

Genetics and breeding of beef cattle

Raluca G. Mateescu

Department of Animal Sciences, University of Florida, Gainesville, FL, United States

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Historical overview of breeding programs

Traditional animal breeding programs based on phenotypic measurements and pedigree structure have been used for a long time to create and select the highly specialized breeds we have today.¹ Breed formation was accomplished by following the example of Robert Bakewell who selected and mated the best with the best until a certain degree of uniformity of type was achieved.² The resulting animals were popularized at livestock shows.³ Ancestry was recorded in herd books and breed societies were founded

with the goal of protecting the purity of the breed.⁴ The selection of the beef breeds was done with the goal of the perceived needs of the industrial revolution. The Angus, Hereford, and Shorthorn breeds were developed between 1750 and 1850.⁵ In the beginning, successful breeding in the breed associations was based on the use of pedigree along with the eye judgment to ensure adherence to formalized breed type.⁶ In 1936, Lush and Black introduced the idea of objective measures of merit in beef cattle and the first heritability estimates for growth were published by Knapp and Nordskog⁷ and

by Koger and Knox⁸ on weight adjustments which fueled research interests. Performance evaluation was first conducted on a "one-to-one" basis by a handful of breeders, researchers, and extension agents. From 1940 to 1960, the elite breeds of today were developed. Central bull testing began in 1941 in Texas^{9,10} and the tests proved to be a successful demonstration of competition based on performance. Beef cattle improvement programs run by extension specialists were started between 1945 and 1950. In 1955, the first beef cattle improvement association was organized in Virginia and was managed by breeders with help from extension agents. The Beef Improvement Federation (BIF) was formed in 1967 to create uniformity, assist in developing programs, encourage education and increase confidence in performance of beef cattle.¹¹ BIF guidelines for uniform beef improvement programs started with the first meeting in 1968 in Kansas City, and continues today where relevant research is presented along with performance updates.

The National Sire Evaluation was the focus of one working committees of BIF and in 1971 the committee developed the guidelines for incorporating the use of reference sires as the method for comparing sires.¹² The first sire summary was published in 1971 by the American Simmental Association. Breeding values for weight, based on an individual's own weight and relative performance, were introduced to the industry during the 1970 BIF meeting at which members of BIF estimated breeding values by playing the computer cow game.¹³ One year later, in 1971, these breeding values were incorporated into breeding programs and in 1974 maternal breeding values (milk production reflected in the weaning weight of calves of daughters of the sires in the pedigree) were introduced.

The mixed model procedure for sire evaluation was performed during 1980 on field data from the American Angus Association and the American Hereford Association. The sire birth-year group constants showed a linear genetic

trend in yearling weight for the Angus (+1.2 kg/yr) and Hereford (+1.5 kg/yr) breeds over two generations (1965–78). Beef breeds recognized AI as a breed improvement tool and at the time, 89% of the sires were genetically directly or indirectly tied through common ancestry. With these ties and the relationships included in a relationship matrix, new analytical procedures were developed to evaluate yearling bulls from across multiple herds.^{14–16} Performance records were sold initially as a within-herd tool. Henderson presented in a symposium to honor J. L. Lush a statistical method which would become the gold standard in predicting additive genetic merit in livestock.¹⁷ The mixed model procedures, which provided Best Linear Unbiased Prediction (BLUP) of breeding values, resulted in a substantial increase in the prediction accuracy by improving the quality of predictions made between contemporary groups such as herds or years, and thus allowing all available data to be used.¹⁸

Subsequent improvements in computer power and developments in computational methods allowed the evolution from univariate sire models to multivariate animal models. In 1984, direct additive effects for the dams were included in the model along with the direct effects for sires.¹⁹ The inclusion of the dam effects resulted in an increase in pedigree connections accounting for nonrandom mating of dams and would later allow for additive effects of dams, also called the additive maternal effect, to be included in the model.²⁰

Comparing genetic merit among breeds was always of interest, which stimulated the development of statistical methods for multibreed analyses. The grading-up programs common to many breed associations resulted in pedigree datasets with animals from other breeds and performance data accumulating from mixed breed composition cattle. Some commercial producers were interested in crossbreeding which opened up a great opportunity to market composite seedstock. Because crossbreeding was very

popular and practiced by many commercial producers, there was a growing need to develop methods to compare genetic merit among breeds. Statistical models using combined data sets or data sets with appropriately structured multibreed data were presented by researchers such as Elzo and Famula²¹ and Elzo and Bradford²² for sire-maternal grandsire models.

