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Opportunities of Genomic Selection in the Improvement of Dairy Cattle Productivity: A Review

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ABSTRACT

This review is aimed to summarize and synthesize the fragmented information in the area of genomic selection in the improvement of productivity in dairy cattle. Genomic selection has been a valuable tool for increasing the rate of genetic improvement with reduced generation interval. In addition, it can be used for selection based on genomic breeding values at an early age for superior breed with great accuracy resulting in enhanced productivity of dairy cattle populations. Genomic selection is particularly used to improve those traits with low-heritability values such as feed efficiency, reproductive traits, especially fertility including adaptation traits. The implementation of genomic selection in developed countries mainly uses purebred and hybrid of *Bos taurus* cattle. Most studies have found that genomic evaluation of pure breeds that serve as a large reference population for high milk production in dairy cows can bring more benefits. Since, most of the research works have been conducted using *Bos taurus* cattle, research focusing on the application of genomic selection on *Bos indicus* cattle is needed to evaluate its impact on the productivity of tropical cattle breeds.

Keywords: Dairy cattle, genomic selection, productivity, genetic improvement
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INTRODUCTION

Genomics is the scientific study of the structure and function of the genome of a species with a large number of nucleotide sequences. It is a new novel approach toward the genetic improvement of livestock (Yadav et al., 2018). Genomic selection (GS) was first described by Meuwissen et al. (2001) and refers to the genetic improvement of animals through selection based on genomic estimated breeding value (GEBV). The GEBV is calculated as the sum of the effects of dense genetic markers across the entire genome and the potentially capturing all the quantitative trait loci (QTL) that contribute to variation in a trait (Borakhatariya et al., 2017). The exhaustive progeny testing of production and reproductive traits based on GEBV is important to extend dairy cattle productivity. Genomic selection has shown a dramatic effect on the reliability of breeding values for animals without records or progeny (Berry et al., 2014). The increase in genetic improvement that supports the accuracy of genomic prediction helps to understand the genetic effects of the offspring of dairy cows (Gutierrez-Reinoso et al., 2021). The total genetic value of the selected candidate is predicted based on the estimated value of the single nucleotide polymorphism (SNP) effect, which is estimated using reference individuals that have been genotyped (Wallén et al., 2017).

The purpose of genome selection is to improve yield by using molecular genetic markers to develop new marker-based genetic evaluation models. Also, Genome selection is also a form of marker-assisted selection (Ibtisham et al., 2017). Genetic markers have covered the entire genome (Ding et al., 2013). Whole genome selection is effective in modern breeding methods for the assembly and selection of superior animals (Ibtisham et al., 2017). It is a better and advance way of selection as it can done at an early age with great accuracy, improved genetic gain with reduced generation interval and increases productivity as compared to traditional breeding methods in particular to improve those traits with low heritability and the traits that are difficult to measure associated with longevity and health (Ibtisham et al., 2017; Wiggans et al., 2017; Yadav et al., 2018; Lozada-Soto et al., 2021).

Genomic information has many new uses, such as pedigree discovery, mating procedures, and guidance in reproductive management. Predictions will use more genetic tests discovered from sequence data and more international genotypes (VanRaden, 2020).

Single nucleotide polymorphism (SNP) markers create the possibility of genotyping cattle in a single analysis with thousands of SNPs, providing enough genomic information to be included in the breeding value estimates. The supply of SNP markers provides new opportunities for selecting the simplest animals suitable for breeding purposes, commonly referred to as genomic selection (Ibtisham et al., 2017). The prediction of GS is based on the principle of connecting many genetic markers with phenotypic performance (Van Marle-Koster et al., 2013). Genomic breeding value is calculated by estimating the SNP effect from the prediction equation. It utilizes both the phenotypic and genotypic data from the reference population (Ibtisham et al., 2017). In addition, genomic selection is used as a tool for an in-depth understanding of the adaptive mechanisms, disease tolerance, and unique traits of native livestock resources. It's the utilization of genome-wide genetic markers to estimate the genetic merit of individual animals (Bouquet and Juga, 2013).

As the middle class of emerging economies continues to grow with rapid increase of urbanization, it is expected that the demand for dairy products will inevitably expand in the near future. In order to meet the ever-increasing demand for food, the animal husbandry industry must increase production efficiency. This may require a further increase in total output without increasing costs, while maintaining or possibly improving product quality (Fleming et al., 2018). Today, due to the low productivity of dairy cows and the restriction of genomic selection to five dairy cow breeds, the demand and supply of food are not balanced. Therefore the aim of this paper is thus to review the significance of genomic selection in the improvement of dairy cattle productivity.

