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NRC Research Press

INVITED REVIEW

Strategies to improve the efficiency of beef cattle production

Stephanie A. Terry, John A. Basarab, Le Luo Guan, and Tim A. McAllister

Abstract: Globally, there are approximately one billion beef cattle, and compared with poultry and swine, beef cattle have the poorest conversion efficiency of feed to meat. However, these metrics fail to consider that beef cattle produce high-quality protein from feeds that are unsuitable for other livestock species. Strategies to improve the efficiency of beef cattle are focusing on operational and breeding management, host genetics, functional efficiency of rumen and respiratory microbiomes, and the structure and composition of feed. These strategies must also consider the health and immunity of the herd as well as the need for beef cattle to thrive in a changing environment. Genotyping can identify hybrid vigor with positive consequences for animal health, productivity, and environmental adaptability. The role of microbiome–host interactions is key in efficient nutrient digestion and host health. Microbial markers and gene expression patterns within the rumen microbiome are being used to identify hosts that are efficient at fibre digestion. Plant breeding and processing are optimizing the feed value of both forages and concentrates. Strategies to improve the efficiency of cattle production are a prerequisite for the sustainable intensification needed to satisfy the future demand for beef.

Key words: efficiency, beef, genetics, microbiome, feed quality.

Résumé : Mondialement, il y a approximativement 1 milliard de bovins de boucherie et comparés à la volaille et les porcs, les bovins de boucherie ont la plus pauvre efficacité de conversion d'aliments à viande. Par contre, ces mesures ne tiennent pas compte du fait que les bovins de boucherie produisent de la protéine de grande qualité à partir d'aliments qui ne conviennent pas aux autres espèces d'animaux d'élevage. Les stratégies pour améliorer le rendement des bovins de boucherie font valoir la gestion opérationnelle et de reproduction, la génétique de l'hôte, l'efficacité fonctionnelle des microbiomes du rumen et respiratoires, ainsi que la structure et la composition des aliments. Ces stratégies doivent aussi prendre en considération la santé et l'immunité du troupeau ainsi que le besoin des bovins de boucherie à s'épanouir dans un environnement changeant. Le génotypage peut déterminer la vigueur des hybrides ayant des conséquences positives la santé, la productivité, et la capacité d'adaptation à l'environnement des animaux. Le rôle des interactions microbiome-hôte joue un rôle clé dans la digestion efficace des éléments nutritifs et la santé de l'hôte. Les marqueurs microbiens et les profils d'expression de gènes dans le microbiome du rumen sont utilisés pour identifier les hôtes qui digèrent efficacement les fibres. La reproduction et le traitement des plantes optimisent la valeur d'aliments des fourrages et des concentrés. Les stratégies pour améliorer l'efficacité de production de bovins sont un prérequis pour l'intensification durable nécessaire afin de satisfaire à la demande future pour le bœuf. [Traduit par la Rédaction]

Mots-clés : rendement, bœuf, génétique, microbiome, qualité d'aliments.

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Introduction

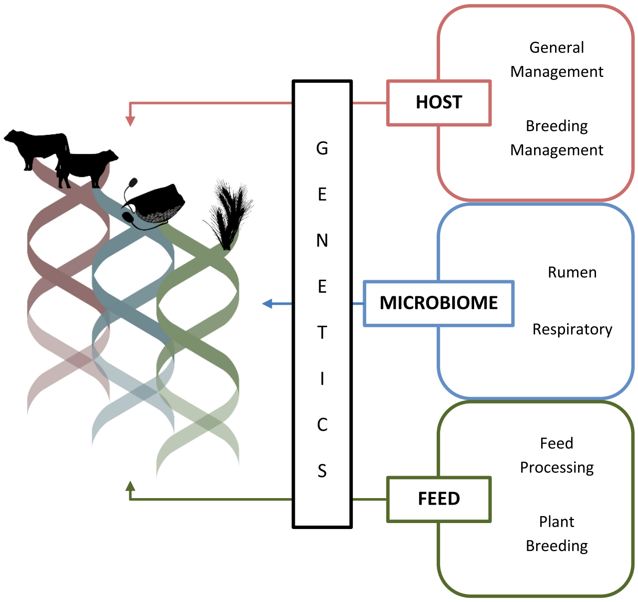
Cattle are unique in their ability to convert lignocellulosic biomass into valuable protein, although compared with other livestock, beef cattle have the lowest production efficiency (Mottet et al. 2017). Meat and milk from cattle and bison are estimated to account for approximately 45% of the global protein supply for humans (Mottet et al. 2017). Although the beef industry is often criticized for its large consumption of grains, only 7%–13% of world beef production is based upon grain-feeding systems (Gerber et al. 2015; Mottet et al. 2018). Even in these systems, grain that is fed is often that portion of the crop that fails to meet the quality grades required for approval as food for humans. Most metrics fail to consider that beef cattle produce high-quality protein from feeds that are largely unsuitable for consumption by humans or other livestock species. Improving the efficiency of beef production has the added advantage of increasing producer profitability as well as reducing their environmental impact on an intensity basis. Although genetic selection has improved the efficiency of beef cattle, this trait is also influenced by diet, environment, management practices, and host microbiomes (Fig. 1). Strategies that improve the sustainable intensification of beef production to satisfy the growing demand for meat production are needed.

Measures of efficiency

Beef cattle efficiency can be expressed in reference to general production efficiency or feed efficiency. General production efficiency measures aim to increase output of production utilizing the same amount of inputs. For example, total weight of calves weaned during a cow's lifetime is the most important output component in the cow–calf production sector as it is a function that accounts for the survival and reproductive performance of cows and the survival and growth rate of their offspring (Burns et al. 2010). General production efficiency can also refer to lifetime production strategies which aim to improve herd health to reduce death loss, thus increasing calf weight per cow exposed to breeding. Similarly, management practices that can also contribute to improving lifetime production efficiency include slaughtering cattle at an optimum age and weight, maintaining optimum heterosis, and ensuring a fertile cow–calf herd.

Previously, feed efficiency was measured on a feed conversion ratio (FCR) or gross feed efficiency basis. These metrics account for the amount of feed required to produce 1 kg of body weight, and are correlated with genetic and phenotypic measures of growth, mature body weight, and composition of gain (Kenny et al. 2018). A feedlot study reported that a 10% improvement in average daily gain lead to an 18% improvement in profit, compared with a 10% improvement in FCR that resulted in a 43% increase in profit (Fox et al. 2001). Similarly, a 5% improvement in feed efficiency can generate four times the economic return of a 5% improvement in average daily gain (Gibb and McAllister 1999). Although FCR is a superior measurement over average daily gain, FCR metrics do not account for the nutritional value of feed consumed or the human nutritional value placed on the output gain (Mottet et al. 2017). Alternatively, metrics that account for the nutrient content of feed (i.e., kilogram of human-edible feed) or the functional end product (kilogram meat protein) can improve the accuracy of efficiency measures, especially when comparing different livestock systems.

Fig. 1. Strategies to improve the efficiency of beef cattle production. [Colour online.]



Ultimately, selection of beef cattle based on increased growth rates and improved feed conversion results in a population with increased mature body size and maintenance requirements, increasing feed intake and associated environmental and economic costs (Crews 2005). Currently, residual feed intake (RFI) is another standard metric for evaluation of feed efficiency in livestock. Koch et al. (1963) defined RFI in youthful cattle as the difference between actual feed consumed and predicted feed intake based on maintenance and growth. Residual feed intake is calculated using a regression equation involving metabolic body weight and average daily gain, where a more efficient animal will have a negative or low RFI, indicating they consume less than predicted whilst maintaining the same level of production (Elolimy et al. 2018). Conversely, a high or more positive RFI indicates an inefficient animal that consumes more than predicted. Dependant on cattle productive stage, RFI can be used to estimate feed efficiency independent of growth rate, body composition, fat deposition, changes in conceptus weight, milk yield, and milk

Table 1. Independent and dependent factors of residual feed intake in beef cattle.