Several researchers developed a method for comparing Expected Progeny Difference (EPD) from multiple breeds which provided factors for adjusting EPDs from different breed associations to values that were comparable across breeds.^{23–26} In the early years, these tables were limited to only birth weights, weaning weights, and yearling growth traits. More recently, the table was updated to include many additional traits and these updates are typically presented during the annual meetings of BIF.

The importance of carcass characteristics and meat quality were recognized as a priority for improvement,²⁷ and several breeds followed the lead of the American Angus Association and began collecting carcass data as early as 1974.²⁸ The performance program was developed by the American Angus Association in collaboration with researchers from Iowa State University in the early 1960s and carcass EPDs started to be published in the mid-1980s. The lack of records on the selection candidates combined with a limited number of records on slaughtered progeny resulted in a low accuracy of prediction. Moreover, the prediction accuracy on young animals of breeding age was even lower, because of the long time required to produce progeny for slaughter. In 1998, genetic merit predictions for ultrasound traits measured directly on breeding stock were published by the American Angus Association. By the year 2000, the list of published EPDs for each breed association had increased considerably, with some breed associations having published more than 15 different EPD.

Quantitative nature of economically important traits—an intrinsic challenge in selection

The principle of genetic improvement is a very simple one: select above average candidates as parents of the next generation and the next generation will be genetically superior. The challenge lies with the nature of the traits which are the focus of selection programs. Most economically important traits with high priority for the industry to improve are quantitative in nature, being controlled by many genes and environmental factors. These types of traits are difficult and expensive to measure on a large number of animals. Thus, there is a lack of reliable performance measures on the selection candidates, their parents and perhaps their offspring, contributing to our inability to cost-effectively rank selection candidates for all traits of interest.²⁹

The first beef cattle traits included in the National Cattle Evaluations (NCE) were weight traits, and they now include birth, weaning and yearling weights, and even mature weights. US breed association do not report the computed Expected Breeding Value (EBV), but rather the EPDs which is one-half the EBV. [Table 2.1](#) shows a summary of traits with reported EPDs for the 16 most prominent US beef cattle breeds. Calving ease has been added to most national evaluation systems and, like weaning weight, includes EPD that reflect direct and maternal contributions.³⁰ Carcass traits have been and are still difficult to measure in seedstock herds where the selection candidates are not following the typical feedlot – slaughter schedule. For these animals, most carcass information is derived from ultrasound measures of mainly rib-eye area, intramuscular fat and fat depth.²⁹ A carcass EPD is not reported for all breed associations. Records of eating quality, a complex of individual traits including tenderness, juiciness and flavor, are mostly limited to tenderness, but this is also

TABLE 2.1 Traits reported in national cattle evaluation for the 16 most prominent beef cattle breeds in the US.

Breed ^a	British				Continental							Indicus				
	AAA	AHA	RAA	ASH	AIC	AGA	AMA	ASA	BAA	NAL	SAL	ABB	ACA	BBU	IBB	SGA
Trait^b																
BWT	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
WWT	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Milk	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
YWT	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
YHT	X															
MWT	X	X													X	
MHT	X															
CCW	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
MRB	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
REA	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
FAT	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
RUMP																
YLD			X			X		X		X	X	X	X			
WBSF								X				X				X
CED	X	X	X	X	X	X	X	X	X	X		X	X	X	X	
CEM	X	X	X	X	X	X	X	X	X			X	X	X	X	
SC	X	X			X						X	X	X		X	X
HPG	X		X			X									X	X
STAY		X	X	X		X		X		X	X		X		X	
GL										X						
DOC	X					X				X	X	X				
RADG	X		X			X										
ME			X													
DTF																
TM		X		X	X	X	X	X	X	X	X		X	X	X	X
A1C																X
BCS																X
TI								X		X						
FI																X
BB																X

