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Genetics and Breeding

Advances in bovine genetics for enhanced milk production: a review

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Abstract. *The global human population is expected to reach approximately 9.7-9.8 billion by 2050 and peak around 10.3-10.4 billion in the mid-2080s which would create a substantial increase in food demand. Demographic growth requires access to large quantities of high-quality protein. Milk and dairy are a fundamental source of nutrition for the humans. Increasing market requirements for dairy products is intensifying the pressure on bovine genetic selection programs. Genetic selection has fundamentally transformed cattle breeding by shifting the paradigm from phenotype-based selection to DNA-based prediction. Molecular markers such as RFLP, SSR, AFLP, and SNPs are a major instrument for precise herd improvement and inbreeding management. Their application in modern animal husbandry addresses the traditional limitations of progeny testing, specifically the long generation intervals. By integrating high-density SNP-chips breeders can effectively enhance breeding efficiency, population monitoring, and genetic conservation. Furthermore, these molecular tools allow for the identification of quantitative trait loci (QTLs) associated with milk fat and/or protein content, and disease resistance. The current review explores the main applications of molecular markers aimed at improving milk production in cattle.*

Key words: bovine genetics, milk production, molecular markers

Introduction

The global human population is expected to peak at approximately 10.3 billion in the mid-2080s. Demographic expansion is poised to exert unprecedented pressure on global food security. This will result in an increased requirement of high-quality protein. Strategic dairy cattle selection is fundamental for improving herd genetics, which directly drives long-term viability and efficiency and is crucial for achieving sustainable production (Gheorghe-Irimia et al., 2023).

Cow‘s milk is one of the main food sources for the human population. It is a liquid food that contains about 87% water, an average of about 4.8% lactose, 3.7% fat and 3.5% protein (Antunes et al., 2023). Milk is a nutrient-rich food with important nutritional value due to its content of calcium, vitamin D (especially in fortified form), protein, vitamin B12, vitamin A, riboflavin, potassium and phosphorus (Górska-Warsewicz et al., 2019). The sufficient content of the amino acid tryptophan, a precursor of niacin, highlights milk as an important source of niacin equivalents (Davoodi et al., 2016).

Since the early stages of cattle domestication (~10,000 years ago), processes of differential selection have led to the development of about 1,200 cattle breeds (FAO, 2015) with different characteristics such as milk yield, milk composition, environmental adaptation, coat color, body size, fertility, and overall resilience (Brito et al., 2021).

The growing demand for animal products creates opportunities to improve the well-being of millions of poor people who depend on livestock for their livelihoods (Odongo et al., 2010). Intensification in dairy farming has emerged as a major response to the increasing demand for food resources to feed the world‘s growing population (Duncan et al., 2013). This typically means intensifying resource use and increasing agricultural output per unit of land. Intensification can increase economic profits and increase food production (economic and social benefits), but it can also lead to environmental degradation if not managed sustainably (environmental impacts) (Salcedo et al., 2025). While intensification aims to increase productivity, it can also lead to complex and sometimes contradictory impacts on the three pillars of sustainability: environmental, economic and social. Sustainable intensification involves agricultural processes or systems in which production is maintained or increased, in line with significant improvements in environmental outcomes (Pretty, 2018).

Consumer market trends are leading to an increased focus on health and dietary functions of food products, and there is an emerging market for dairy products (Jakubowska et al., 2024). The main focus in dairy products is on milk proteins, which are rich in bioactive substances (Auestad and Layman, 2021). This

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area of product development is expected to undergo significant expansion based on the sequencing of the bovine genome (Thompson et al., 2009).

There are currently more than 270 million dairy cows in the world with an average milk yield of over 2600 kg per cow per lactation period. However, only 33 countries have an average national milk yield of over 6000 kg per cow per lactation period (FAO, 2018), which represents only a small fraction (about 13%) of the global population, but more than 40% of the total global milk.

Modern animal husbandry aims to prioritize the genetic improvement of herds (van der Werf, 2022). Cattle breeding plays a major role among the livestock sectors due to the diversity of products obtained from it, which are of essential importance for the food security of humanity (Tampaki et al., 2025). Sustainable development in the field of cattle breeding requires optimal and precise management of genetic resources in the long term.