Independent	Dependent
Growth rate	Production system (confined vs. grazing)
Body composition	Dry matter intake measurement
Fat deposition	Diet composition
Conceptus weight	Genetics
Milk yield	Feeding (restricted vs. ad libitum)
Milk composition	Production status (pregnant, dry, milking, growing, and finishing)
Body size	Maturity (parity and age)
Body weight	Comparative intake is predicted
Gender	—
Age	—

composition (Basarab et al. 2003; Basarab et al. 2007). Similarly, RFI has been found to be moderately heritable (h^2 = 0.16–0.43) in growing cattle (Berry and Crowley 2013). A major disadvantage of RFI is that it requires accurate measures of individual animal feed intake. To meet the criteria for evaluation, individual animals are acclimatized to a feed intake measurement system for a 21 d period, followed by a 45–50 d measurement period that requires body weight to be recorded on two consecutive days at the beginning, end, and at regular intervals throughout the feeding period (Manafiazar et al. 2017; Kenny et al. 2018). A limitation of RFI is its dependence on production system and feeding management as well as its reliance on a predicted dry matter intake (DMI) based on maintenance and growth requirements (Table 1). However, RFI, unlike growth rate, DMI, and FCR, is independent of body size, weight, production, gender, and age (Kenny et al. 2018).

Improving feed efficiency of beef through selection for low RFI aims to use less feed to achieve the same level of output. Selection of low RFI cattle has been shown to correlate with a reduction in feed intake, decreased enteric methane (CH_4) production, and improved feed conversion, with no effect on body weight or growth (Elolimy et al. 2018). Additionally, selection for low RFI had no effect on calving, pregnancy, or weaning rates (Arthur et al. 2005; Basarab et al. 2011; Callum et al. 2018). Improving efficiency using RFI as an indicator also has the potential to decrease land use and subsequent demands for forage and feed production, whilst also reducing agricultural impacts on biodiversity and environmental pollution (Fig. 2). Though not easily quantified, these factors should be considered when evaluating the consequences of selecting for efficient beef cattle.

Changes in efficiency of beef cattle

Cattle that were imported from Britain to the Americas were a dual purpose animal used primarily for milk and draught, and only after their usefulness for draft declined were they produced specifically for meat. It was not until the mid-1800s that Shorthorn, Aberdeen Angus, and Hereford breeds (British breeds) were incorporated into the Canadian beef herd for the purpose of beef production. At the start of the 20th century, farmers and ranchers selected beef cattle for smaller frame size resulting in cattle that matured and fattened earlier. This resulted in a beef population that was dominated by smaller, compact animals with increased prevalence of dwarfism genes (Willham 1982). Carcass size of slaughter cattle was approximately 250 kg, and this trend only started to be reversed in the early 1970s due to the selection for increased growth rate and larger framed cattle through cross breeding (Berg 1975; Berg et al. 1979; Gregory and Cundiff 1980; Fredeen et al. 1981). Larger framed, leaner and faster growing European continental breeds including Charolais, Limousin, and Simmental were crossed with British breeds, producing offspring that grew faster, were leaner and had increased frame size and heavier carcasses. Thus, since the 1960s, there has been a steady increase in finished carcass weight of Canadian beef cattle ranging from ~250 kg in 1960 to ~400 kg in 2019. However, during the period from 1970 to the mid-1990s, mature cow maintenance requirements also increased due to selection for increased growth rate and body size (Evans et al. 2002). In the mid-1990s to present day, selection for a balanced animal with a moderate frame that is early maturing has improved the efficiency of the Canadian beef herd.

Despite past detrimental selection pressure, the production efficiency of beef cattle production has improved dramatically in the past 50 yr. Comparing numbers from 1977 to 2007, the same amount of beef is produced with 69.9% of the animals, 81.4% of the feed, 87.9% of water, and 67.0% of land in the US (Capper 2011). In Canada, over the last 30 yr, the improvement in the production efficiency of beef has resulted in a 14.0% decrease in kilogram carbon dioxide equivalents produced per kilogram of live weight and a 24.0% reduction in the amount of land required to maintain the Canadian beef herd (Legesse et al. 2016). Continued improvements in beef cattle efficiency are a requirement for meeting human food demands while maintaining economic stability and environmental sustainability.

Monogastrics vs. ruminants

Despite historical improvements in beef cattle efficiency, the industry is still publicly criticized for the relatively lower feed efficiency of beef cattle compared with monogastric livestock and poultry. A variety of factors account for this difference in efficiency including: diet, environmental dependency, body size, maintenance requirements, and gestation period (Table 2). Ruminant production is often criticized for its inability to compete with the efficiency of monogastrics, yet more than 80% of the feed consumed by monogastrics (poultry and

Fig. 2. Benefits of increasing the efficiency of beef cattle production. [Colour online.]

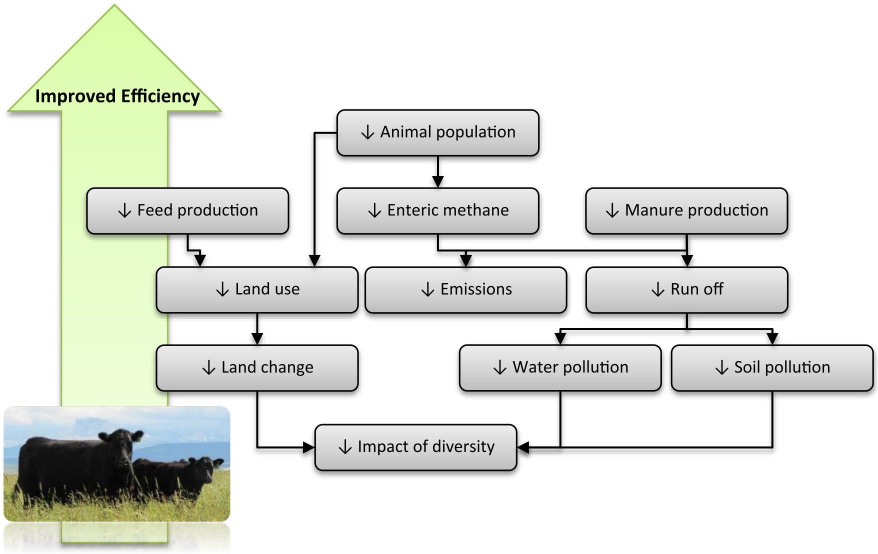


Table 2. Comparison of production attributes in poultry and beef production.

Production attribute	Poultry	Beef
Gestation	21 d	283 d
Offspring	Up to 200 eggs yr^{-1}	1 calf yr^{-1}
Age at slaughter	42–56 d	540 d
Environment	Controlled	Extreme variability
Diet	Grain-based	Forage-based
Maintenance requirements	Low	High
Genetic turnover	High	Low
Feed conversion efficiency	2:1	6:1

pork) could be considered as food for humans as compared with about 5% of that consumed by ruminants (Mottet et al. 2017). In grazing and mixed systems, roughages are the main (>80%) dietary component, and for the most part, these sources (i.e., grasses, silage, and crop residues) do not compete with food for humans (Mottet et al. 2018). It is only within the last 3–4 mo before slaughter that intensively produced feedlot cattle consume a high grain (90% dry matter) finishing diet to improve system efficiency, as keeping youthful cattle destined for slaughter on high forage diets at low gains results in more days on feed, more emissions, and lower profits.

Increasing the amount of concentrates in beef cattle diets can improve production efficiency, though it detracts from the benefits associated with the ability of ruminants to convert low-nutrient feeds into high-quality milk and meat. As diet has a large impact on the efficiency of all livestock, ingredients of the diet must be considered to properly compare the environmental footprint of different livestock production systems. Efforts to find representative metrics considering the nutrient composition of feeds and their competition with human consumption is a more balanced approach to compare the relative efficiencies among livestock sectors (Table 3). For example, a comparison of global ruminants and monogastric production systems found that ruminants require less human-edible food to produce 1 kg of meat than monogastrics (2.8 vs. 3.2 kg for beef cattle and monogastrics, respectively). However, ruminants consume 133 kg of dry matter (DM) to produce a kilogram of protein, whereas monogastrics use only 30 kg of DM (Mottet et al. 2017).