TABLE 2.1 Traits reported in national cattle evaluation for the 16 most prominent beef cattle breeds in the US.—cont'd

Breed ^a	British				Continental						Indicus					
	AAA	AHA	RAA	ASH	AIC	AGA	AMA	ASA	BAA	NAL	SAL	ABB	ACA	BBU	IBB	SGA
Trait ^b																
DMI	X	X	X			X										
\$EN	X															
\$W	X															
\$F	X			X												
\$G	X															
\$B	X															
US		X														
TSI		X														
\$BMI		X		X												
\$BII		X														
\$CHB		X														
HB			X													
GM			X													
\$CEZ				X												
TSI					X											
P30D						X										
RFI						X										
\$COW						X										
FPI						X										
EPI						X										
API									X							

^a Breed: British: AAA, American Angus Association; ABB, American Brahman Breeders Association; ACA, American Chianina Association (includes Chiangus); AGA, American Gelbvieh Association; AHA, American Hereford Association; AIC, American International Charolais Association; AMA, American Maine Anjou Association; ASA, American Simmental Association; ASH, American Shorthorn Association; Continental: BAA, Braunvieh Association of America; BBU, Beefmaster Breeders United; IBB, International Brangus Breeders Association; NAL, North American Limousin Foundation; RAA, Red Angus Association of America; SAL, American Salers Association; Indicus: SGA, Santa Gertrudis Association.

^b Trait: \$B, dollars beef; \$BII, Brahman influence index; \$BMI, british maternal index; \$CEZ, calving ease index; \$CHB, certified Hereford beef index; \$COW, maternal productivity; \$EN, cow energy value; \$F, feedlot index; \$G, grid value; \$W, weaned calf value; A1C, age at first calf; API, all-purpose index (\$/cow exposed, all purpose sire scenario); BB, breed back; BCS, body condition score; BWT, birth weight; CCW, carcass weight; CED, calving ease direct; CEM, calving ease maternal; DMI, dry matter intake; DOC, docility; DTF, days to finish; EPI, efficiency profit index; FAT, fat depth (usually over rib); FI, fertility index; FPI, feeder profit index; GL, gestation length; GM, grid master; HB, heard builder; HPG, heifer pregnancy rate; ME, maintenance energy requirements; MHT, mature height; Milk, weaning weight maternal; MRB, marbling/intramuscular fat; MWT, mature weight; P30D, pregnant at 30 days; RADG, residual average daily gain; REA, rib eye area; RFI, residual feed intake; RUMP, fat depth over rump; SC, scrotal circumference; STAY, stayability; TI, terminal index; TM, maternal total ($1/2$ bull's WW EPD + bull's MK EPD); TS, teat size; TSI, terminal sire index; US, udder suspension; WBSF, Warner-Bratzler shear force (tenderness); WWT, weaning weight direct; YHT, yearling height; YLD, retail beef yield/percent retail cuts/yield grade; YWT, yearling weight.

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I. Beef cattle production

difficult to measure. As a solution, marbling is used as a surrogate for tenderness/eating quality. More recently, a quantitative trait locus (QTL) in the region of the calpain and calpastatin genes was considered for marker-assisted selection, using a Single Nucleotide Polymorphism (SNP) that varies among breeds, most notably between *Bos indicus* and *Bos taurus* breeds. Measures of reproductive performance present difficulties as well, since inventory recording systems have not been used by most breed associations until relatively recently, so it is impossible to determine if a female not presented as a dam calved or not.³¹ Reproductive EPD have, therefore, been limited to scrotal circumference, and more recently, heifer pregnancy. Many other traits of potential economic importance like feed intake are also problematic to measure on a large number of animals, especially under grazing conditions. Other traits like energy requirements for maintenance have been predicted from data on mature weight, body condition score and potential for milk production.³²