History of genomic selection

In the absence of molecular knowledge, breeders have effectively used traditional animal breeding (TAB) methods to produce high-quality animals (Garner et al., 2016). In the TAB method, estimated breeding values (EBV) is predicated on animal own and family physical performance like shape, color etc., which remains questionable because of low reliability of such methods (Ibtisham et al., 2017). The chicken genome was the first farm animal that was fully sequenced in 2004 (Tixier-Boichard et al., 2011) followed by the sheep (2007), cattle (2009) and goat (2013).

Genomic estimates for dairy cattle were first released for Holsteins, Brown Swiss and Jerseys in 2009 while for Ayrshires and Guernsey it was in 2013 and 2016, respectively(Wiggans et al., 2017). The first commercially available bovine genomic was chip BovineSNP50 (Matukumalli et al., 2009). Genomic technology has been well established in developed countries (Van Marle-Koster and Visse, 2018). Genomic assessment has been successfully implemented within United States (US), Canada, United Kingdom (UK), Ireland, New Zealand, Australia, France, Netherlands, Germany and Scandinavian countries. The adoption of this technology in dairy producing countries has led to major changes in the global dairy industry. Genome selection has been successful in increasing the rate of genetic gain though the genetic structure of quantitative variation is still poorly understood (Weller et al., 2017). Bulls in most countries have been used as reference populations for genomic selection. Female reference populations are now becoming more and more popular, especially in terms of unique traits such as feed efficiency, methane emissions, and detailed reproductive measures. Genomic selection is now being used on a large scale in the dairy industry and is being used to improve all livestock populations (Yadav et al., 2018)

Genomic selection in developed countries has been supported by conventional genome prediction and a number of studies have been carried out in multiple breeds, while in developing nations, conventional genome prediction has been carried out in only a few breeds of farm animals (Mrode et al., 2019). Moreover, in developed countries, whole-genome sequence analysis and GS are being applied to the breeding programs of the five major farm animals (cattle, sheep, goat, chicken, and pig) (Meuwissen et al., 2016; Mrode et al., 2019). However, in developing countries, genomic technology is used to assess genetic diversity and mixing and select features to identify genomic regions and variants that cause variation (Mrode et al., 2019; Tera et al., 2019). After the application of GS, genetic diversity has been preserved in American Angus and, in certain cases(Lozada-Soto et al., 2021) while Scott et al. (2021) described that genomic selection increased inbreeding per year and causes loss of genetic diversity, decreased long-term response to selection and reduced animal performance. The major challenges for the application of GS in developing countries are poor breeding infrastructure that basic to conventional breeding, lack of routine recording of reliable phenotypes and good analytical tools to synthesize the data, and providing timely feedback to help improve farmer management and husbandry techniques (Mrode et al., 2019).

Implementation of genomic selection

Genomic selection is now implemented in all major farm animal species (Bank, 2022). Its primary goal is to accelerate genetic trends by narrowing generation gaps and improving selection accuracy, especially for young animals (Misztal et al., 2021). Due to its market-oriented selection goal, the dairy industry is well positioned for quick adoption of the GS (Mueller et al., 2022).

Genomic contains a group of current and valuable technologies that are implemented as real tools for commercial dairy cattle breeding programs (Gutierrez-Reinoso et al., 2021). Genomic selection in dairy cattle breeding programs enables breeders to recognize genetically superior animals at a much younger age (Schefers and Weigel, 2012). The implementation of GS in breeding programs requires improved selection procedures, especially in species with long reproductive cycles, sex-restricted trait records, and complex traits. The selection of bulls with dairy traits was hampered by the long progeny testing period. On the other hand, dairy breeders have taken advantage of technological advances in reproduction and genomics in conventional breeding programs which makes it possible to increase the genetic gains in traditional milk production traits and low-genetic traits such as health and fertility. As the demand for dairy products increases, it is important for dairy farmers to optimize the use of existing technologies and consider any technologies currently being studied in various fields (Fleming et al., 2018). Genomic assessment has been implemented in developed countries. In almost all countries where genomic selection is implemented, bulls that have been tested for offspring have been used to form a reference population (Ding et al., 2013). The implementation of GS regularly includes estimating the SNP effects in a reference population that involves the individuals with phenotypic records and genotypes (Mrode et al., 2019). Implementations of GS have accelerated the genetic gain progress by adjusting the existing breeding program design (Bank, 2022).