The comparative environments of beef and poultry production can also account for differences in efficiency as cattle inhabit and grow in environments not suitable for other production systems including those with harsh climates and nutrient deficiencies. Ruminant production is successful across all biomes including temperate and tropical rainforests to deserts and alpine regions. Alternatively, in intensive monogastric production systems, environments are adjusted to suit the animal with most monogastrics housed indoors in environmentally controlled barns. In the US, it is estimated that >99% of broilers and >97% of pigs (USDA 2017) are

Table 3. Feed conversion ratio (FCR) using different metrics in comparing world monogastric and ruminant production systems.

FCR metric		Livestock (FCR)	
Intake (kg feed)	Output (kg)	Ruminants	Monogastrics
DM	Protein	**133**	30
Human-edible DM[a]	Protein	5.9	**15.8**
Human-edible DM[a]	Meat	2.8	**3.2**
Human-edible DM[a] + SBC	Protein	6.7	**20.3**
Protein	Protein	2	**14**
Protein-edible feed	Protein	0.6	**2**
Protein-edible feed + SBC	Protein	1	**4.2**

Note: Adapted from Mottet et al. (2017). DM, dry matter; SBC, soybean cake. Bold text indicates a higher FCR.

[a] Feeds that compete with human consumption, including only cereal grains, pulses, soybeans, and roots.

raised in intensive housing allowing for genetic selection within a narrow range of environmental parameters. If these animals are removed from these controlled environments, they face adverse effects on health and mortality (El-Deek and El-Sabrout 2019). For example, free-range broilers had double the mortality rates and finished 141 g lighter than those raised within confinement (Durali et al. 2012).

Unlike housed monogastrics, selection for efficiency in cattle must consider climate, with extreme heat and cold increasing the energy requirements for maintenance and growth (NASEM 2016). The environmental adaptability of beef cattle has a large influence on animal productivity and can occur at the expense of production. For example, compared with *Bos taurus* breeds, *Bos indicus* breeds exhibit increased adaptability to warm climates, although they have lower reproductive and feed efficiency rates (Rodrigues et al. 2017). Animal production under controlled environments eliminates these environmental influences, but it is unlikely to be an economic or spatially viable strategy for beef cattle (Gaughan et al. 2018). Alternatively, increasing the efficiency of dairy cattle through intensification via housing is well established across several developed and developing nations. For example, composite breeds of *B. indicus* and *B. taurus* are kept in housing in tropical countries to improve milk production efficiency as a result of a reduction in environmental stressors such as parasites and heat (O'Neill et al. 2010). Similarly, *B. taurus* dairy cows are also often housed indoors in temperate countries. Similar to monogastrics, these dairy breeds exhibit less genetic variability than beef cattle, and dairy genetic pools are often less suited to coping with environmental challenges.

The low reproductive cycle of cattle (<1 calf cow^{-1} yr^{-1}) compared with chickens (~180 eggs hen^{-1} yr^{-1}) and even pigs (~20 piglets sow^{-1} yr^{-1}) also slows the rate of genetic progress and, therefore, plays a major role in the slow rate of efficiency gains obtained via genetic selection (Nielsen et al. 2013; Zuidhof et al. 2014). The maintenance of the producing cow herd also accounts for 65% of the feed energy required for the beef production cycle (Nielsen et al. 2013). It is theorized that a 20% increase in reproductive rate of the cow herd would reduce the total feed energy requirement per kilogram of edible product by approximately 12% (Dickerson 1978). Additionally, assessment of feed efficiency in beef cows is difficult as they are largely maintained on pasture, where measurement of feed intake is challenging.

Although ruminants in sub-Sahara Africa frequently have reproduction rates of less than 50%, they provide milk and protein to stakeholders with little to no input (Otte et al. 2019). Many of the people within these developing regions would not meet their dietary protein requirements without cattle as a source of meat and milk. Reducing the carbon footprint of cattle in these systems could be easily obtained through improvements in nutritional and management practices that increase milk production, reducing the time to slaughter, and improving reproductive efficiency.

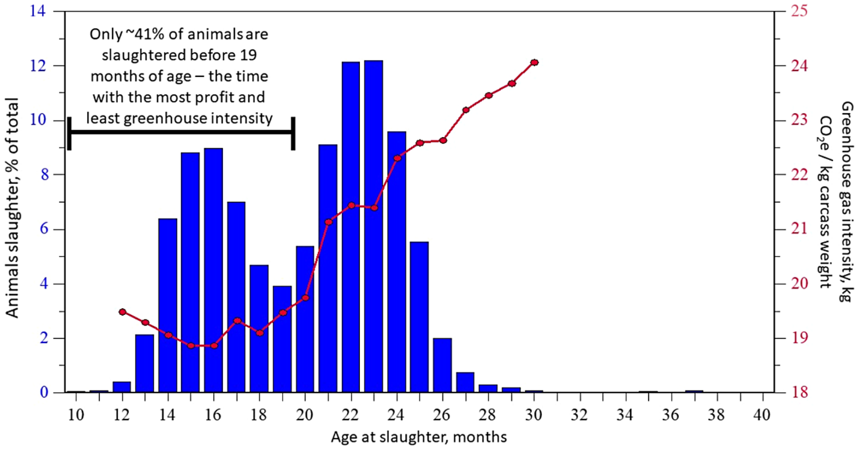
Strategies to Improve Efficiency

Management

Production management

Increasing carcass weight, reducing age at slaughter, maintaining optimum heterosis, and using multi-trait selection indices for feeder cattle and fertile replacement heifers are management practices that have a large impact on the sustainability of beef production. The improvements observed in the environmental footprint of the North American beef herd over the past 70 yr reinforces that increasing carcass weight and reducing age at slaughter is one of the simplest approaches to reducing the environmental footprint of beef production and improving production efficiency. Cattle with larger frame and carcass weight divert energy towards production more efficiently than smaller framed animals that divert more energy towards

Fig. 3. Slaughter by age and greenhouse gas intensity per kilogram of carcass weight of Canadian beef cattle (data obtained from Canadian Cattle Identification Agency database as of 1 June 2009). [Colour online.]



maintenance (Castro Bulle et al. 2007). Beef breeding programs should focus on selecting for faster growing and moderate to large framed crossbreed cattle, reducing the number of animals required to produce the same quantity of meat. However, large framed cows have higher feed input costs and are less fertile if there is limited forage of sufficient quality in extensive grazing systems (Evans et al. 2002). As grazing and mixed (grazing and feedlot) systems account for more than 90% of the world's beef production, improvements in this sector are critical to improving the efficiency of beef cattle production. Without the use of controversial growth promoters like hormonal implants and beta-agonists, decreasing the optimum age at slaughter and ensuring that cattle are moved from the cow–calf to a feeder system and sold before their growth rate plateaus ensures that consumed energy is directed towards gain. Alternatively, establishing finishing targets for feeder cattle, such as 420–450 d to reach slaughter weights of 612 kg for calf-fed feeder cattle and 510–540 d to reach 658 kg for yearling feeder cattle, results in improved efficiency, increased profit, and decreased intensity of greenhouse gas emissions (Fig. 3).

Segmentation of the beef industry is a major constraint to efficiency improvement. Beef production is frequently challenged by the lack of vertical or cooperative integration of data across the production cycle. In addition, no single-coordinated breeding strategy is followed as each breed association and seed stock producer has their own breeding objectives. Similarly, the use of artificial insemination and other breeding technologies is limited, slowing the rate of genetic progress (Burns et al. 2010). The geographic distribution of cow–calf and feedlot sectors as well as the large number of cow–calf producers makes vertical integration challenging. One of the biggest advantages of cooperative integration is the ability to amalgamate data across the sector, enabling advanced data analytics to be applied to achieve common breeding and production goals. A large specialised program that drives improvements in efficiency in a calculated and coordinated manner would be more effective than the diverse breeding goals that are currently employed in the beef industry. Integration would also allow increased product consistency and large-scale genomic reference pools would improve the predictability of traits related to performance and efficiency. Alternatively, the biggest restriction to the adoption of vertical integration in the beef sector is the differential production goals of each sector (cow–calf, feedlot, and packing segments). The biological optimum for the grazing-based cow–calf sector and the grain-based feedlot sectors is often antagonistic. Similarly, breeding decisions by the cow–calf sector will not be made in the interest of the feedlot sector if they are unwilling to share the economic cost.