Advances in genomic technologies and genomic selection

Starting in 1990, advances in molecular genetics held the promise that DNA information would lead to greater genetic improvement compared to that based only on phenotypic records. Research efforts were focused on Marker-Assisted Selection (MAS), which consists of two steps: 1) detect and (fine) map genes underlying the traits of interest, i.e., quantitative trait loci (QTL); and 2) include the QTL information into the BLUP-EBV.³³ Although the first step of mapping QTL resulted in many QTL being detected, the repeatability of the mapping studies was low where many QTL positions moved or completely disappeared from one study to the next. This is attributed to the majority of QTL having very small effects, which, in combination with the multiple testing situation (testing

thousands of markers), results in a substantial “Beavis effect” of overestimated effects of significant markers.³⁴ In genome-wide association studies (GWAS), the number of tests equals the number of genotyped independent SNPs, which in livestock is typically many thousands. To account for multiple-testing, very stringent P-values are used and, consequently, only QTL with a large effect are found. DGAT1 is one of the very few large QTL detected for fat content in milk,³⁵ while for most traits investigated no reliable QTL were found. Even in dairy cattle, where many QTL mapping studies were conducted on very large populations to ensure sufficient power to detect these effects, less than 10% of the genetic variance of the breeding objective could be explained by these QTL. Hence, by 2005, although the MAS approach was successful for simple traits controlled by one gene, it provided disappointing results for many complex traits which resulted in the limited use of MAS in livestock breeding. In 2001, Hayes and Goddard³⁶ predicted that 50 to 100 genes affected dairy traits, which was considered a high estimate at that time. In the following 15 years, results from GWAS and genomic selection suggested that complex traits are controlled by many genes with very small effects. In 2016, Goddard et al.³⁷ estimated that between 2,000 and 10,000 genes may affect dairy traits.

Three breakthroughs have resulted in the current widespread use of DNA information: 1) the development of genomic selection methodology,³⁸ 2) the identification of many thousands of SNP markers across the entire genome, and 3) high throughput genotyping technologies (SNP chips) which allow for a cost effective genotyping solution for large number of SNPs. It is important to point out that the seminal paper describing the approach of genomic selection and the statistical methods for accurately estimating the genetic merit from a set of genetic markers spanning the entire genome was published before these markers were available. The subsequent genome sequencing of many of the

livestock species resulted in the discovery of thousands of SNPs across the genome which enabled the SNP-chip genotyping technologies to be developed for most livestock species. In cattle, the 1,000-bulls sequencing project has revealed 30 + million SNP markers.³⁹ The first high-density and high-throughput genotyping assay was the 10K SNP chip commercialized by Affymetrix.⁴⁰ Because the number of markers on this panel was insufficient for many genomic studies, a higher density Illumina BovineSNP50 chip (~50,000 SNP) was developed by a consortium of animal scientists using SNP discovery populations in Holstein, Angus and mixed breeds of beef cattle.⁴¹ This assay has become the international standard for genomic selection (GS) and GWAS in cattle. Subsequently, the Illumina BovineHD BeadChip containing 777,962 SNPs (777K) became available and is being used in discovery research.

Genotyping was embraced by a number of breed associations, and producers of registered cattle are currently driving the implementation of genomic selection within their breeds. However, there is still a great portion of producers not genotyping their cattle because it requires a significant economic investment which is usually difficult to offset unless they retain ownership of weaned calves. This technology can be used in commercial herds to reduce the risk associated with buying herd bulls. A traditional EPD for young bulls is exclusively based on parental average EPDs for all traits, except birth weight and possibly weaning weight. For these young animals, genomic-enhanced EPDs are more reliable than traditional EPDs. The decrease in risk is proportional to the reduction in the possible change in value for each EPD as a result of higher accuracy. There is a great potential for the genomic technology to generate considerable value across the entire beef production chain, from the producer to the end product and to the consumer⁴², but currently, the seedstock sector incurs most of the genotyping expense. Within the seedstock

sector, genotyping technologies have been used largely as a marketing tool, and the ability to increase genetic improvement has been a secondary goal. Enhanced marketing results in increased returns on investment which tend to be much higher in the seedstock sector compared to the commercial sector. Many small producers of registered cattle do not have the ability to take advantage of marketing; therefore, the genotyping costs are not economical as they cannot recoup any of their investment. It is expected that this challenge will be overcome in time as the prices of genotyping continue to decline and beef producers continue to become more educated about the value of genomic testing in generating EPDs with greater accuracy.

