes in current breeding objectives. For example, this may increase the favouring of animals that can use non-conventional feed sources. This, in turn, may allow the use of marginal lands that cannot be used for crop production. In this regard, an important topic is also the resilience of cows against perturbations in the environment and for stable performance (König and May, 2019). Thus, breeding for efficiency may need to include the performance of cattle in diverse environments.

Conclusions

In this review, we concentrated on the challenges due to climate change for cattle breeding. GS is the latest technology to revolutionise selective breeding. We discussed GS and its role in breeding cattle in response to climate change, particularly considering important traits that improve production efficiency and play a crucial role in adaptation to climate change. Because GS is more cost-efficient and allows changing a cattle population faster than a traditional pedigree-based breeding programme, GS should be the preferred breeding programme. Given animal agriculture's large EI amid increasing demand for animal protein, the sustainable intensification may allow for reaching production goals and preserving environmental quality. In already intensified production populations, feed efficiency, health, fertility and adaptation may be more important than increasing production, particularly as heat stress can reduce and limit the rate of increase in production. Unused genetic potential in the adaptation of cattle to climate change can exist in native cattle breeds which needs to be investigated

and maintained to preserve global cattle genetic diversity. Focused and increased investments in new and advanced technologies will become essential. Future global challenges are only likely to be met by new techniques, such as the adoption of genomic and reproductive technologies (such as artificial insemination and embryo transfer) for livestock improvement. The continued readiness of cattle breeders to adopt recent technologies is essential. Undoubtedly, the next two decades will bring new tools to help us meet the challenges highlighted in this review.

Ethics approval

Not applicable.

Data and model availability

Not applicable.

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Conceptualisation (IS, EN) and drafting the manuscript (IS). Writing of introduction (IS), global challenges (IS, EN), genomic selection (IS), breeding towards lower greenhouse gas emissions (EN), improving feed efficiency (ML, TM), breeding functional and adaptive traits (EN), contrasting environments (EN), global genetic variation (JK), genomic introgression (IS), existing and future challenges (IS, ML, EN) and conclusions (IS, EN). All authors revised the draft and approved the final manuscript.

Declaration of interest

The authors declare that they have no conflicts of interest.

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