Breeding management

Heterosis is defined as the performance superiority of crossbred progeny over the average of its parents, and retained heterozygosity is a measure of the relative percentage change in heterosis of the progeny compared with the first generation (Basarab et al. 2018). Applying breeding management strategies to maintain heterosis in a herd can have many benefits to beef cattle efficiency. Single-nucleotide polymorphism (SNP) panels are a genomic tool that can predict genomic breed composition, retained heterozygosity, and heterosis of beef cattle (Akanno et al. 2017). A 10% change in retained heterozygosity resulted in 51 ± 20 d longer survival in the herd, 35.7 ± 15.2 kg more calf weight weaned per cow exposed over five parities, and a 1–2 d decrease in age at first calving. These gains equated to a CA$161 increase in yearly profit per heifer when averaged over five parities in an intensive beef production system (Basarab et al. 2018). Additionally, genomic retained heterozygosity and retained heterosis were positively and linearly correlated to cow fertility, longevity, and lifetime productivity (Basarab et al. 2018).

Genomic retained heterozygosity also improved calf health and resilience from birth to weaning and decreased "all-caused" mortality and morbidity in feeder cattle. Genotypes of 552 calves born in 1 yr that were tracked from weaning to 60 d post-weaning revealed that the odds of calves with low genomic retained heterozygosity (gRHET < 0.05) getting sick or dying was 2.45 times higher than calves with a high genomic retained heterozygosity (gRHET ≥ 0.05) (Case et al. 2019). Similarly, a US study reported that each 1% change in heterozygosity resulted in a 1.14% increase in the probability of a female staying in the breeding herd until 4 yr of age (Genho 2019).

Maintaining hybrid vigor can also improve the sustainability of beef cattle production through breeding animals that are more resistant to environmental fluctuations brought about by climate change. For example, *B. indicus* exhibit a natural genetic tolerance to heat and parasites, whereas *B. taurus* breeds are cold tolerant and produce higher quality beef (Rodrigues et al. 2017). Identification of genes that makes *B. indicus* breeds more tolerant to environmental and nutritional stress could be successfully incorporated into a *B. taurus* herd through selective cross-breeding (Gaughan et al. 2018). Slick hair, thyroid hormone receptor, fibroblast growth factor, and heat-shock protein genes are involved in thermo-tolerance in ruminants and are candidates to select for increased adaptability of beef cattle to warmer climates (Gaughan et al. 2018). Whole genome sequencing and marker-assisted selection may also be able to accelerate the selection for climate-adapted beef cattle, without disadvantageous effects on production attributes. Genomic tools that use parentage information, breed, and an estimate of hybrid vigor are being developed to support cross-breeding decisions in commercial production herds (Basarab et al. 2018).

Genetics

Genome sequencing

Development of SNP panels offers the ability to predict the efficiency of an animal at a young age, immediately providing information on their breeding potential, optimum age at slaughter, and their possible immune robustness. In a validation study conducted to assess an SNP panel for genetic improvement associated with feed efficiency, 63 SNPs showed variation (19.4%) in feed-efficiency traits (Abo-Ismail et al. 2018). Of these, the ciliary neutrotrophic factor receptor (*CNTFR*), oncostatin M receptor (*OSMR*), and the growth hormone receptor (*GHR*) genes associated with the Jak-STAT signaling pathway showed potential as genetic markers that could be used to select for improved feed efficiency. The Jak-STAT pathway is involved in cell development, insulin signaling, and lipid and glucose metabolism (Abo-Ismail et al. 2018). *GHR* encodes for a receptor for growth hormone which influences growth, function and metabolism, and cellular storage of carbohydrates, proteins, and lipids (Di Stasio et al. 2005). Similarly, inter-animal variation in RFI has been associated with nutrient digestibility (10%), body composition (5%), heat increment of feeding and fermentation (9%), physical activity (9%), and energy expenditure due to protein turnover, tissue metabolism, and stress (37%) (Herd and Arthur 2009; Basarab et al. 2013). Protein turnover, ion pumping associated with Na^+/K^+ ATPase and mitochondrial proton leakage accounted for 20% of the total inter-animal variation in basal energy expenditure (Bottje and Carstens 2009). Understanding the biological and physiological pathways underlying variation in RFI can focus selection on those genes that are most pertinent to efficiency (Cantalapiedra-Hijar et al. 2018; Kenny et al. 2018).

Genome-wide association studies (GWAS) use available genotypes in the form of SNPs to identify genomic regions that are associated with phenotypic variation, including those associated with efficiency (Akanno et al. 2018). Using GWAS, seven SNPs with significant dominance (within-locus) associations were detected for birth weight, weaning weight, pre-weaning daily gain, yearling weight, and marbling score, all economically important traits related to efficiency. These SNPs were mapped to six putative candidate genes that had biological functions related to the regulation of gene expression, glucose and lipid metabolism, and fat deposition (Akanno et al. 2018). However, regions associated with these production traits have large confidence intervals, making it difficult to identify causative mutations directly associated with these traits, and only a few causative mutations have been validated to date.

Marker associations with RFI have been reported in cattle, and putative quantitative trait loci have been mapped (Saatchi et al. 2014). However, these quantitative trait loci are defined as population specific and have little overlap with other populations of cattle (Saatchi et al. 2014). A meta-analysis of GWAS revealed a common pathway of genes involved in valine, leucine, and isoleucine catabolism that were related to RFI in three metagenomic studies (Duarte et al. 2019) and one transcriptomic study (Khansefid et al. 2017). These branched-chain amino acids have diverse metabolic roles and are associated with protein synthesis and energy generation within the rumen as well as protein turnover in body tissues. Increased activity of these genes may increase maintenance requirements and reduce the efficiency of beef cattle (Herd and Arthur 2009).

Screening for animals that exhibit greater disease resistance can positively affect general production efficiency through decreasing death loss and incidences of morbidity. Though the average heritability of most health and disease traits is low (<0.20), natural variation exists within a population, implying that genetic selection for these traits is achievable (Berry 2014). For example, selection for increased resistance to disease can be achieved either directly through specified health traits, or indirectly through correlated traits such as body condition score and increased survival, assuming that these traits are correlated with immune health. In Holsteins, traits such as antibody-mediated immune response and skin thickness were used to predict immune responses and were found to be moderately heritable (0.25–0.35) (Mallard et al. 2015). Furthermore, high immune responders were found to have increased average daily weight gain as compared with low immune responders (Mallard et al. 2015). Exploitation of the genetic variance in the susceptibility to bovine respiratory disease (BRD) may also be another strategy to improve the efficiency of livestock production due to its prevalence within the beef cattle industry. Heritability estimates of susceptibility to BRD range from 0.07 to 0.22, and 0.05 to 0.07 for maternal indirect selection (Berry 2014). In a GWAS, Holstein cattle with superior antibody-mediated and cell-mediated immune responses were genotyped using the Illumina Bovine SNP50 BeadChip (Thompson-Crispi et al. 2014). A total of 186 SNPs were associated with antibody-mediated immune responses, and 21 SNPs were associated with cell-mediated immune responses. Various pathways including antigen processing were identified as being important for host defense. Most health and immunity-related genome sequencing has been conducted in dairy cattle due to the assumption that the immune system of beef cattle is more robust than that of dairy cattle. However, large-scale benefits of more research conducted in this area with specific relation to BRD immunity could result in substantial gains in production efficiency for feedlot cattle.

Genotype to phenotype

Genomic selection criteria that associate genetic variance with genotypes provide the potential to develop accurate molecular breeding values (MBVs) for selection of candidates at an early age without the need to measure these traits once a reference database is established. Use of MBVs paired with use of reproductive technologies can both reduce the generation interval and increase genetic progress towards selection for beef cattle with superior efficiency. With this increase in affordability of beef cattle genotyping, MBVs of traits related to breeding objectives could be accurately predicted. MBVs predicted up to 35% of observed variability in carcass traits with a prediction range from 0.43 to 0.59 across beef cattle breeds (Akanno et al. 2019). For growth and carcass traits, MBVs accounted for up to 18% and 8%, respectively, of genetic variation in a multi-breed analysis, and up to 28% and 42%, respectively, in single breeds of beef cattle (Weber et al. 2012).