The achievement of genomic selection mostly depends on the extent of linkage disequilibrium (LD) between markers and quantitative trait loci (QTL), the quantity of animals within the training set (TS), and the heritability of traits (Brito et al., 2011). However, the challenge of implementing genomic selection is to collect all available biological samples (hair, semen or blood from live animals) and quantify sufficient quality and quantity to establish a training population of specific species. In modern times, the amount of animal DNA has made a great genetic contribution to improvement, and it should come from. All animals should have accurate phenotype information for genome prediction, but the genotypes of significant ancestors, even if there is no phenotype information, can also be used to generate population haplotypes, so as to proceed from low-density genotypes to high-density genotypes. The SNP panels should be used to genotype animals, and appropriate verification procedures should be used to determine the most suitable genome prediction algorithm (Van Marle-Köster et al., 2013).

Generally, the implementation of genomic selection is a two-step process. Firstly, the effect of each of the genome-wide SNP markers on the trait of interest is quantified in a reference population due to the effect of each DNA marker and reference populations must be very large to estimate these effects accurately. Secondly, the genomic selection implementation stage involves genotyping candidate animals and summing, across the animal's SNPs in which the allele count is multiplied by the estimated SNP effect from the reference population. The result of this process is the direct genomic value, which is an estimate of the genetic value based on DNA information (Berry et al., 2014). The implementation of GS is technically harmless as it simply enhances the efficacy of the "breed the best to the best" approach and contributes to the improvement of the livestock productivity (Bank, 2022).

Genomic selection and marker-assisted selection

In addition to phenotypic information, genomic information is also used to improve reliability, which is called marker-assisted selection (MAS) (Ibtisham et al., 2017). The application of molecular genetics in livestock began with the use of DNA markers to identify genes or genomic regions that control traits of interest. Various types of molecular markers are used to characterize the genetic polymorphism of dairy cows and the application of MAS. The MAS method is effective for traits with simple genetic determinism, but produces unsatisfactory results under many more complex conditions. The two key reasons for low productivity are the limited part of genetic variation and the low association between population-level markers and QTL (Boichard et al., 2016). It utilizes both phenotypic as well as genotypic information. The selection of animals for MAS is the connection between the marker, and the linked QTL. Marker-assisted selection can help us overcome the limitations of traditional breeding methods, especially for low heritability, sex-restrictive traits, and traits that appear in animal life. It also helps to maximize the genetic gain by reducing the generation interval (Yadav et al., 2018).

Genome-wide association studies (GWAS) such as quantitative trait loci (QTL), single nucleotide polymorphisms (SNPs), or single-step genomic best linear unbiased prediction (ssGBLUP) methods included in global dairy programs for the estimation of marker-assisted selection-derived effects (Gutierrez-Reinoso et al., 2021). As described by Rabier et al. (2016), GS is a type of MAS, in which densely labeled maps of chromosomes can be used to accurately estimate the breeding value of an animal without the need for information about its phenotype or phenotype of close relatives. Such method could be more suitable in developing countries where such information cannot be obtained from the farmers keeping dairy cattle due to the absence of well-organized herd records.

Genomic selection is more accurate and easier to implement than marker-assisted selection (De Roos, 2011). Until a few years ago, the application of genomic selection was not thought to be feasible because the number of genetic markers detected in most livestock species was insufficient and relatively expensive. In recent years, with the development of DNA technology and genome sequencing, the detection of thousands of SNPs has greatly reduced the cost of genotyping, which has led to the practical application of genome selection in many developed countries (De Roos, 2011). This implies that many developing nations can take the advantages of relatively inexpensive genome sequencing so as to apply genomic based selection. It is apparent that genetic markers such as microsatellites, SNPs, and most recently whole genomes are tools used to characterize genetic diversity between and within populations. For developing countries, SNP has been reported to be superior to other markers because it is simple, can distinguish variants and is used to identify genes with important economic characteristics, such as myostatin for animal muscles, and is inexpensive (Worku and Tadesse, 2017).