The genomic selection approach proposed in 2001 by Meuwissen et al.³⁸ estimates the breeding value from markers evenly spaced throughout the entire genome. In this approach, the overall breeding value of any animal is predicted by summing up the estimated genetic effect of each genetic marker (Fig. 2.1). The genetic effect of the markers is estimated in large populations of cattle with recorded phenotypes and marker genotype information which are referred to as reference populations. The estimated effects can then be used for selection of candidates with genotypic information, but without any phenotypic records. The effectiveness of the genomic selection approach relies on a large number of genotyped cattle and the number of markers on the genome. The challenge related to the number of genotyped markers in cattle was solved with the advent of large-scale and cheap genotyping methods.

Among all livestock industries, the dairy industry was arguably the most successful in implementing this genomic selection approach. Several advantages made it easier for the dairy industry to adopt genomic selection including widespread use of AI, availability of large reference populations of bulls with highly accurate estimates of genetic merit, individual animals

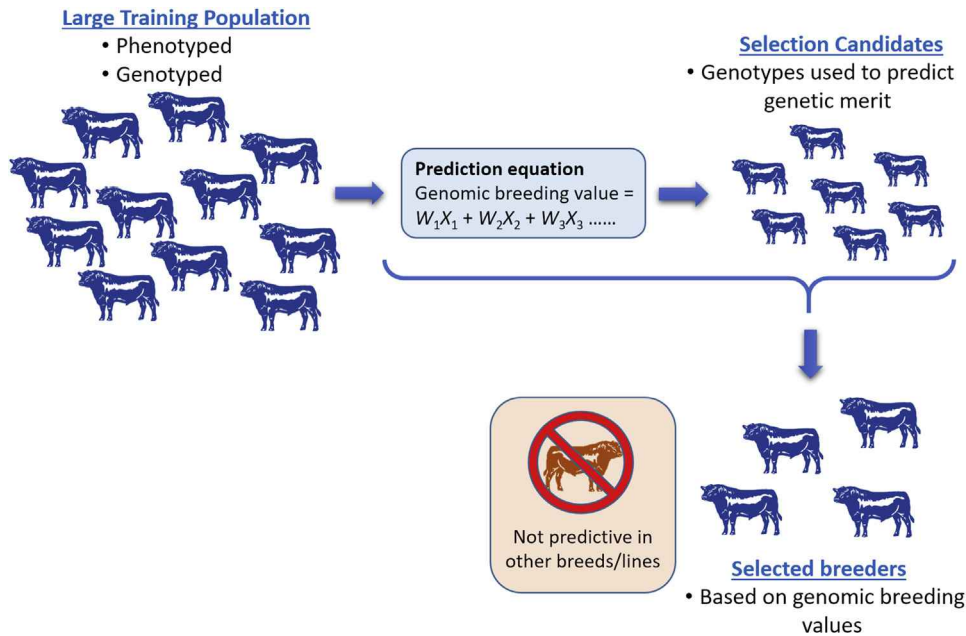


FIG. 2.1 Principle of Genomic Selection. A training population with many individuals genotyped and phenotyped is used to derive a genomic prediction equation. This equation is then used to estimate the genomic breeding value of genotyped individuals without phenotypes.

with high EBV sufficient to offset the costs of genotyping.

