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Review article

Oligosaccharides, polyamines and sphingolipids in ruminant milk

Daniela Giorgio[a,*], Adriana Di Trana[a], Salvatore Claps[b]

[a] Scuola di Scienze Agrarie, Forestali, Alimentari e Ambientali (SAFE), University of Basilicata, Viale dell'Ateneo Lucano, 10, 85100 Potenza, Italy
[b] Unità di Ricerca per la Zootecnia Estensiva (ZOE), Council for Agricultural Research and Economics (CREA), Via Appia, Bella Scalo, 85054 Muro Lucano, PZ, Italy

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ABSTRACT

As a result of the widespread applications and the use of milk and milk products in human nutrition, intense scientific interest has focused on identifying the components in milk that may be relevant to improving human health. Milk contains a heterogeneous mixture of secretory compounds with a wide variety of chemical and functional activities. Among these compounds, many indigenous minor bioactive compounds are present. This review provides an overview of the available knowledge on the polyamines, oligosaccharides and sphingolipids occurring in goat and sheep milk compared to cow milk. It has been highlighted that goat milk is richer in polyamines than is milk from other mammals and that the former represents a very appealing source of human-like oligosaccharides. Furthermore, it is interesting to note the effect that breed and polymorphism at the CSN1S1 locus exerts on the polar lipid content and oligosaccharides profile. Goat and sheep milk production plays an important role in the nutrition and economy of many countries around the world, especially in the Mediterranean area. Information on the bioactive properties of goat and sheep milk is an important tool for their use as a nutritional source for infants, in medicinal foods and for developing new markets.

1. Introduction

Milk from various mammals contains a heterogeneous mixture of secretory components with a wide variety of chemical and functional activities. Beyond the nutritional components that contribute to meeting our dietary requirements, milk and dairy products provide a broad range of bioactive compounds that protect neonates and adults against pathogens and illnesses. The term *bioactive components* refers to compounds that either exist naturally in food or are formed or formulated during food processing and may have physiological and biochemical functions when they are consumed by humans (Park, 2009). In recent decades, increased awareness of the association between diet and health has led to a new field of research to clarify the role of food products containing bioactive components in health promotion and disease prevention.

Among food products, milk has been shown to be an important source of health-promoting compounds (Ebringer et al., 2008; Park, 2009; Mills et al., 2011). Bioactive peptides, whose release may occur during gastrointestinal digestion or food processing, and bioactive lipids, such as conjugated linoleic acids, are the most studied components in milk and dairy products (Park, 2009; Park and Nam, 2015; Claps et al., 2017). In addition to the major bioactive components reported above, mammary secretions are known to contain a great number of other indigenous minor bioactive components with considerable potential benefits, such as hormones, cytokines, oligosaccharides, nucleotides and minor components, which can have a profound impact on the development and maintenance of metabolic, immunological and physiological processes and thus contribute to the development of functional dairy products (Silanikove et al., 2010).

Although numerous studies have examined the bioactive properties of several components in milk with regard to some health-related variables, intense scientific interest has been focused on human and bovine milk. To date, bioactive components in goat and sheep milk have not been explored sufficiently. Dairy goat and sheep farming are a vital part of the national economy in many countries, especially in the Mediterranean area, where small ruminant farming systems often represent the only possible animal production activity connected to the utilization of marginal lands and production of typical products (De Rancourt et al., 2006).

In this context, this paper provides an overview of the available knowledge about a number of minor bioactive milk components (polyamines, oligosaccharides, sphingolipids) that occur naturally in goat and sheep milk compared to cow milk, with respect to their beneficial properties for human health and potential applications in functional foods.

* Corresponding author.
E-mail address: giorgio_daniela@alice.it (D. Giorgio).

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2. Polyamines

The biologically active polyamines putrescine (PUT), spermidine (SPD) and spermine (SPM) are aliphatic molecules with amine groups distributed along their structure. They are ubiquitous compounds that occur in living organisms either as free cations or conjugates bound to phenolic acids and polyanionic macromolecules such as proteins and nucleic acids (Tiburcio et al., 1997). The importance of polyamines in cellular growth, differentiation and proliferation is well established. Polyamines influence the transcriptional and translational stages of protein synthesis, stabilize membranes and modulate neurophysiological functions; they may also act as intracellular messengers (Gugliucci, 2004; Larqué et al., 2007). The presence of SPD and SPM in human breast milk has been reported to decrease the intestinal permeability of macromolecules and reduce the frequency of food allergies in children (Dandrifosse et al., 2000). In addition, these polyamines have been shown to display a significant antiglycation effect at physiological concentrations, suggesting a new role for polyamines in diabetes (Gugliucci and Menini, 2003; Gugliucci, 2004; Méndez and Leal, 2004; Jafarnejad et al., 2008; Soda, 2015). Polyamines are essential to male and female reproductive processes and play an important role in spermatogenesis, oogenesis and embryo/foetal development (Lefèvre et al., 2011). Notably, the polyamine levels decrease with age, and anti-ageing properties were demonstrated for spermidine (Minois, 2014). The importance of polyamines in cell function is reflected in the strict regulatory control of their intracellular levels. The bodily pool of polyamines is maintained by endogenous or *de novo* biosynthesis, intestinal microorganism and dietary intake (Kalač, 2014). The external source provides more polyamines than endogenous biosynthesis does; thus, diet may be a useful source of these substances, especially under circumstances of rapid growth and cell proliferation (as in newborns or during the recovery of injured tissues) (Gugliucci, 2004; Ali et al., 2011). Furthermore, dietary polyamines may become important with ageing, as cell proliferation slows with age, and ornithine decarboxylase activity (the first rate-limiting enzyme in polyamine biosynthesis) also decreases (Minois et al., 2011).