Impacts of genomic selection on the dairy cattle

Genomic selection can be considered as a modular approach to genetic improvement, and its simplicity and effectiveness can bring genetic improvement in the livestock industry within a short period. Moreover, due to the effectiveness of its multi-disciplinary approaches to improving livestock production, the application of GS could result in increased productivity, profitability and sustainability (Bank, 2022). Genomic selection could also reduce the necessity of progeny testing a bull paving the way for the implementation of selection them at a very early age by limiting the costs related to the lengthy progeny testing procedure. Genomic selection could have also a significant impact on breeding programs for dairy calves if accurate marker data for the reference population is constantly accessible. The population structure, accessibility of dense marker maps, and size of the reference population all affect how useful GS is (Borakhatariya et al., 2017). Some of the impact of genomic selection in the improvement of dairy cattle productivity has been highlighted in the following subheadings.

Improved predicting of the genetic value

Genetic improvement has played an important role in improving the efficiency of economic important traits in the livestock industry (Ibtisham et al., 2017). Genomic selection has further resulted in rapid rates of genetic gains especially in dairy cattle in developed countries resulting in a higher proportion of genetically proven young bulls being used in many breeding programs (Mrode et al., 2019).

Genomic selection has profoundly affected the genetic improvement of dairy cows. They evaluate the artificial intelligence organization that buys young bulls based on the genomic. Heifers and bulls are usually genotyped before 1 month of age, and some embryos are genotyped before implantation (Wiggans et al., 2017). In dairy cows, GS leads to higher accuracy in predicting the genetic value of young animals. The intensity of selection is increased as GS can be used to test a larger potential animal population compared to the traditional offspring test structure which expensive and unaffordable to many developing nations (Matthews et al., 2019). Genomic selection has led to a rapid increase in genetic gains, especially in dairy cows in developed countries, resulting in a higher percentage of young bulls with genome proof being used for breeding. It should be stressed however that such success stories depend on a sound traditional genetic evaluation system. Genomic predictions in developing countries are mainly dairy cows and beef cattle, usually with a small reference population (500-3,000 animals), and mainly involving dairy cows. Input variables are often pre-corrected phenotypic records, and in addition to genomic best linear unbiased prediction (GBLUP), a small reference group makes the implementation of various Bayesian methods feasible (Mrode et al., 2019). Genomic selection of dairy cows has been used to find markers and improvements in traits related to milk production, dairy cow health, udder health, and dairy cow structure.

When applying genomic selection, accurate breeding values can be obtained at birth, and the cost is much lower than that of offspring testing, which is another benefit of application of GS for the genetic improvement of local dairy cattle in developing nations. Moreover, accurate breeding values allow early selection of young candidates to be used at the age of 1 year and allow selection immediately after bulls mature, reducing the generation interval from six years to only two years (Cuyabano, 2014). Genetic evaluations that use genomic information aim at increasing the accuracy of breeding value predictions and focused mainly on sire's EBV (Jimenez-Montero et al., 2012).

Genomic estimated breeding values (GEBVs) can be predicted for any genotyped individual animals by using only its SNP genotypes and estimated SNP effects in GS. For multiple ovulation and embryo transfer (MOET) or for *in vitro* embryo production (IVP), GS could be utilized to precisely choose young female donors with high genetic value, as well as bulls for semen collection (Mueller et al., 2022).

The future of animal breeding companies is dependent on the application of GS, which increases genetic gain by reducing generation interval and increasing reliability (Granleese et al., 2015; Ibtisham et al., 2017; Lozada-Soto et al., 2021). Genetic gain in dairy cattle has increased as a result of the application of GS in a number of nations (Garca-Ruiz et al., 2016; Meuwissen et al., 2016; Doublet et al., 2019). The use of GEBV rather than EBV can be expected to yield greater genetic gains, and the selection of young bulls and heifers without test records was more successful by using genomics as a selection tool (Lee et al., 2020). In particular, for animals without phenotypic data, the GEBV was more reliable than the EBV in terms of reproducibility. Without phenotypic information, selection was somewhat more accurate in young bulls and heifers, and the accuracy of selection increased even more when genomic data were used (Lee et al., 2020).