In contrast with the dairy industry, a multitude of challenges slowed down the adoption of genomic selection in the beef industry. The US beef industry consists of many different breeds selected to fit various beef cattle production systems and environments over a wide geographic area. The beef industry includes more than 80 distinct breeds, although at the seedstock level the top five breeds comprise nearly 80% of all registered animals. A main limitation is the lack of widespread use of AI which constricts the availability of high-accuracy sires for the reference population. In addition, given the substantial differences among the breeds, a separate reference population is required for each breed which further limits the number of animals available for the training population. Compared to the dairy industry which has an industry-wide breeding objective, many

different traits are economically important in different beef industry sectors (e.g., carcass traits are the key profit driver for the processors, but not for the commercial sector). There is also no beneficiary willing to pay for the development of phenotyped and genotyped training populations, such as the AI studs provided for the dairy industry, owing to the limited use of AI in the beef industry. Consequently, the development of training populations in the beef cattle industry has been somewhat disjointed. Some companies, such as GeneSeek (formerly Igenity) and Zoetis (formally Pfizer Animal Genetics), saw this void as a business opportunity⁴³ and paid for the genotyping of semen collections from AI sires put together by individual researchers⁴⁴ or they developed their own training populations. This involvement of commercial genomics companies introduced a proprietary component into the process of ranking animals based on genetic merit⁴³ and made it difficult to obtain

validation data for the resulting genomic predictions.⁴⁵ Other breed associations have developed their own training populations by genotyping AI bulls and obtaining 50K genotypes from the influential bulls that were genotyped at the US Meat Animal Research Center (US-MARC) in Clay Center, Nebraska, as part of the 2,000 Bull Project. Breed associations, in collaboration with the National Beef Cattle Evaluation Consortium, used these data to develop within-breed genomic prediction equations. The advantage of this model is that the breed association has access to the genotypic information and can use this information in conjunction with new performance and pedigree information in the breed database to continuously improve prediction equations.

Another limitation lies with the segmented nature of the beef cattle industry which is composed of five main sectors: seedstock, commercial, feedlot, processor, and retail. There are several thousand seedstock breeders and over 750,000 commercial producers. Animals change ownership multiple times in the production chain, and phenotypic performance in downstream segments (e.g., feed efficiency in the feedlot, carcass quality, eating satisfaction) is rarely relayed back to the breeding sector. In contrast to more vertically integrated industries, segmentation of beef cattle industry results in market inefficiency because breeders are rarely rewarded for developing improvement programs that maximize profit for the entire industry. Additionally, in the absence of phenotypes from the commercial, feedlot, processing, and retail sectors, it is difficult to make genetic improvement for traits that are measured in those sectors.

Future genomic information

High density SNP chips (800K) are now commercially available and being used in discovery research. Under the assumption that linkage disequilibrium (LD) is preserved between the SNP and QTL across breeds, this high-density SNP chip is expected to allow pooling of training

data sets across breeds. When cost is the limiting factor, genotype imputation allows increasing the size of the population with high density genotypes or whole-genome sequences. The imputation from low density SNP panels to 50K or 770K SNP panels has been shown to be highly accurate in beef cattle where there is a high level of LD across the genome. This imputation is highly accurate especially for those breeds that have a large reference population of animals with high density genotypes.^{46,47} The imputation to whole-genome sequence is more challenging because the low minor allele frequency variants which have a high incidence are much more difficult to impute accurately. For variants with a minor allele frequency above 5%, imputation from the 777K to full sequence is moderately accurate,⁴⁸ while variants with a frequency lower than 5% are imputed extremely poorly.⁴⁹ Sequencing genomes of animals in such a way as to maximize the number of haplotypes available in the reference population or animals genetically related to all other animals in the population could increase the accuracy of imputation.^{50,51}

Availability of large populations of beef cattle with full sequence information will positively impact association analyses, and the ability to fine-map genes for economically important traits has the potential to lead to a better understanding of the genetic architecture of complex traits.

Where genomic selection can have a great impact for the beef industry?

Genomic selection is most advantageous for traits that are difficult to select for traditionally. The greatest benefit from genomic selection in dairy cattle is the reduction in the generation interval associated with progeny testing. In beef cattle, growth rate, a trait with high economic priority, can be measured on selection candidates at a young age so progeny testing is not needed, making genomic selection less beneficial. However, several other economically important traits in beef cattle, such as feed conversion efficiency,

beef quality and thermotolerance, are difficult to improve via traditional selection programs. Because phenotypic records for these types of traits are very difficult and expensive, the high cost associated with developing large reference populations of beef cattle is very difficult to justify even for large companies with their own breeding program. For these traits, the best approach may be a multibreed training population and nonlinear analysis based on high-density SNP panels or genome sequence data.