Genetic diversity and genomic assessment

Most traits of economic importance are of quantitative nature, i.e., are influenced by multiple genes and environmental factors (Zhang et al., 1998). Knowledge of the factors influencing cattle productivity, as well as the genetic diversity underlying the genetic potential of breeds, is extremely important for the management and sustainable use of resources in livestock farming. In this regard, in recent years, numerous studies have appeared to assess genetic diversity, linkage disequilibrium and the correlation between haplotypes and productivity in cattle (Dlamini et al., 2022).

Genetic progress in dairy cattle depends on the accuracy of genetic assessments, selection intensity, and generation interval (Kern, 2014). Key genes responsible for milk production or composition should be identified based on a multidisciplinary approach combining different lines of evidence such as gene locus, gene expression profile, gene expression regulation, function of the encoded protein, and previously reported associations between gene markers and the phenotypes studied (Raschia et al., 2018).

Whole-genome sequencing (WGS) and high-throughput genotyping, used in modern studies of animal genetics, have successfully replaced the use of so-called pedigree-based methods for determining their breeding value (Lee et al., 2024). In addition, genome evaluation provides more precise monitoring of inbreeding and the detection of rare genetic variants. According to Ristanic et al. (2024) the level of inbreeding in a population is an important parameter for monitoring its genetic diversity and its management (Ristanic et al., 2024). Traditionally, inbreeding was calculated by estimating inbreeding coefficients based on the pedigrees. The progress of modern genotyping methods enabled the increased use of genomic information for more precise estimation of inbreeding coefficients (Getmantseva et al., 2026).

GWAS (Genome Wide Association Study) allows for the detection of single nucleotide polymorphisms (SNPs) associated with desirable traits by scanning the genome, providing insights into the genetic architecture of these traits, and facilitating the development of genomic selection tool variations (Rekik et al., 2024). Furthermore, genetic testing of both cows and bulls prevents the spread of a number of genetic diseases (Kasimanickam et al., 2025).

Overall improvements in the genetics of dairy cows over the past 20 years have led to enormous increases in milk yield (Figure 1); however, maximizing milk yield has been accompanied by a decrease in reproductive performance and a higher incidence of metabolic and infectious diseases in the early postpartum period (Siatka et al., 2017).

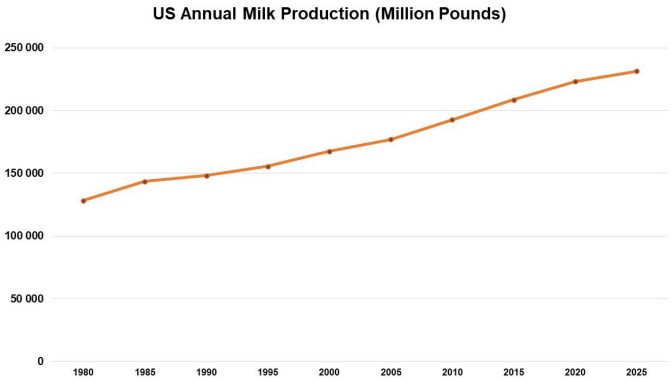

Figure 1. Increase in cow's milk production in the USA states for the last decades;
Source: https://esmis.nal.usda.gov/publication/milk-production

The productive qualities of cattle depend directly on their genetic predispositions, as well as on the conditions of breeding, nutrition, season, climatic features and the sequence of lactation. For example, a higher percentage of fat is observed in milk produced in autumn and winter (Patel et al., 2022). A number of genetic variants of the major proteins of cow's milk have been observed and characterized. These variations range from single nucleotide substitutions, which can lead to amino acid change in the polypeptide chain, to mutations affecting large stretches of the DNA molecule, such as deletions and duplications (Daniloski et al., 2022).

Genomics in cattle breeding has been developing rapidly in recent decades, with the focus mainly on identifying potential loci relevant to the formation of the phenotypic expression of QTL (Quantitative Trait Loci) traits (Ghavi Hossein-Zadeh, 2024). Genomic selection allows for the accurate identification of phenotypically superior breeding animals and provides flexibility to breeders based on their production targets (Džermeikaitė et al., 2025). In genomic selection, some indices can be used to effectively evaluate genomic predictions to provide greater accuracy and achieve much faster genetic improvement (Ardicli et al., 2024). The effectiveness of selection depends to a significant extent on the degree of accuracy and reliability with which the genetic predispositions of animals can be assessed (Rabier et al., 2016). The goal of genomic evaluation is to improve productivity efficiency in a population using molecular genetic markers (Tade and Melesse, 2024).