Genomic sequencing using SNPs and GWAS has limitations with regard to predicting efficiency. These studies do not consider gene expression or if a sufficient number of genes are expressed to generate functional biochemical pathways. Unlike marker-assisted selection, genomic selection is based on associating thousands of genetic markers spread densely across thousands of reference animals (Hayes and Goddard 2010). The merit of these approaches will depend on examination of whether selection for gene expression links to quantifiable differences in beef cattle efficiency, and if these genomic selections align with environmental adaptability. Further research is required to quantify the requirements of these breeding technologies, so producers are encouraged to adopt these approaches in their breeding programs.

Efforts to correlate genotypic variation with phenotypic expression are underway. The Canadian Cattle Genome Project is a large-scale international initiative that was employed to develop genomics-based tools for genetic selection to increase the efficiency and sustainability of dairy and beef cattle production (Stothard et al. 2015). The obtained dataset contained 379 whole-genome sequences taken from mostly *B. taurus* breeds, and facilitated efforts to associate genotypic variation to phenotypic differences. The Functional Annotation of Animal Genomes project also aims to understand how variation in gene sequences and functional expression determines phenotypic diversity (Andersson et al. 2015). The expansion of this program will inform the development and exploitation of improved models for predicting complex phenotypes from sequence information. Though the mentioned studies can have wide reaching potential for improving efficiency in developed nations, the implementation of genomic sequencing within developing nations remains a challenge. The efforts of genomic sequencing can result in small and sustained improvements in the developed world, but in developing nations, a focus on improved nutrition, management, reproductive performance, and resilience to disease are likely to generate the greatest gains in efficiency.

Efficiency in the rumen microbiome

The microbial community plays a quantifiable and important role in influencing the efficiency of beef cattle production. Both confined beef (Carberry et al. 2012; Carberry et al. 2014) and dairy cattle (Jewell et al. 2015) with low RFI had lower proportions of *Prevotella* within their rumen microbiome. However, *Prevotella* has also been shown to be a common member of the rumen microbiota in less efficient cattle (Jewell et al. 2015). Other genera associated with efficient cattle include *Coprococcus* (Zhou et al. 2018), whereas *Butyrivibrio*, *Anaerovibrio* (Myer et al. 2015), and *Lachnospiraceae*, *Lactobacillaceae* and *Veillonellaceae* have been associated with less efficient cattle (Li and Guan 2017). Members of *Coprococcus* are involved in the acrylate pathway which converts lactate to propionate, a pathway that was more common than the conversion of succinate to propionate in efficient dairy cows (Shabat et al. 2016). Additionally, *Coprococcus catus* was enriched in the rumen of efficient dairy cows that exhibited increased propionate and butyrate production, a shift in fermentation that may reduce the availability of metabolic hydrogen to reduce carbon dioxide to CH_4 (Shabat et al. 2016). This suggests that the observed variation in the abundance of a particular bacterial taxa can lead to varied production of short-chain fatty acids, which supply up to 70% of energy to the animal (Bergman 1990).

Recent work has estimated that approximately 20% of the variation in production and efficiency traits in beef cattle (i.e., average daily feed intake, average daily gain, and FCR) were explained by variation in the microbiome (Paz et al. 2018). Using functional predictions based on metagenomic data, bacterial taxa associated with feed efficiency were identified to be involved in starch, carbohydrate, and protein metabolism. Similarly, inefficient dairy cows had enriched enzymes in the rumen that were associated with protein digestion and absorption, amino acid biosynthesis, and CH_4 production (Shabat et al. 2016). Animals that were more efficient possessed a lower number of Kyoto Encyclopedia of Genes and Genomes pathways and inferred metabolites, possibly a reflection of precision energetic metabolism within these individuals. In crossbred steers, the relative abundance of 20, 14, 17, and 18 microbial genes explained 63%, 65%, 66%, and 73% of the phenotypic variation in feed conversion efficiency, average daily weight gain, RFI, and daily feed intake, respectively (Lima et al. 2019*a*). Microbial genes encoding for proteins related to hemicellulose and cellulose degradation, vitamin B_{12} synthesis, and amino acid metabolism were associated with more efficient (low RFI) cattle, suggesting that these genes may be useful predictors of efficiency. However, given that the composition of the microbiome is overwhelmingly determined by the nature of the diet (Henderson et al. 2015) and the apparent variation in the rumen microbial indicators associated with RFI, their usefulness is yet to be proven. Furthermore, most rumen microbiota have yet to be cultured in the laboratory and characterizing their specific enzymatic and metabolic activities will likely be a key step in defining their impact on feed efficiency (Callaway et al. 2010).

Metatranscriptomics revealed 30 differential metabolic pathways and 11 CAZymes that were enriched in inefficient beef steers, with only two pathways and one CAZyme more enriched in efficient steers (Li and Guan 2017). This reinforces the possibility that efficient cattle possess a rumen microbial population with a less diverse range of metabolic activities than inefficient cattle. Other metagenomic studies have also indicated that more efficient cattle have a rumen which is defined by a microbial population with low species richness and gene content (Shabat et al. 2016). The feed efficiency phenotype of dairy cows was able to be predicted with an accuracy of 50% based on species and gene composition of the rumen microbiome (Shabat et al. 2016). Alternatively, microbial populations with greater uniformity may be less likely to adapt to abrupt changes in diet composition. This could be a concern for feedlot cattle rapidly transitioned from a forage to a concentrate diet and for grazing cattle consuming a diverse range of forage species (Belanche et al. 2019).

Diet is the major factor that determines the composition of the rumen microbiome (Henderson et al. 2015), although intrinsic relationships between host genetics, rumen microbial population, and phenotypic feed efficiency have also been demonstrated (Guan et al. 2008; Hernandez-Sanabria et al. 2013; Li et al. 2019). Similarly, breed, sex, and diet all influenced the composition of the rumen microbiota in beef cattle with the relative abundance of approximately 34% of microbial taxa being predicted as being heritable ($h^2 \geq 0.15$) (Li et al. 2019). These moderately heritable rumen microbial features were identified to be associated with feed efficiency traits including FCR, average daily gain, and DMI, although none of the microbiota were strongly correlated with RFI. It is assumed that host genetics can influence the rumen microbiome through changes in rumen physical features that can enhance the activity of certain microbiota. Coevolution of rumen microorganism and the host may also explain the genetic effects on host taxa, where the abundance of certain bacteria function under specific host-association patterns. For example, a host SNP associated with variation in the ruminal abundance of *Ruminococcus* was shown to be located within the Ras association (*RalGDS/AF-6*) and pleckstrin homology domains 1 (*RAPH1*) genes. This gene is associated with cell migration and nutrient absorption by rumen epithelia cells. Similarly, downstream GWAS found that 19 SNPs within the *B. taurus* autosome were associated with microbial taxa, including six bacterial genera (unclassified *BS11*, *Ruminococcus*, unclassified *Lachnospriaceae*, *YRC22*, unclassified *Mogibacteriaceae*, and unclassified *Victivallaceae*) (Li et al. 2019). Although host efficiency may be influenced by rumen microbiota, these relationships could be confounded by diet as the host–microbiome relationship was stronger in beef cattle fed a high forage than a high grain diet (Carberry et al. 2012). Consideration of the host–microbiota relationship could allow manipulation of the microbiome through genetic selection and may play a future role in selection for improved feed efficiency.

Microbial CH_4 production

Understanding of the relationship between the microbial metagenome and CH_4 production in cattle may also offer an opportunity to improve the efficiency of beef production. Stoichiometry calculations suggest that enteric CH_4 production represents an energetic loss in ruminants of 2%–12% of gross energy intake (Johnson and Johnson 1995). Sequencing of the rumen microbiome has revealed distinct microbial profiles associated with low and high CH_4 producing cattle.