Feed efficiency is becoming a popular trait for genomic selection because of the large impact on producer profitability and the possibility to contribute to reducing the environmental footprint for production of beef. Feed efficiency can be measured in many different ways, but accurate measures of dry matter and nutrient intake are required. Residual feed intake (RFI), also known as net feed intake, has become increasingly popular and is considered the standard measure of metabolic efficiency. The RFI is defined as the difference between the actual and predicted dry matter intake for an animal, where the prediction is based on the weight and growth of the animal. The advantage of the RFI is that, conceptually, the RFI measure is independent of growth and mature size. To further eliminate the impact of these traits on the RFI, body condition score or other energy expenditure related traits could be included in the RFI calculation. Feed efficiency in beef cattle is a complex trait and the result of multiple factors and biological processes which are also under the influence of physiological status and environmental/management conditions.

Genomics and sustainability

Productivity is at the heart of creating a sustainable food system. The latest scientific advances in genetics, animal nutrition and husbandry techniques, allowed U.S. farmers and ranchers to produce 20% of the world's beef with only 6% of the global cattle. Producing the

26.2 billion pounds of beef in 2017 was accomplished with a 53% smaller herd than would have been required to produce the same amount in 1975.

By 2050, the world's population is expected to grow from 7.6 billion people to 10 billion, which will pose enormous challenges to securing an abundant and safe food supply. Advances in genomic technologies and research can be part of the solution by allowing further improvement in animal productivity, disease resistance, adaptability to increased variability in the climate (e.g., heat, drought, rainfall), and improved nutritional quality while minimizing environmental impact. The necessary increase in total agricultural output is estimated by the Food and Agriculture Organization of the United Nations at 60% to meet future demands for food. The demand for animal protein is expected to be higher with some estimates that milk production will need to increase by 63%, and meat production by 76%.⁵² Most of this increase is expected in the developing world, while in the developed world both meat and milk consumption are likely to increase by less than 15%.⁵³ This will have to be accompanied by increases in efficiency of food production, improved animal health and welfare, and a reduction in the environmental footprint for beef and dairy operations. A similar challenge was met in the developed world in the last 75 years through increases in production efficiency mostly achieved through improvements in genetics combined with better nutrition, improved management and, more recently, advances in genomics. Therefore, it is expected that upcoming advances in genetics and genomic technologies will further increase efficiencies in animal production and a sustainable solution to the increased demand for animal protein. Genomic solutions will be required as they hold the promise to meet these demands by increasing livestock production efficiencies in the developing world.

Feed efficiency is at the core of any discussion of sustainability given its great potential to impact beef profitability and food security.

The main benefit of selecting beef cattle for improved feed efficiency or low residual feed intake (RFI) is a reduction in feed intake without compromising growth and product quality⁵⁴ which translates to reduced feed costs and increased overall profitability. In addition, increases in feed efficiency are associated with a reduction in greenhouse gas emissions per animal^{55,56} and decreases in manure production⁵⁷ which will result in an overall reduction in the environmental footprint. The main challenge for producers is to collect sufficient individual records because feed efficiency is both expensive and time consuming to measure on a large number of animals in order to identify those that have the genotype to increase efficiency of production. The genomic selection approach where high density genotypes and recorded phenotypes in a reference population are used to predict genetic merit of candidates for selection offers a potential alternative for estimating RFI in genotyped animals without phenotypic data. However, the high cost associated with measuring RFI is usually a big impediment to developing a large enough reference population which translates into lower accuracy of the predicted genomic EBV. One approach evaluated as a solution for increasing the reference population size was a multibreed evaluation where information from different breeds can be combined to increase the accuracy. However, this approach resulted only in a small increase in the accuracy of genomic EBV.^{58–60} This marginal improvement can be attributed to SNP by breed interactions and to the low relationships between animals from different breeds. Many studies using candidate gene approaches^{65–68} or genome-wide association studies (GWAS)^{61–64} revealed a large number of genetic markers associated with feed and its components traits. This information can be used in developing cost-effective SNP marker panels to predict a large proportion of the variation in feed efficiency traits. A set of 63 SNPs was associated with 19.4% of the variation in feed

efficiency identified by Abo-Ismaïl⁶⁹ could allow for a low cost test for estimating molecular breeding values.