Genetic improvement through selection based on breeding value offers enormous potential for improving animal performance. However, this is time-consuming, as the generation interval in cattle is long and it takes considerably longer for the desired traits to develop. Furthermore, for milk production as a sex-limited trait, it is not possible to select a male animal based on its own

performance (Rosa, 2013). To minimize these problems, marker-based selection can play a major role in achieving genetic improvement in animals before the actual target traits develop. Selection can also be done based on marker value before birth, which is called marker-assisted selection (MAS). According to Abdel-Azim and Freeman (2002) MAS has the potential to increase genetic gain faster and is expected to be more effective than traditional selection systems.

Since the majority of economically important traits show complex or multicomponent inheritance patterns that are influenced by environmental factors; therefore, the main challenge is not simply the discovery of QTL, but rather the disentanglement of genes and regulatory elements that control gene expression (Andersson and Georges, 2004). This requires the integration of multiple resources, including genetic and physical maps, QTL markers, EST libraries, microarrays, and whole genome sequencing, to delineate the molecular mechanisms that control complex biological systems (Green et al., 2007). It should be noted that genomic studies are an improved method for selecting young animals, the reliability of which is confirmed by subsequent evaluation of the offspring.

Marker assisted selection

Sequencing of the cattle genome began in December 2003, led by Richard Gibbs and George Weinstock at the Baylor College of Medicine's genome sequencing center in Houston, Texas, USA (Burt, 2009). The taurine genome has been sequenced, analyzed, and partially annotated by the Bovine Genome Project which is a collaborative project involving several groups and funding from the United States, Canada, United Kingdom, France, Australia, and New Zealand.

Genome sequencing reveals millions of genetic markers which allows to accurately predict and rapidly improve milk yield, composition, and quality. The development of Next Generation Sequencing (NGS) technologies has enabled rapid and cost-effective generation of sequence data for SNP discovery in cattle (Zwane et al., 2019). NGS technologies have identified a large number of SNPs with many variants remaining to be detected, especially in cattle breeds that are phylogenetically distinct from the more extensively studied European breeds (Choi et al., 2013).

Genetic markers are specific sequences in DNA molecules located in different chromosomes, which are used to study the functions of certain genes, to track their heritability, to identify different individuals, breeds or biological species. They are widely used in a number of fields such as medicine, agriculture, forensics and plant and animal breeding. Most often, genetic markers are associated with closely located regions or genes that determine certain traits. These can be both genes associated with the development of various diseases, and a number of loci that affect the productivity of farm animals. In order to be used for breeding purposes, markers must be polymorphic, that is, exist in more than one variant (Amiteye, 2021). Markers are mainly divided into morphological, chromosomal, biochemical and molecular markers (DNA markers).

SNP markers allow for genotyping cattle in a single analysis with thousands of SNPs and providing genomic information for breeding value assessment. Breeding value prediction based on genomic evaluation data is based on the principle of linking multiple genetic markers to phenotypic presentation (Fleming et al., 2018). According to Sitkowska et al. (2026), the use of very large numbers of SNP data enables researchers to efficiently identify statistical associations between SNPs and phenotypes, allowing for the pinpointing of biologically significant candidate genes located near the significant SNPs for further investigation. Establishment of SNP markers affecting milk yield and composition allows for the development of genetic maps which contain all loci that directly influence productive traits in cattle.

Genetic maps

Detection and mapping of genes, genetic markers and QTL can be used to enhance genetic improvement of breeding stock through marker or gene assisted selection. High density SNP marker genotypes have increased the feasibility of QTL detection and mapping using historical population-wide linkage disequilibrium (LD) (Kolbehdari et al., 2009). During the last decade, the number of markers, used for QTL mapping in dairy cattle, has been consistently increasing, which led to higher precision of mapping (Figure 2).