Methanobrevibacter were 2.5 times more abundant in high than low CH_4 producing beef cattle, whereas *Succinivibrionaceae* were 75.9% more abundant in low than high CH_4 producing cattle (Wallace et al. 2015). Alternatively, sheep selected for low and high CH_4 emissions did not differ in the proportion of methanogens in the rumen but did have increased abundance of *Methanosphaera* spp. and a decreased abundance of *Methanobrevibacter gottschalkii* (Shi et al. 2014). However, metatranscriptomic analysis revealed that high emitting sheep had an enriched abundance of transcripts encoding for enzymes involved in methanogenesis. This reiterates that methanogenic activity rather than the abundance of methanogens influences CH_4 production (Shi et al. 2014).

Although the importance of the rumen microbiome in nutrient utilization and feed efficiency is well established, strategies to favorably alter the microbial population over the long term have met with limited success. Dietary additives can immediately alter the microbiome, but sustained changes and continuous administration of an additive are frequently required to maintain these responses. For example, monensin was shown to reduce enteric CH_4 emissions in the short term, but this reduction was not sustained over 4 wk of continuous administration (Guan et al. 2006). Alternatively, the CH_4 inhibitor 3-NOP is extremely effective in inhibiting the activity of methanogens within the rumen if it is administered daily with no evidence of adaptation (Jayanegara et al. 2018). However, an in vitro incubation found that once all 3-NOP is utilized, CH_4 production returns to pre-treatment levels within 5 h (Duin et al. 2016). Similarly, the addition of 3-NOP to a high forage diet resulted in a consistent reduction in CH_4, though once removed, CH_4 production returned to pre-treatment levels (Romero-Perez et al. 2015). This suggests that methanogens are capable of entering a state of dormancy upon exposure to inhibitors, and once administration ceases, return to a metabolically active state. Similarly, although some studies suggest that the decrease in CH_4 with 3-NOP results in energetic savings being redirected towards body weight gain, these findings are not consistent with some studies reporting that 3-NOP increased H_2 eructation (Vyas et al. 2016).

An additional limitation to long-term alteration of the rumen microbiome is that once the mature rumen microbial population is established, it exhibits a high resilience to change. For example, total rumen transfaunation did not permanently alter the microbiome, with it returning to its original state in some individuals within 7 d (Weimer et al. 2010; Zhou et al. 2018). Similarly, two transfers of rumen contents from bison into beef cattle increased the diversity and evenness of the bacterial communities in the rumen 1 and 27 d after rumen transfer (Ribeiro et al. 2017), but some phylum quickly returned to pre-transfer abundances. Early dietary intervention may be a more viable approach to programming the rumen microbiome. For example, the microbiome of lambs was shown to be altered when lambs were fed linseed oil during pre-weaning with this change persisting for 10 wk after linseed oil supplementation ceased (Lyons et al. 2017). Similarly, a single dose of bromochloromethane to pre-weaned goat kids resulted in a change in the methanogen population that persisted for 3 mo (Abecia et al. 2014). However, long-term studies examining manipulation of the rumen microbiome during early life have yet to be conducted.

Alteration of feed

Grain processing

Derivation of energy from feed by ruminants is dependent upon their symbiotic association with the complex microbial community within rumen. This complex community is responsible for converting a diverse range of feeds into nutrients to meet the host's energy and nutrient requirement for maintenance, growth, and production. Promoting the activity of the rumen microbiota is essential for rapid colonisation and fermentation of feed. The host itself plays an important role in causing physical damage to feed through mastication and rumination, breaching physical barriers that impede the rapid colonisation of feed by rumen microbiota (Terry et al. 2020). Several feed processing techniques may also be employed to further promote this, improving the ability of microbiota to derive energy and nutrients from feed.

Processing index (PI) is calculated as the ratio of volume weight of rolled grain to its original unprocessed volume weight, and is commonly used in commercial feedlots as a measure of the degree of mechanical disruption of grains (Moya et al. 2011). A lower PI is indicative of more severe processing (Ribeiro et al. 2016*b*). Processing grains to such an extent that the production of organic acids by rumen microbiota exceeds the buffering capacity and their absorption across the rumen epithelium can result in a sustained reduction in rumen pH. This can reduce microbial diversity and function, resulting in a decline in feed intake, digestibility, and efficiency (Terry et al. 2020).

Several studies have demonstrated that increasing grain processing to an extent that rumen pH declines below 5.2 can have negative consequences for animal health and production (Moya et al. 2011; Ribeiro et al. 2016*b*). Excessive processing of barley and wheat increased DMI and decreased gain-to-feed ratio, salable meat yield, and rib eye area in feedlot steers fed a high grain diet (Moya et al. 2011; Ribeiro et al. 2016*b*). Alternatively, feedlot steers fed dry- or tempered-rolled barley to a lower PI were more feed efficient than those fed barley with a higher PI (Wang et al. 2003). Tempering is a process that involves adding water for 24 h prior to rolling, resulting in fewer fine particles than dry rolling. This can reduce the rate of starch degradation and reduce the risk of the buffering capacity in the rumen being exceeded by the production of organic acids (Nikkhah 2012). Tempering barley improved milk yield, feed efficiency, and digestibility of starch by 5%, 10%, and 4%, respectively, compared with dry rolling in dairy cows (Christen et al. 1996). Similarly, tempering of barley before rolling increased DMI, average daily gain, and gain-to-feed ratio of steers fed a high grain barley diet (Wang et al. 2003). Increasing the degree of processing of barley (slight, medium, and crushed) improved feed conversion efficiency by 10% in beef bulls fed a high-concentrate diet (Mathison et al. 1997). Grain processing increases the extent of ruminal and total tract starch degradation and can alter ruminal and post-ruminal starch digestion by impacting its accessibility to rumen microbiota. Reduction to a smaller particle size breaches recalcitrant barriers and increases the feed surface area available for microbial colonisation (Ribeiro et al. 2016*b*).

Improving forage utilization

Improving dietary fibre degradation is important for improving efficiency as fibre can limit intake and diet digestibility. Mechanical processing including chopping, shredding, and pelleting can increase the surface area for microbial attachment, reduce gut fill, and increase feed intake (Adesogan et al. 2019). Alkali treatment is also an effective method for breaking down the fibrous components that restrict microbial degradation. Alkali treatments including ammonia, sodium hydroxide, oxidative lime, calcium oxide, and calcium hydroxide have been successfully employed to increase ruminal fibre degradation and the nutritional value of low-quality feeds (Chang et al. 2001; Adesogan et al. 2019). Ammonia fibre expansion technology (AFEX) is another alkali-based technology that has extended the potential for utilizing highly fibrous feed in ruminant diets. AFEX involves exposing recalcitrant fibre to steam and anhydrous ammonia at high pressure and temperature for 1 h, followed by rapid depressurization and ammonia recovery (Teymouri et al. 2005). This combination of physical and chemical treatment disrupts hydrogen, ether, and ester bonds, partially solubilizes lignin, and hydrolyses hemicellulose to a greater extent than conventional alkali treatments (Teymouri et al. 2005; Balan et al. 2009).

The AFEX treatment of barley straw, wheat straw, corn stover, and rice straw increased in vitro dry matter disappearance by up to 128% (Beauchemin et al. 2019). Similarly, AFEX-treated barley straw increased dry matter, neutral detergent fibre, and acid detergent fibre degradation, whilst also reducing CH_4 produced per gram digested dry matter in an artificial rumen (Griffith et al. 2016). Feeding AFEX-treated rice straw to lactating dairy cows increased neutral detergent fibre intake and milk production when included in the diet at 7% of dry matter (Weimer et al. 2003). Compared with non-treated wheat straw, AFEX treatment increased intake, digestibility, and milk production in lactating buffalo and crossbred dairy cattle (Mor et al. 2018). Though there is enormous potential for AFEX, increased processing and transport costs associated with this technology must be considered (Adesogan et al. 2019).

