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GENETIC ASPECTS OF LACTOSE SYNTHESIS IN DAIRY CATTLE

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Abstract. Market requirements, dictated by the growing needs of consumers, make it necessary to conduct breeding works to improve the performance characteristics of farm animals. The effectiveness of the breeding goal depends on both the genotype of the animals and the environmental conditions. Genomic selection using single nucleotide polymorphism (SNP) is increasingly used in the selection and evaluation of dairy cattle breeds. In recent years, many experiments have been carried out to determine the relationship between the occurrence of the genotype and performance traits of livestock. The analysis of milk composition carried out so far focused mainly on such milk production traits as milk yield (kg), fat yield (kg), fat content (%), protein yield (kg) and protein content (%). So far, no large-scale experiments have been carried out to test the content of lactose in milk and evaluate possible relationships with other milk performance traits. Lactose synthesis in the epithelial cells of the mammary gland serves as a major factor influencing milk volume production. Due to that conducting such an analysis seems to be beneficial for milk producers for economic reasons. An additional advantage may be the use of the obtained results in marker-assisted selection (MAS). The present review summarizes knowledge about lactose synthesis by covering and linking several aspects of cow's milk.

Key words: lactose synthesis, marker-assisted selection (MAS), mastitis, metabolic disorders, dairy cattle.

INTRODUCTION

Market requirements, dictated by the growing needs of consumers, make it necessary to conduct breeding works to improve the performance traits of farm animals. The aim of genetic selection is to improve the performance characteristics of animals from generation to generation to obtain offspring with better performance parameters than the parents. Traditional selection methods are mainly based on the phenotypic selection of individuals for breeding. Due to the low heritability of traits, they are not very effective in practice, therefore, other solutions are sought to improve breeding results. The alternatives to traditional selection methods are gene--assisted selection (GAS) and marker-assisted selection (MAS) (Dekkers 2004; Veerkamp and Beerda 2007).

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In recent years, many experiments have been carried out to determine the relationship between the occurrence of the genotype and performance traits of livestock. Thanks to the efforts towards genome mapping within the BovMap project, a map of the cattle genome was obtained, which could be used to identify quantitative trait locus (QTLs) within the genome of this species (Świtoński 2008). Most traits of economic importance in livestock are either quantitative or complex. In dairy cattle, milk yield and composition are typical polygenic traits (Georges et al. 1995).

In the QTLs regions, new candidate genes that are responsible for the economically important performance traits of animals are still being sought. So far, the search for candidate genes within QTLs in dairy cattle has focused mainly on functional traits as milk yield, fat yield and content, protein yield and content. Many studies conducted to identify the QTLs responsible for milk performance traits showed that QTLs were present mainly in chromosomes 1, 3, 6, 9, 14 and 20, while in other chromosomes QTLs were found less frequently (Khatkar et al. 2004). Several studies have reported the segregation of at least one QTL in the middle of chromosome 6 (BTA6), close to marker BM143 (Olsen et al. 2005). Recently, an approach based on the improved bovine genetics through molecular marker selective breeding has been becoming widely accepted and has revolutionized dairy cattle breeding.

The efficiency of milk synthesis can be improved by taking advantage of the accumulated knowledge of the transcriptional and posttranscriptional regulation of genes coding for proteins involved in the synthesis of fat, protein, and lactose in the mammary gland. Research in this area is relatively new, but research conducted over the past 10 years allows conclusions to be drawn about possible effects of lactose synthesis on milk production traits in dairy cattle (Osorio et al. 2016).

LACTOSE AND ITS IMPORTANCE IN MILK

Milk and its derivatives contribute essential play a key role in healthy human nutrition and health. The nutritional value of milk is primarily determined by the content of basic chemical components, especially high-value proteins, and easily digestible fat, as well as carbohydrates, vitamins, and minerals (Marangoni et al. 2019). The basic function of the lactating mammary gland is to produce milk, providing nutrients for growth and development of the offspring. The main constituents of bovine milk are lactose, proteins, and lipids. Cow milk contains around 5% of lactose, which represents about 40% of total solids. The lactose content of cows' milk varies with the breed of cow, individual animals, udder infection (mastitis) and stage of lactation. The lactose content decreases progressively and significantly during lactation. While the concentration of lactose in milk is inversely related to the concentrations of lipids and proteins. The inverse relationship between the concentrations of lactose and lipids and protein reflects the fact that the synthesis of lactose draws water into the Golgi vesicles what caused diluting the concentrations of other milk constituents (Fox et al. 2015).