Table 1 : Impact of genomic selection on genetic gain

Breed	Country	Added genetic gain	References
Holstein-Friesian	US	50-100%	Garca-Ruiz et al., 2016
Jersey	Australian	100%	Scott et al., 2021
Holstein-Friesian	Australian	160%	Scott et al., 2021
Montbéliarde	France	50 %	Doublet et al.,2019
Normande	France	71%	Doublet et al.,2019
Holstein	France	33%	Doublet et al.,2019

Improved heat tolerance

Dairy cattle production in many tropical and subtropical regions of the world has been impaired by extreme environmental temperatures. In many sub-tropical countries, high humidity is also another problem that affects the performances of dairy cattle. Temperature and humidity levels above a certain threshold will reduce milk production in dairy cows, and genetic variation is related to yield loss. In order to allow selection to improve heat resistance, GEBV for heat resistance of dairy cows was developed, and genomic selection can be used to improve heat resistance of dairy cows. Heat tolerance has been included in a multi-trait selection index, correlations with other production and functional traits and the net economic effect, given current and predicted future incidence of heat stress events, considered to achieve a balanced outcome (Nguyen et al., 2016).

Dairy cows are extremely susceptible to the decline in milk production as a result of heat stress. With the increasing frequency and duration of heat stress events, the feed intake of dairy cows will be profoundly reduced. However, the magnitude of heat stress effect can vary from one to the other individual animals. Identifying dairy cows that are more tolerant to heat stress conditions will be thus an important strategy in selecting and managing dairy herds that are more adaptable to future climates (Garner et al., 2016).

Breeding for heat stress tolerance may be accelerated through genomic selection, using genome-wide DNA markers that predict heat stress tolerance in a given livestock population. The whole genome is used as a selection feature to scan and identify regions in the genome rich in genes which are directly or indirectly related to environmental adaptation (Onzima, 2019). Genomic selection for heat tolerance in dairy cows is a step towards by ensuring a valuable source of nutrients and improving animal welfare. In the future, heat stress events are expected to increase (Garner et al., 2016). In dairy cattle, temperature and humidity exceeding thresholds of various livestock species could lead to a significant decline in feed intake, milk production, and fertility. Decline in performance traits are usually associated with physiology changes including increased core body temperature, respiration and panting rates, sweating, and endocrine system changes, which are important to health and productivity of farm animals (Garner et al., 2016; Sammad et al., 2020). High-yielding lactating dairy cows are the most susceptible to the harmful effects of heat stress among domesticated animals. The ambient temperature for high producing *Bos taurus* cattle at which body temperature begins to rise is approximately 25 °C. However, this will vary depending on production status (lactating vs. non-lactating, growing), pregnancy status, diet and climatic variables including solar radiation, wind speed and relative humidity (Wheelock et al., 2010; Garner et al., 2016).

With more frequent and prolonged heat stress events is expected to happen in the future, GS for heat tolerance has been reported to enhance the resilience and welfare of dairy cattle globally (Garner et al., 2016). Genomic predictions for heat tolerance with accuracy of 0.39 to 0.57 and 0.44 to 0.61 have been reported for Holstein and Jersey cattle breeds, respectively. These predictions suggest that GS is a promising approach to accelerate genetic gains in selecting cattle for improved heat tolerance. It has been observed that as more and more cows are added to the reference population, the accuracies of genomic evaluation for heat tolerance should improve (Nguyen et al., 2016).

Genomic selection was used on two negatively correlated traits for production and adaptation, which have heritability estimates of moderate and low values, respectively. Genomic introgression resulted in a more favorable genetic alteration for both productivity and adaptability traits when compared to within-population breeding. When the adaptation trait was given a lower selection weight than the production trait, genomic introgression from highly adapted with low productivity populations into highly productive with low adaption populations was reported to be the most successful genetic improvement strategy. When the selection weight for the adaptation trait was larger than the selection weight given to the production trait, genomic introgression from highly productive populations to highly adapted populations was also found to be successful. This shows that genomic introgression has the capacity to enhance both production and adaption traits although they are negatively correlated to each other (Strandén et al., 2019).

Enhanced dairy cattle health

Some characteristics, such as resistance to infectious and non-communicable diseases and adaptability to the environment, have been introduced as new selection indicators for dairy cows. The genetic background of immune response traits has been shown to be related to dairy cow function and production traits (Konig and May, 2019).

Genomic selection is an attractive tool for improving dairy health characteristics. Between 2008 and 2014, genomic selection has resulted in a 3–4-fold change in the rate of improvements in health and productive life span (García-Ruiz et al., 2016; Matthews et al., 2019). Genomic selection has played a vital role in the elimination of genetic diseases, such as bovine leukocyte adhesion defects, uridine monophosphate synthase (DUMPS) defects, and complex vertebral malformations (CVM) (Charlier et al., 2008).