Supplementation of fibrous feed with exogenous fibrolytic enzymes is proposed as an effective method for improving fibre utilization of cattle. A meta-analysis found that cattle with <50% forage in their diet had increased average daily gain if exogenous fibrolytic enzymes were added to the diet (Tirado-González et al. 2018). Alternatively, when diets contained greater than 50% forage, feed intake, average daily gain, and gain-to-feed were not improved (Tirado-González et al. 2018). Across multiple studies (Ribeiro et al. 2016*a*; Tirado-González et al. 2018; Terry et al. 2019), it is consistently reported that the effects of enzymes varies and is confounded by multiple factors including enzyme type, specificity, rate of application, and dietary composition. Enzyme application, unlike other dietary additives, must also compete with digestion rates and ruminal residence times to be effective within the rumen (Terry et al. 2019). However, if the variability in enzyme responses could be overcome through novel enzyme discovery and delivery, they could play a role in improving the feed efficiency of ruminants.

Food wastage

It is currently estimated that 30% of cereals, 45% of roots and tubers, 45% of fruits and vegetables, and 20% of oilseeds and pulses are wasted globally [Food and Agriculture Organization (FAO) 2019]. There is large potential for food waste to be incorporated into ruminant diets, possibly improving diet quality as these wastes are often higher in protein or water-soluble carbohydrates than standard feeds. Using food that does not meet the quality grade for human consumption reduces the extent to which components in ruminant diets compete with food for humans. For example, incorporation of unsalable carrot or pumpkin waste at up to 40% of dry matter in ensiled corn or sorghum did not alter silage quality and improved in vitro dry matter digestibility (Forwood et al. 2019; Hooker et al. 2019). Similarly, grazed forages, hay, silages, and grains are often contaminated by a wide range of mycotoxins, toxic molecules produced by fungi, often as a result of unfavourable ensiling and storage conditions (Gallo et al. 2015). Ruminants are considered to be less susceptible to the negative effects of mycotoxins than monogastrics due to the ability of the rumen microbiota to degrade, deactivate, or bind these toxic molecules (Gallo et al. 2015).

By-products from the preparation of food for humans or biofuel production can also be effectively utilized as feed for ruminants. For example, replacement of soybean meal with soybean cake had no effect on DMI, volatile fatty acid production, or apparent digestibility in dairy cows (Silveira et al. 2019). Similarly, dried distillers' grain readily replaces cereal grains in ruminant diets due to its rich energy and protein content (Hünerberg et al. 2014). Additionally, a meta-analysis found that when distillers grain plus solubles replaced forage in total mixed rations, it increased the average daily gain and final body weight of backgrounding cattle (Griffin et al. 2012). A limitation to the use of high-fat products is that total dietary fat content should remain below 6% to minimize the negative effects of fats on fibre digestibility (Johnson and Johnson 1995).

Not only does inclusion of human food wastage in ruminant diets increase its nutrient content, incorporating wastage from crop and biofuel production contributes to the economic sustainability of these systems. If food that did not make human quality grades was not able to be fed to ruminants, these unsalable by-products could become a net liability and result in significant reductions in revenue. It has been estimated that ∼86% of global livestock DMI consists of feed materials unsuitable for human consumption (Mottet et al. 2017). For example, in 2018, dried distillers' grain accounted for more than 25% of total revenue generated as a result of ethanol production from the fermentation of corn (Irwin 2018). Similarly, approximately 85% of the world's soybeans are pressed annually into soybean cake and oil, of which 97% of the resultant meal is processed into animal feed, a principle driver of soybean production (Mottet et al. 2017). In Canada, over 75% of malt barley fails to make the quality grade required for human consumption and is relegated to livestock feed (Ribeiro et al. 2016*b*). Producers that produce malt barley for beer processing are dependent upon the livestock industry to purchase crops that do not make the grade for human consumption. Without the value of these by-products, such enterprises would not be profitable as by-product disposal would represent a financial and environmental liability. Incorporation of these feeds into beef cattle production should not be considered as a part of the carbon footprint of beef production as they would be diverted to landfills, burned or composted if they had no value as a ruminant feed. Consequently, the contribution of ruminants to circularity in the food chain should be considered in efficiency assessments.

Plant breeding

The nutritional value and the degradability of dietary components are dependent on a range of environmental and genetic factors. Climate change influences crop production through altered weather patterns, increased soil salinity, drought, and susceptibility to disease and insect attack (Haque et al. 2018). Intensive selection for traits that improve the robustness of crops against these challenges and increase the derivation of energy and nutrients during ruminal fermentation can improve the feed efficiency of beef cattle (Adesogan et al. 2019).

Improvements in fibre degradability are usually observed when lignin or indigestible neutral detergent fibre content is reduced. Genetic selection for crops with decreased concentrations of these components can improve the degradability of forages. The brown-midrib mutation of corn, sorghum, and pearl millet reduces lignin content, and a brown-midrib corn silage-based total mixed ration improved feed efficiency of beef heifers by 11.5% as compared with conventional corn silage (Saunders et al. 2015). Additionally, brown-midrib corn silage increased total volatile fatty acid production and decreased the proportion of acetate to propionate, resulting in a 23.6% increase in net returns ($ per steer). Similarly, compared with control lines, in vitro dry matter and neutral detergent fibre digestibility were increased in two lignin down-regulated alfalfa lines (Getachew et al. 2018). Likewise, lignin down-regulated alfalfa hay increased neutral detergent fibre intake and digestibility when fed to young lambs (Mertens and McCaslin 2008), but not to dairy cattle (Weakley et al. 2008).

Development of forages that yield higher concentrations of water-soluble carbohydrates can also improve the efficiency of ruminal production. A perennial ryegrass that was selected for higher concentrations of water-soluble carbohydrates, improved milk production and total tract neutral detergent fibre and acid detergent fibre digestibility in dairy cows as compared with conventional ryegrass (Miller et al. 2001). Further research should investigate the possibility of breeding forages with high sugar concentrations as long as there are no negative consequences on forage yield. The major difficulty with selecting plants based on their potential to improve feed efficiency in cattle is that this goal must be accomplished without compromising the yield of digestible dry matter. For example, earlier brown-midrib hybrids had lower yields than conventional hybrids, which may negate the benefits associated with improvements in digestibility (Adesogan et al. 2019).

Health and immunity

Genetic selection for improved animal health or disease resistance has the potential to compliment genetic gains associated with selection for improved feed efficiency. Unlike traditional prevention and treatment strategies for diseases, genetic gain is cumulative and can persist over generations. Improving the health and immunity of cattle can complement advancements in feed efficiency by improving production efficiency through a reduction in morbidities and mortalities.

Respiratory tract microbiome

Bovine respiratory disease is the most common cause of morbidity and mortality in feedlot cattle, resulting in production, welfare, and economic losses (Holman et al. 2015). Infection with BRD decreases feed efficiency and life-cycle efficiency as BRD causes 65%–80% of morbidities and 45%–75% mortalities in North American feedlots (Beef Cattle Research Council 2019). Similarly, respiratory disease was found to be negatively correlated with average daily gain, marbling score, and hot carcass weight across 18 feedlots over 5 yr (Reinhardt et al. 2009). In a further evaluation of 5976 feedlot cattle, BRD was associated with a 0.37 kg d^{-1} loss in average daily gain and a reduction in carcass weight of 8.16 kg (Schneider et al. 2009). These studies demonstrate the importance in maintaining respiratory health to achieve overall beef production efficiency.

Resident microbiota colonising the respiratory tract have a critical role in fighting against bacterial pathogens that result in BRD. Identification of microbes within the respiratory tract that precipitate the development of BRD can enhance the understanding and inform strategies to treat or prevent the disease. Breed differences in disease susceptibility have shown that increased genomic heterozygosity was associated with a decrease in the incidence of BRD as compared with purebred populations (Snowder et al. 2005). Similarly, factors including inheritance, the genetics of the dam, and environmental factors (i.e., uterine environment and colostrum) influence the genetic susceptibility of the offspring to respiratory disease (Snowder et al. 2005).