In bovines, lactose is the major disaccharide molecule found in milk molecule composed by glucose and galactose. Lactose synthesis and secretion by the mammary gland involve the expression of a large number of genes. Glucose is the primary precursor for the synthesis of lactose and its concentration in the lactating mammary epithelial cells is higher than usual (Lin et al. 2016). Compared with non-lactating dairy cows, lactating dairy cows have an approximately 4-fold higher requirement for glucose (Bell and Bauman 1997).

Animal nutrition has a substantial effect on milk composition including lactose concentration. Fasting, caloric deprivation, and dietary carbohydrate restriction have negative effect on glucose uptake by the mammary gland for lactose synthesis (Ollier et al. 2007; Sadovnikova et al. 2021b). Glucose is a dietary factor that affects milk synthesis, but whether glucose supplementation can affect lactose synthesis in dairy cow mammary gland is not well understood.

There are only few studies have focused on the effects of glucose supplementation on the expression of genes involved in lactose biosynthesis (Lin et al. 2016).

Lactose is an important energy source in milk for the newborn. It also plays a primary role in milk production because it represents the main osmotic constituent in milk and draws water into the mammary epithelial cells (Osorio et al. 2016). The synthesis of lactose by the mammary gland is the major factor influencing milk volume, where the concentration of lactose in milk is positively associated with milk volume and negatively associated with the osmolarity of salts in milk. Lactose has more opportunities for hydrogen binding and hydration than the inorganic salts in milk (i.e., Cl, Na), which explains lactose concentration in milk is inversely correlated with its osmolality and positively correlated with milk volume. The inverse correlation between the concentration of lactose and inorganic salts in milk also maintains milk as isosmotic to blood, which is essential for sustained milk synthesis. Lactose also acts as the primer for oligosaccharide synthesis, where it serves as the reducing end of the oligosaccharide core (Fox et al. 2015; Sadovnikova et al. 2021a).

The lactose content in milk is still a new research object in the field of functional properties of dairy cattle. Lactose synthesis is mainly studied for its important role in driving milk yield. However, the relations between the biosynthesis pathways of the different major milk components such fat, protein, and lactose, are much less studied. A difference in energy balance, probably through its effects on glucose metabolism, affects lactose synthesis and milk yield (Costa et al. 2019a, 2019b).

BIOSYNTHESIS OF LACTOSE

The biosynthesis pathway and the other roles of glucose in milk synthesis by the mammary gland are well known. Glucose uptake in the mammary gland plays a key role in milk production and is considered a rate-limiting step in milk production (Zhao and Keating 2007). The uptake of the glucose from the circulatory system is regulated by facilitative glucose transporters, whose genetic expression also directly affects milk synthesis (Zhao 2014).

Glucose after absorption by the basolateral membrane of mammary epithelial cells is phosphorylated to glucose-6-phosphate and then joined with uridine diphosphate (UDP) to form UDP-glucose. The UDP-glucose is then converted to UDP-galactose by the UDP-glucose pyrophosphorylase 2 (UGP2) and phosphoglucomutase 1 (PGM1) in the cytoplasm and enters the Golgi, through the UDP-galactose transporter 2 (SLC35A2), where the lactose is synthesized by combining one molecule of UDP-galactose with one of glucose by lactose synthase composed by β-1,4-galactosyltransferase 1 (B4GALT1) and α-lactalbumin (LALBA) (Osorio et al. 2016; Hettinga 2019). Given the important function of these genes in lactose synthesis, they are a reasonable candidate for use in improving milk production traits in dairy cattle. The control of expression of the main genes coding for proteins related to lactose synthesis is poorly characterized.

β-1,4-galactosyltransferase *1* (B4GALT1) is a Golgi-resident enzyme, which is needed for the biosynthesis of lactose in mammals. It has been reported that the amount of B4GALT1 enzyme increases during lactation period to meet the demand for lactose synthesis. Beginning in late pregnancy, the B4GALT1 level in the mammary gland is estimated to increase about 50-fold in preparation for lactose biosynthesis (Lin et al. 2016). Bovine *B4GALT1* is associated with milk production traits including milk, lactose, protein, and total solids production. It has been shown that *B4GALT* determining the level of lactose synthesis and affects the synthesis of other milk constituents, although the mechanism by which this can operate is unclear. Understanding the transcriptional and translational control of *B4GALT1* can be critical to improving milk yield and efficiency of milk production (Shahbazkia et al. 2012; Osorio et al. 2016).