The creation and use of genetic maps has revolutionized dairy cattle breeding, allowing breeders to select the most productive individuals for reproduction (Weigel et al., 2024). With the help of genetic maps, specific loci in the genome that influence certain traits can be identified. Of particular importance are those maps that contain markers that influence indicators with low heritability, such as milk productivity, the amount of protein and fat in milk, growth and fattening abilities, reproductive capabilities, etc. (Zamorano-Algandar et al., 2023). Therefore, the only applicable approach for QTL identification and candidate gene detection in large farm animals is the combination of different pieces of evidence supporting the functionality of identified genomic regions in relation to multigenic traits (Ogorevc et al., 2009). The purpose of QTL mapping studies in livestock populations is to identify genes or markers which could be used in breeding programs through marker assisted selection (MAS) (Matějíčková et al., 2013).

Number of QTLs Per Trait (as of 20.04.2026)	
Milk yield	8,035
Milk protein yield	3,997
Milk protein percentage	9,798
Milk fat yield	9,518
Milk fat percentage	11,909
Milk C14 index	4,848
Milk kappa-casein percentage	4,832

Figure 2. Number of QTLs, affecting milk production in dairy cattle;
Source:https://www.animalgenome.org/cgi-bin/QTLdb/index

The main types of maps are Linkage Maps, Physical Maps and Functional Maps. Linkage maps are used to track certain traits which are inherited together. They use molecular markers (like microsatellites) to determine the relative distance between genes on a chromosome (King, 2023). Physical maps provide information of the amount of nucleotides between the genes (O'Rourke, 2014). Functional maps are used to identify QTLs among the whole genome (Wu et al., 2005).

Recently, the application of a new experimental design (daughter or granddaughter design), resulted in several reports, which showed, that there are QTL for milk production traits segregating on BTA6 (Kühn et al., 1999). Mapping QTL can also help us to understand how many QTL significantly contribute to the trait variation in a population and how much variation is due to the additive effects of QTL and how much is due to dominant and epistatic effects of QTL (Zeng, 2013).

Selection programs

The development of intensive dairy systems has been fueled by a consistent flow of innovations and technological breakthroughs, among which conventional genetic selection played a major role over the past decades (Brito et al., 2021).

The breeding program should set clear goals that encourage breeders to adopt modern scientific methods to accelerate genetic progress and improve the breeding value of animals, suitable for the development of dairy cattle breeding in the 21st century (Cleveland, 2026). All breeding programs operate with limited resources allocated to breeding activities with the aim to maximize return on investment (Obšteter et al., 2021). The purpose of selection programs is to accelerate the rate of genetic change or selection response per unit of time toward a given breeding objective (Hayes et al., 2009). Furthermore, the goal of the selection program is to improve performance, body structure, health and fertility in the population, to obtain resilient animals for the different dairy production systems. Farmers should use the full potential of genomic evaluation to achieve their own breeding goals.

The selection of individual traits by the breeder to optimize performance for their specific breeding system and profitable milk production also includes the preparation of individual breeding plans with the selection of genomically evaluated animals while taking into account additional traits such as calving ease, health traits, reproduction and crossbreeding (Ule et al., 2024).

Scientifically designed breeding schemes along with increasing computerization of the industry were the main causes of the tremendous increase in milk production per cow (Figure 3). Modern breeding programs are based primarily on genetic markers, unlike phenotype-based programs applied in the past. Key genes responsible for milk production or composition traits should be identified on the basis of a multidisciplinary approach combining different pieces of evidence such as gene location, gene expression profile, regulation of gene expression, function of coded protein, and previously reported associations between markers on the gene and the phenotypes under study (Raschia et al., 2018).

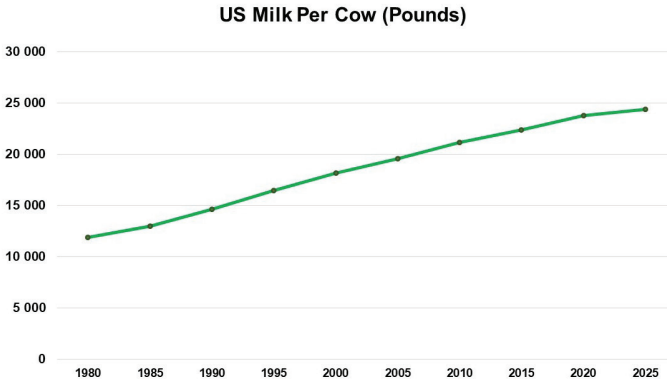

Figure 3. Increase in milk production per cow in USA for the last decades;
Source: https://esmis.nal.usda.gov/publication/milk-production