Genetic improvement in climate resilience traits

Climatic stress is a major factor limiting production efficiencies in beef cattle in tropical and subtropical environments and in dairy cattle throughout most of the world. This stress is expected to increase due to climate change. More than half of the cattle in the world are maintained in hot and humid environments, including about 40% of beef cows in the US. Substantial differences in thermal tolerance exist among breeds and among animals within breeds indicative of opportunities for improvements through selection. For example, *B. indicus* cattle exhibit increased resistance to many environmental stressors relative to *B. taurus*, but tend to have slower growth, lower fertility and poor meat quality as they have not been as intensively selected for these traits as specialized *B. taurus* breeds. Use of genomic tools to produce an animal with superior ability for both thermal adaptation and food production represents an energy-efficient sustainable approach to meet the challenge of global climate change. Although swine, poultry and dairy cattle are more severely affected by heat stress than beef cattle, their confinement and intensive production systems make climate control via housing design and management interventions feasible. Beef cattle, particularly those in the cow-calf segment, are typically reared in extensive systems with limited opportunities for controlling environmental stress. Moreover, fewer solutions are available in developing countries to alleviate the effects of climate change given the limited facilities and management resources. Genetic improvement is one of few feasible strategies for ensuring adequate and sustainable production of beef protein in an increasingly hot world.

Genomic research to find genes associated with mechanisms to combat climate issues are underway. Hamblen et al.⁷⁰ found that several animal characteristics such as coat score and temperament influence core body temperature responses to heat stress in Brangus heifers. In the same study, core body temperature measured under similar environmental conditions in a population of Brangus heifers of the same age and managed uniformly showed a high level of variation which is indicative of opportunities for improvements in performance through genetic selection. A major dominant-acting genetic effect that improves heat tolerance^{71,72} is associated with the “slick” coat trait in Senepol cattle. The causal variant comprises a single base deletion producing a frameshift mutation resulting in a truncated isoform of the prolactin receptor.⁷³ Introgression of the slick trait in breeds susceptible to heat stress is possible, but a slow process. Nevertheless, introgression of the slick coat trait into dairy genetics has begun with US Holstein cattle⁷⁴ and offers a significant potential for genetic improvement of dairy cattle in the tropics.

New genomic technologies

Genome editing is a powerful new technology that can efficiently alter the genome of organisms and provides a precise way of introducing desirable alleles into the elite germplasm of a given breed, without the need to bring along the unwanted genetic material that accompanies traditional backcrossing and introgression strategies. The current genome-editing tools are based on the use of nucleases: zinc-finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeats/associated nuclease Cas9 (CRISPR/Cas9).^{75–77} The basic working principle of all these nucleases begins with the creation of site-specific DNA double-strand breaks at the required location in the genome. These double-strand breaks in the

DNA are then repaired through one of the two repair pathways: non-homologous end joining or homology directed repair pathways. The non-homologous end joining pathway is a major DNA repair pathway in cells and ligates the ends at the break directly without a template. Nucleotide deletions or insertions can occur during the non-homologous end joining repair process resulting in indels and repair error related frameshift. As a result, gene knock-out can be efficiently made by nuclease-assisted non-homologous end joining. Compared to non-homologous end joining pathway, the frequency of the homology directed repair is much lower in cells. However, because the repair is accomplished through homologous recombination between a donor DNA template and the target genomic locus, this pathway results in a precise insertion of the donor DNA. Nuclease-assisted HDR is, therefore, used to generate targeted gene knock-in or allele replacement. These nuclease-based genome editing techniques, particularly CRISPR/Cas9, due to its simplicity and high efficiency, have triggered a revolution in a wide variety of biological systems. In animal agriculture, genome editing opens up new possibilities for accelerating genetic selection and creating animals that are hornless, disease-resistant, and heat-tolerant, as well as being producers of less methane and less waste compared to animals in the current production systems.

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