α-lactalbumin (LALBA) is an important whey protein that regulates the production of lactose in milk. The expression of *LALBA* is very low during pregnancy and increases significantly with parturition (Lin et al. 2016). It has been found positive correlation observed between the expression of *LALBA* and milk yield in a large transcriptomics analysis of the bovine mammary tissue from late pregnancy to end of lactation. Increasing the expression of *LALBA* can be an effective way to increase milk yield improving the efficiency of milk production, but without affecting milk quality. Due to that, understanding the transcriptional control of *LALBA* appears necessary (Osorio et al. 2016). The role of *LALBA* is to increase the specificity of *B4GALT1* for glucose, so its concentration is usually highly correlated with the amount of lactose in milk (Fox et al. 2015).

The conversion of glucose to UDP-galactose is catalyzed by the UDP-glucose pyrophosphorylase 2 (encoded by *UGP2* gene) and phosphoglucomutase 1 (encoded by *PGM1* gene). The UDP-galactose is then transported into the Golgi by the solute carrier family 35 member A2 (*SLC35A2*). Previous studies have shown that expression of *PGM1* is strongly correlated with the amount of lactose in milk. It has been demonstrated that genes controlling conversion of glucose to UDP-galactose (*UGP2* and *PGM1*) may be rate limiting in the lactose synthesis (Mohammad et al. 2012; Sadovnikova et al. 2021a).

SLC35A2 encodes UDP-galactose translocator (UGT). This protein has been shown to be localized to the Golgi apparatus. SLC35A2 transports nucleotide sugars from the cytosol into Golgi vesicles. It is also responsible for pyrimidine nucleotide-sugar transmembrane transporter activity. *SLC35A2* is associated with milk production traits including milk, lactose, protein, and total solids production (Lin et al. 2016; Hadley et al. 2019). *SLC35A2* expression should be defined as gene appear to be rate-limiting for lactose synthesis during secretory activation (Sadovnikova et al. 2021a). Due to that, understanding the transcriptional control of *SLC35A2* seems crucial.

LACTOSE AS BIOMARKER

Understanding of the factors that regulate lactose synthesis stands to direct strategies not only for improving milk production and composition, but also health in cattle (Sadovnikova et al. 2021b). Due to low variability of lactose concentration low variability, it has been considered a low-informative trait. There are only few studies have examined the phenotypic and genetic variability of this component. Some investigations have reported interesting findings, particularly its negative relationship with somatic cell count (SCC). Miglior et al. (2007), Alessio et al. (2016), Costa et al. (2019b) and Lim et al. (2020) have demonstrated that a certain informative variation in lactose within and across lactations exists in cattle.

Mastitis is the most prevalent disease of dairy cattle, causing substantial economic loss for the dairy industry. Developing new techniques to diagnose Inflammation of the bovine udder in its early stages improves herd health and seems to be beneficial for milk producers for economic reasons. Early bovine mastitis detection may improve treatment strategies and milk yield and reduce the use of antibiotics. As reported before, the lactose content of cows' milk varies depending on occurrence udder infections and stage of lactation. Milk from first-calving cows has higher lactose content than milk from cows in later lactations. Lactose content tends to decrease when clinical or subclinical udder inflammation is present and SCC increases. Mastitis is usually more common in herds with a high percentage of multiparous cows, because primiparous cows tend to be less susceptible to udder inflammation. The milk of multiparous cows has generally higher SCC than the milk of primiparous cows. In reference to this concentration of lactose in milk can be used as a strong indicator of mastitis (Petrovski et al. 2006; Koeck et al. 2010; Ebrahimie et al. 2018; Antanaitis et al. 2021).

Mastitis causes an increased level of NaCl in milk and depresses the secretion of lactose. Lactose, along with sodium, potassium, and chloride ions, plays a major role in maintaining the osmotic pressure in the mammary system. Therefore, any increase or decrease in lactose content is compensated for by an increase or decrease in the soluble salt constituents (Fox et al. 2015).

Besides the association with mastitis, lactose concentration is also strictly related to energy balance and available blood glucose. Ketosis is one of the most frequent metabolic diseases affecting dairy cattle. A difference in energy balance, probably through its effects on glucose metabolism, affects lactose synthesis and milk yield. Glycemia and energy balance in cows are positively correlated with lactose content (Reist et al. 2002; Lemosquet et al. 2009; Larsen and Moyes 2015). Lactose content seems to be negatively related to β-hydroxybutyrate (BHB). Milk from subketotic and ketonic cows tends to show lower lactose concentration and higher BHB than healthy animals, especially in early lactation (Cant et al. 2002; Loker et al. 2012; Belay et al. 2017). These results suggest that the relationship between milk lactose and gluconeogenesis in dairy cows should be further investigated, to detect and propose novel health indicators in milk.

Haile-Mariam and Pryce (2017) reported favorable correlations of lactose concentration with longevity and fertility. Both milk lactose concentration and fertility depend on cow energy balance. Moreover, a positive association of lactose content with fertility in the subsequent lactation has been reported by Bastin et al. (2016).