Dairy cattle breeding programs have focused on productive traits, while traits with low heritability, such as fertility, have been subjected to a direct selective pressure (Brito et al., 2025). However, genetic variation in fertility traits is significant, indicating potential for selection for improved fertility (Dechow et al., 2004). Selective breeding is traditionally based on EBV (Estimated Breeding Value), obtained as a result of the joint analysis of relevant phenotypic and pedigree data for the animals, after correction for environmental and other non-genetic factors (Soufleri et al., 2025).

Genetic polymorphism and its effect on milk productivity

The composition of cow's milk proteins is an important factor in the profitability of the dairy industry (Bobe et al., 1999). The difficulties in determining quantitative traits arise from the fact that their genetic basis consists of a number of genes, the products of which, obtained as a result of their expression, form the phenotypic characteristics (phenotypic profile) of the individual (MacKay et al., 2009). The main problem facing the researcher is to establish the degree of influence of each individual gene on the trait, while the target gene should not be considered as a separate functional unit when compiling the expression profile, but as part of a whole system of genes involved in the formation of individual phenotypic features.

Numerous scientific studies prove the influence of a number of genes on the quantity and composition of cow's milk. Among the candidate genes in dairy cattle are DGAT1, SCD, CSN2, CSN3, SREBP1, PLEC, PRLR, LGB, etc. Single nucleotide polymorphisms (SNPs) in the diacylglycerol acyltransferase 1 (DGAT1), stearoyl-CoA desaturase 1(SCD1), fatty acid synthase (FASN), oxidized low-density lipoprotein receptor 1 (OLR1), prolactin (PRL), signal transducer activator of transcription 5A (STAT5A) and growth hormone receptor (GHR) genes have been shown to affect the composition of bovine milk in different cattle populations (Alim et al., 2013). The diacylglycerol O-acyltransferase encoded by DGAT1 gene, according to previous studies, largely affects milk protein and fat composition (Li et al., 2021).

An experiment by Fox and Morrissey (1977) demonstrated the influence of the amount of kappa-casein in milk and the thermostability of milk.

According to Da and Law (1983), the kappa-casein

content in milk directly affects the size of micelles, with increasing the amount of kappa-casein leading to a decrease in micelle size.

A study by Bovenhuis et al. (1992) on the influence of milk protein genes on productive qualities in a large number of first lactation cows showed that the kappa-casein gene influenced the total amount of protein in milk, and the beta-lactoglobulin gene influenced the amount of fat, protein and total milk. In addition, the results of the study showed that the beta-casein gene significantly influenced the amount of milk, as well as the protein and fat in it. Miluchova et al. (2023) reported higher protein yields in Holstein-Friesian cattle with the A1A2 and A2A2 genotypes of the CSN2 gene, as well as higher milk fat concentration in animals with the A1A1 genotype. In a previous study, we determined the frequencies of CSN2 alleles in Holstein-Friesian cows reared in Bulgaria, where allele A was present at a frequency of 0.4 and allele A2 at 0.6 (Bekyarova, 2026).

A study of Yordanova et al. (2021) reveals that cows with genotype AA of LGB gene have the highest milk fat content and the lowest milk protein content. Cows with genotype AB of the same gene have the highest milk protein concentration. Furthermore, in recent research we established the frequencies of LGB alleles in Holstein-Friesian cattle reared in Bulgaria, where allele A was present at a frequency of 0.73 and allele B at 0.27 (Bekyarova and Koynarski, 2026, in press).

Such results may constitute a step forward towards the implementation of marker-assisted selection in breeding programs.

Conclusions

Sustainable livestock production has been and will continue to be significantly influenced by the global genetic improvement of livestock. A structured breeding program with a clear breeding goal is the best way to maximize the impact of various reproductive and molecular biotechnologies used for the genetic improvement of cattle. Even though genomic sequencing has been conducted in cattle extensively in recent years, the available data are still insufficient to provide a complete explanation of the genetic mechanisms for milk production traits.

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