Genomic assessments to estimate the genetic risk of specific health events in dairy cows include genetic predictions for placental residual, ketosis, true gastric displacement, mastitis, and claudication (Vukasinovic et al., 2017). Incorporating genomics into the herd improvement program has significantly improved productivity and health characteristics. The rate of genetic changes in milk production traits has increased by 50-100% (García-Ruiz et al., 2016). Milk production traits on chromosomes 6, 14 and 20 were found to affect the whole genome and quantitative trait loci (QTL) of milk production on chromosome 14 (Khatkar et al., 2012). Also, Matejickova et al. (2013) reported the importance of QTLs on chromosomes 6 and 14 to the percentage of milk protein. The information from genome analysis represents an important alternative to the production of databases that are of great interest to animal science and new genome editing applications, speeding up the genetic evaluation process of dairy cows (Gutierrez-Reinoso et al., 2021).

Selection of reproductive traits

Genetic improvements have been achieved in several species by combining within breed selection by applying reproductive technologies such as artificial insemination and embryo transfer to effectively disseminate elite genomes. Any genetic improvement activity in dairy cattle requires information on productive and reproductive performance traits in the given population (Rahman et al., 2021). The improved reproductive performance of males and females is the basis of a profitable dairy and beef production system (Berry et al., 2014). Knowledge of key genes and haplotypes, including their regulatory mechanisms, as markers of productivity traits, improves current and future dairy cow selection strategies. Advances in genetics that improve the accuracy of genome-based predictions have also increased the understanding of genetic effects in the offspring of dairy cows. However, crosses within inbred lines severely increased homozygotes, and collected the negative effects of inbreeding, such as decreased reproductive performance (Gutierrez-Reinoso et al., 2021).

The genetic improvement rate of reproductive performance traits of dairy cows is relatively slow due to their low heritability which usually ranges between 0.02 and 0.32 (Berry et al., 2014; Garcia-Ruizn et al., 2016). Moreover, the low heritability of classic fertility traits derived from calving and insemination data has slowed the genetic improvement of traditional animal breeding. Therefore, improving reproductive performance has considerable benefits to the overall profitability of dairy cattle breeding by reducing the cost of insemination and veterinary treatment, shortening the calving interval and reducing the involuntary elimination rate.

There is an increasing interest to find novel measures of fertility that have a better heritability or using genomic information to assistance genetic selection for fertility (Tenghe, 2017). Fertility rate is an important part of the efficiency of dairy production, so increasing fertility rate is very important to reduce production costs (Shao et al., 2021). Additionally, the GS has considerably improved the genetic gain for fertility a trait that is very difficult to improve through classical selection methods due to its low heritability (Scott et al., 2021). Genomic selection approach to genetic improvement offers the opportunity to make change in traits formerly less tractable to selection (hard-to-measure traits) or traits that are require slaughtering of the animal (Bank, 2022). Genetic variation is more related to the physiology of the reproductive process. Fertility traits are strongly influenced by the environment, genetic variation associated with multiple reproductive traits, and opportunities for selection (Pinedo et al., 2018).

The analysis of the US national dairy database found that generation intervals have decreased dramatically over the past 6 years, and selection intensity for lowly heritable traits has increased considerably. Genetic trends rapidly increased for fertility, lifespan, and udder health. These results clearly demonstrate the positive impact of genomic selection in US dairy cattle, even though this technology has only been in use for a short time (Wiggans et al., 2017)

Specific reproductive characteristics currently assessed through genomic analysis include ovulation rate, uterine health, pregnancy rate, non-recurrence rate, and dystocia (Pinedo et al., 2018). Genomic analysis provides the ability to locate lethal genes that affect fertility outcomes. As explained by VanRaden et al. (2011) observing specific genomic regions, identified new birth defects in dairy cow breeds. Reproductive technologies, such as embryo transfer and multiple ovulations will have a major impact on genomic selection.

The traits used for genetic evaluation of fertility in dairy cows can be divided into two aspects of fertility. The first is the ability of the cow to recover after calving and the time interval from calving to the first service. The second is the ability of cows to conceive, and maintain pregnancy after fertilization, the time interval between the first and last fertilization, and the rate of non-milk return after delivery (Tenghe, 2017). The reliability of calving interval breeding values for bulls without progeny increased by 27 percentage units from 20% to 47% and in Australia and the United Kingdom, the reliability of fertility breeding values increased by 22 and 29 percentage units, respectively from using genomic selection (Berry et al., 2014). In combination with multiple ovulation and embryo transfer (MOET), GS may be used to choose the best embryos to create the next generation of animals resulting in a reduced generation interval considerably (Meuwissen et al., 2016).