In summary, the addition of new traits such as lactose concentration in selection indexes will improve the estimated breeding values (EBV) accuracy and allow for faster genetic improvement of traits of interest, such as mastitis resistance, udder health, and energy balance in future generations of dairy cows (Costa et al. 2019a).

GENOME-WIDE ASSOCIATION STUDIES FOR LACTOSE CONCENTRATION

Lactose content in milk is currently determined in most herd-testing schemes and it is usually routinely recorded in the framework of the official milk recording procedures. In conjunction with the increased availability of milk data from infrared predictions, lactose percentage has been included in scientific studies and reports, together with other milk production traits such as milk yield, fat percentage, and protein percentage (Costa et al. 2019b). Genome-wide association studies for lactose yield and lactose content are meagre in the available literature. The first study on expression profiling of genes involved in milk oligosaccharide metabolism in mammalian species was conducted Wickramasinghe et al. (2011). The conducted research confirmed that *B4GALT1* on chromosome 9, related to the transport of glucose, was significant for lactose biosynthesis. In particular, the expression of this gene was higher in the first part of lactation, corresponding to peak milk yield. Moreover, results showed that he majority of the genes involved in oligosaccharide metabolism are expressed in the milk somatic cells. Other studies for lactose content in dairy cattle have performed by Lopdell et al. (2017), and Wang and Bovenhuis (2018). Major genomic regions associated with lactose concentration were identified on chromosomes 2, 3, 12, 16, 20, and 28. Additionally, most of these regions also showed significant associations with fat and protein. These findings highlight novel candidate genes and variants involved in milk lactose regulation.

CONCLUSIONS

Lactose is the major carbohydrate of milk produced in the mammary gland of mammals. Expanding the knowledge of the transcriptional and post-transcriptional regulation of genes en-

coding proteins involved in lactose in the mammary gland could affect both the milk characteristics and the health status of dairy cattle. So far, the search for candidate genes within QTLs in dairy cattle has focused mainly on functional traits as milk yield, fat yield and content, protein yield and content. It is definitely worth to considering to looking for other QTLs responsible for other performance traits of livestock, such as the lactose content in milk. Nowadays there are not many experiments involving the testing of lactose content in milk and the assessment of possible relationships with other milk performance characteristics have been carried out. The lactose content in milk is still a new research object in the field of functional properties of dairy cattle. Lactose synthesis is mainly studied for its important role in driving milk yield. However, the relations between the biosynthesis pathways of the different major milk components such fat, protein, and lactose, are much less studied.

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GENETYCZNE ASPEKTY SYNTEZY LAKTOZY U BYDŁA MLECZNEGO

Streszczenie. Wymagania rynkowe, dyktowane rosnącymi potrzebami konsumentów, stwarzają konieczność prowadzenia prac hodowlanych w celu poprawy cech użytkowych zwierząt gospodarskich. Skuteczność celu hodowlanego zależy zarówno od genotypu zwierząt, jak i warunków środowiska. Coraz częściej w ocenie wartości osobników ras mlecznych stosuje się selekcję genomową wykorzystującą polimorfizm pojedynczego nukleotydu (ang. *single nucleotide polymorphism*, SNP). W ostatnich latach przeprowadzono wiele doświadczeń w celu określenia zależności pomiędzy występowaniem genotypu a cechami użytkowymi zwierząt gospodarskich. Przeprowadzone dotychczas analizy składu mleka skupiały się głównie na takich cechach użytkowości mleka jak wydajność mleka (kg), wydajność tłuszczu (kg), zawartość tłuszczu (%), wydajność białka (kg) oraz zawartość białka (%). Do tej pory nie przeprowadzono na dużą skalę doświadczeń polegających na badaniu zawartości laktozy w mleku oraz ocenie ewentualnych zależności z innymi cechami użytkowości mlecznej. Synteza laktozy w komórkach nabłonkowych gruczołu mlekowego jest głównym czynnikiem wpływającym na objętość produkcji mleka. Przeprowadzenie analiz zależności pomiędzy zawartością laktozy w mleku a cechami użytkowości mlecznej wydaje się korzystne ze względów ekonomicznych dla producentów mleka. Dodatkowym atutem może być wykorzystanie otrzymanych wyników w selekcji wspomaganej markerami (MAS). Niniejsza praca podsumowuje wiedzę na temat syntezy laktozy, obejmując i łącząc kilka aspektów dotyczących mleka krowiego.

Słowa kluczowe: synteza laktozy, selekcja wspomagana markerami, mastitis, zaburzenia metaboliczne, bydło mleczne.