Bacteria frequently associated with BRD include *Mannheimia haemolytica*, *Pasteurella multocida*, *Histophilus somnus*, *Pasteurella multocida*, *Trueperella pyogenes*, and *Mycoplasma bovis* (Klima et al. 2014; Zeineldin et al. 2019). These bacteria are opportunistic pathogens that are present within the respiratory tract of both healthy and BRD-infected cattle. Consequently, factors that alter immunity and the microbiome could provoke atypical colonisation and the development of dysbiosis within the lungs. Commensal bacteria can inhibit the proliferation of bacterial pathogens through competition for nutrients, competitive exclusion, and the production of antimicrobials (Zeineldin et al. 2019). Feedlot cattle with BRD exhibited less bacterial diversity in their nasopharynx before and after (60 d) feedlot placement, with the nasopharynx of healthy cattle being enriched in *Micrococcaceae*, *Lachnospiraceae*, *Lactobacillaceae*, and *Bacillaceae* (Holman et al. 2015). In calves diagnosed with BRD, the respiratory tract microbiome was shown to be characterised by a reduction in bacterial richness and evenness (Holman et al. 2015; Timsit et al. 2018). Alternatively, although deep nasophyaryngeal and pharyngeal swabs revealed shifts in bacterial taxa between healthy and BRD calves, there was no difference in the diversity of the microbial community (Lima et al. 2016; Zeineldin et al. 2017). This demonstrates that the microbiota colonising the respiratory tract of cattle may be able to be manipulated to minimize the negative effects of respiratory disease on production efficiency.

Mannheimia haemolytica is a Gram-negative bacterium that is found throughout the respiratory tract of ruminants. However, upon exposure to external stressors, it can rapidly colonise the lung and cause acute fibrinonecrotic pleuropneumonia (Shanthalingam et al. 2016). Modulation of the disease through use of natural microflora inhabiting the respiratory tract was recently investigated (Amat et al. 2019). A single dose of a intranasal probiotic consisting of a mixture of six *Lactobacillus* strains reduced nasal colonisation of *Mannheimia haemolytica* in dairy calves (Amat et al. 2020) and caused no adverse effects on the health and growth performance of beef calves (Amat et al. 2020). Similarly, the ecological network of nasopharyngeal microbiota from treated calves became more integrated, suggesting that selection for a more stable microbiome can result in a population with increased resistance and resilience to pathogens. This technology illustrates the enormous potential to use natural therapeutics to reduce BRD and raises the possibility of its use to combat other diseases that arise as a result of the displacement of commensal microbiomes.

As the microbiota colonising the respiratory tract have an important role in BRD, determining the origin of these colonisers may inform strategies to improve respiratory health. The earliest potential source of microbial colonisation of the calf occurs as it passes through the birth canal of the dam. Bacterial communities found in the upper respiratory tract of dairy calves were highly similar to those found with the vaginal canal of the dam, with 73%–87% of operational taxonomic units being shared at 3, 14, and 35 d after calf birth (Lima et al. 2019*b*). This illustrates that the maternal vaginal microbiota has a strong impact on the calf upper respiratory tract microbiota, and thus there may be a maternal influence in the incidence of BRD. If suitable probiotics could be identified, seeding of the birth canal with these bacteria may provide the calf with resilience against BRD.

Future Directions

Genomic selection from genotyping of ruminants and their feed promises a long-term strategy for improving the efficiency at which beef cattle can utilize feed nutrients. However, genetic screening currently requires costly genotyping, a practice that is still too expensive for wide spread adoption by stakeholders, particularly in developing countries. Future development of genomic techniques can improve the cost of genetic profiling, increasing the viability of genetic selection programs. Alternatively, a combination of nutritional, breeding, and feed management strategies, as well as performance selection of cattle, represents a viable approach to increase production, decrease feed requirements, and reduce the environmental footprint of cattle. There are a myriad of genomic approaches to improving efficiency in beef cattle, an example of two of the most recently emerging strategies are outlined below.

Exosomes are vesicles formed within animal and plant cells that are involved in cell communication and nutrient delivery (Akuma et al. 2019) and have the potential to radically improve efficiency. Exosomes consist of a lipid bilayer and contain a diverse range of biological compounds including messenger RNA (mRNA), microRNA, membrane receptors, protein, and lipids (Akuma et al. 2019). Understanding the function of these complexes in regulating gene expression could identify new avenues for improving the efficiency of beef cattle production.

In animals, exosomes are secreted mainly by red blood cells, platelets, and lymphocytes (Mandal 2017), and they are present in biological fluids including milk, urine, blood plasma, and amniotic fluid (Keller et al. 2007). The exosomes insert their contents into target cells through phagocytosis or membrane fusion and can be delivered orally, through an intranasal spray or through intravenous injection (Mitchell et al. 2020). Customised molecules could be inserted into donor cells, including mRNA genes that code for proteins that target specific cells.

Exosomes have the potential to be used in the development of biomarkers for health or productive status and as a therapeutic. Research has been conducted to differentiate the cargo profiles of exosomes as influenced by dairy cows differing in metabolic health (Crookenden et al. 2016), uterine health, and fertility status (Koh et al. 2018; Mitchell et al. 2020). Currently, ruminant exosome research has been conducted in dairy cattle; however, an Australian project has been funded with the aim of identifying tick-resistant beef cattle through characterization of exosomes.

Editing exosomes also has the potential to be used in plants to improve their robustness against climate change or change their chemical composition so as to be more suitable as a feed for ruminants. For example, exosomes in the apoplasts of Arabidopsis leaves were shown to be enriched in defense and stress-related proteins as a result of exposure to abiotic stress (Rutter and Innes 2017).

Genome editing may also be used in genomic selection programs to increase genetic gain within beef production systems. CRISPR technology is more cost effective, precise, and highly efficient compared with other genomic technologies like zinc finger nucleases and transcriptional activator-like effector nucleases (Zhang et al. 2019). Genome editing has previously focused on disease resistance, welfare traits, and some production characteristics, and has produced cattle with resistance to tuberculosis (Gao et al. 2017), increased muscling (Proudfoot et al. 2015), and elimination of the horned trait (Carroll et al. 2016). Gene editing was employed to modify alleles so as to allow the expression of genetically engineered cattle that would produce leukocytes resistant to leukotoxin-induced cytolysis, demonstrating the feasibility of breeding lines of cattle genetically resistant to *Mannheimia haemolytica* (Shanthalingam et al. 2016). Leukotoxin is recognised as a critical virulence factor and is primarily responsible for the induction of respiratory disease and death in calves. Successful gene editing within plants has also been shown using CRISPR technology which has resulted in genetic resistance against fungi, increased yield during drought stress, and increased genetic variation within certain crops (Gao 2018).

Though there are ethical concerns with the use of exosome and gene-editing technologies, a case has been made to allow for the editing of genes that have already been naturally mutated within a species. For example, the POLLED trait arises from a naturally occurring mutation that eliminates horn growth in cattle, and gene editing of the associated allele could avoid welfare concerns regarding the dehorning procedure (Van Eenennaam 2019). Another difficulty with gene editing is that editing of complex traits can result in unintended genetic consequences as quantitative traits are controlled by the expression of many genes (Van Eenennaam 2019). Similarly, exosome delivery needs to target specific proteins without causing other unintended metabolic changes. These technologies should focus on known single-effect targets to correct genetic defects, with conventional breeding and selection having a larger role in complex traits like feed efficiency. Similarly, gene editing and exosomes could introduce specific alleles including those that contribute to heat tolerance and disease resistance more easily than herd selection (Van Eenennaam 2019). If the ethical constraints on the use of exosome and CRISPR technologies can be addressed, these techniques could contribute to improving the efficiency of beef cattle production.

Conclusion

Though dietary modification and genetic selection has resulted in superior beef cattle populations, the efficiency status of beef cattle is influenced by other factors including diet, environment, management practices, host genetics, and gastrointestinal and nasophyaryngeal microbiomes. Evaluation of beef cattle efficiency should account for their unique ability to utilize forage, environmental adaptability, value in providing high-quality protein, and their role in providing sustainability to crop and biofuel production systems through the use of by-products. For the future sustainability of beef cattle production, successful integration of selective breeding, meta-omics, and nutritional advances is required. Additionally, a combination approach considering the complex relationship between host genetics and host microbiota should contribute to genetic breeding programs that utilize screening panels that target well-defined genomic traits. This multi-faceted approach to improving efficiency should be coupled with strategies that improve host health and survivability in the face of climate change. Strategies to improve the efficiency of cattle production are a prerequisite for the sustainable intensification that is needed to satisfy the future demand for beef.

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