Improved feed efficiency

Feed is a major component of variable costs associated with dairy production systems and an important consideration for breeding goals (Wallén et al., 2017). Improving feed efficiency is thus economically significant. Including of feed efficiency in the breeding objectives of any genetic improvement programs could be achieved by approximating the quantity of energy required for milk production, maintenance and reproduction. It has been always an expensive practice to accurately measure the feed intake of a large number of dairy cows. Genomic selection is an important tool to introduce feed efficiency into dairy cattle breeding programs (Li et al., 2020). Genomic selection for yield alone increases feed intake while results in a larger negative energy balance and more body tissue mobilization during lactation (Rahman et al. 2021). Since traits are heritable, breeders who use breeding values can assent the reliability of genomic predictions. The genomic prediction accuracy of the dairy cow's dry matter intake and residual feed intake (RFI) has been estimated to be around 0.4 (Pryce et al., 2014). Genomic selection and mid-infrared technology are the two methods that are being applied for predicting feed efficiency in dairy cows. Genomic selection requires feed intake data to form the predictions and need to be validated in independent populations. The size of the reference population and its relationship to the predicted population remain as the limiting factors for achieving high prediction reliability for feed efficiency (Li et al., 2020). Residual feed intake (RFI), as one proposed feed efficiency definition trait, is defined as the difference between an animal's actual feed intake and its predicted feed intake calculated from various energy related with other traits such as milk production, metabolic body weight and change of body weight (Manzanilla-Pech et al., 2016). Genomic prediction reliabilities for RFI averaged 34% for all phenotyped animals and 13% for genotyped animals and genomic information increased the prediction reliabilities for RFI compared with using only pedigree information (Li et al., 2020).

Genomic selection and traditional Best Linear Unbiased Prediction (BLUP) breeding programs are related to the genetic improvement of feed efficiency in dairy cattle populations. Changes in genetic gain over time and achievable choices have always been the accuracy of milk production and remaining feed intake, as a measure of feed efficiency. When including feed efficiency in genomic BLUP schemes, it was potential to achieve high selection accuracies for genomic selection, and all genomic BLUP schemes gave better genetic gain for feed efficiency than BLUP using a pedigree relationship matrix (Wallén et al., 2017).

Generally, feed efficiency is a genetically complex trait that can be described as units of product output such as milk yield per unit of feed input. Feed efficiency is a heritable trait and could be improved through the application of GS. Thus, dairy cattle with a large reference population can successfully implement GS to enhance feed efficiency (Brito et al., 2020). The estimated heritability for RFI is reported to be 0.14 with either a pedigree or genomic model (Li et al., 2020). The accuracy of genomic predictions for feed efficiency are still low but are expected to increase as the training populations are enlarged and additional functional information is taken into account (Brito et al., 2020).

CONCLUSION

Genomic selection improves the health and reproductive traits of dairy cows, can be used at any age, shortens the generation interval, increases the rate of genetic gain, and reduces the rate of inbreeding per generation. Since heat stress events are expected to increase in the future due to climate change effects, selection of animals having a better heat tolerance is an alternative solution. Genomic selection for heat tolerance in dairy cows has facilitated the selection process with much accuracy. Genomics plays a crucial role in introducing new and difficult to measure characteristics such as feed intake, health, and disease. Genomic assessments are also useful tools to estimate the genetic risk of specific health events in dairy cows. Reproductive characteristics could be assessed through genomic analysis. The feed efficiency in the genomic best linear unbiased prediction (BLUP) program resulted in high selection accuracy of genomic selection, and all genomic BLUP programs provide better genetic gains for feed efficiency. Programmatic genomics data collection procedure is more critical in breeding. In GBV -based genomic selection decisions, a larger reference population is needed to improve the accuracy of genome breeding values. More research is thus needed to determine the value of reference populations for genomic selection of *B. taurus* and *B. indicus*. Moreover, the application of genomic selection in the genetic improvement of tropical dairy cattle is limited and should be used as a reliable way of improving the milk production potentials of local cattle.

Authors' contributions

The first author drafted the manuscript by intensively reviewing and searching for recently published information in the subject area while the second author edited and reshaped the manuscript.

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