Milk is the first source of exogenous polyamines for newborn babies and animals. High levels of polyamines, especially spermine, have been shown to be immunoprotective by decreasing the permeability of the intestinal mucosa to antigenic macromolecules during the infant breastfeeding period (Dandrifosse et al., 2000). It is generally accepted that the content of milk bioactive substances in mammalian species reflects differences in the offspring's requirements. Interspecies differences in milk polyamine concentration are associated with different requirements for milk constituents, conditioned by different growth rates of newborns (Motyl et al., 1995). The available data on polyamine concentrations in human and ruminant milk are given in Table 1. Variations in the polyamine levels were analysed in human milk during the immediate postnatal period by Buts et al. (1995), Pollack et al. (1992) and Romain et al. (1992). Although the results of the various analyses are not uniform and show distinct variations, it is clear that human milk contains substantial amounts of polyamines, mainly SPM and SPD, with a smaller quantity of PTR. In spite of several reports on polyamine contents in human and rat milk, there is a deficit of information on milk-borne polyamines in other animal species. Bardócz et al. (1993) analysed polyamine content in various foods consumed by humans, such as full cream milk from bovine species (Table 1). Motyl et al. (1995) investigated the polyamine levels in cow milk during the first month of lactation and found that the concentration of milk fat and protein is significantly correlated with the polyamine level. In particular, a significant positive correlation was found between protein and SPD concentration ($r = 0.79$, $P < 0.01$) as well as between fat and SPD concentration ($r = 0.78$, $P < 0.01$). The authors suggested a relation between the polyamine biosynthesis rate and secretion activity of milk constituents in the mammary gland during lactation. Cow milk and dairy products have lower polyamine contents than human milk does because of the high rate of polyamine degradation in the former by highly active enzymes such as diamine oxidase or polyamine oxidase (Löser, 2000). Studies on polyamines in milk from small ruminants are very limited (Ploszaj et al., 1997; Prosser et al., 2008; Galitsopoulou et al., 2015). Comparing colostrum and milk from two goat breeds (German Brown and Polish White) over 90 days of lactation, Ploszaj et al. (1997) indicated that goat colostrum and milk are rich in polyamines and that their total concentration is higher than that observed in milk from other mammals. On the whole, the SPM concentration (3.18 μmol/L in German Brown goats and 3.80 μmol/L in Polish White goats) was similar to that determined in human milk, whereas the SPD content (39.67 μmol/L in German Brown goats and 26.00 μmol/L in Polish White goats) was higher than that in humans; the PTR level (6.00 μmol/L in German Brown and 5.12 μmol/L in Polish White) was highest among other mammals (human, cow, rat and sow). The results presented by Ploszaj et al. (1997) highlight a relation among polyamine patterns, goat age, offspring number, lactation period, milking time and individual variation. In the lactation stage, the SPM and SPD milk concentrations remained relatively stable over 90 days of lactation, whereas PTR decreased during the first month of lactation. This study also reveals considerable interbreeding differences in milk polyamine level during the entire experimental period. According to the authors, interbreeding variabilities in the milk polyamine level result from the breed-related specificity of enzyme activity involved in polyamines synthesis in the mammary tissue (adenosylmethionine decarboxylase, SAMDC).

Very little is known about polyamine levels in sheep milk. Recently, Galitsopoulou et al. (2015) examined the early post-partum variation of polyamine content in sheep and goat milk from indigenous Greek breeds (Chios and Eghoria, respectively) (Table 1). The results of this study showed that species variation had a significant effect on PTR, SPD and total polyamine levels ($P < 0.001$) but not SPM concentration ($P = 0.707$). A significant species × lactation day interaction was also detected. More specifically, the PTR level, which was the lowest in both milk species, decreased with advancing lactation in goat milk but exhibited a distinct maximum concentration on the 3rd day post-partum and decreased significantly thereafter in sheep milk. The SPD concentration in sheep increased slightly for the first two lactation days and remained relatively constant thereafter, but it decreased considerably after the 5th post-partum day in goat milk. The evolution profile of SPM was quite similar in both milk species.

Variations in the polyamine levels were also analysed in infant formulas. Studying the composition and nutritive value of goat milk formulas, Prosser et al. (2008) observed that the concentrations of polyamines in goat milk powder and infant and follow-on formula are slightly higher than in their cow milk counterparts (Fig. 1). However, the levels present in goat or cow infant formula are much lower than those in human breast milk (Romain et al., 1992). Based on the findings reported above, it is important to determine the levels of polyamines in

Table 1
Mean polyamine concentration (nmol/dL) in human, goat, sheep and cow milk.

	Period[a]	Putrescine	Spermidine	Spermine	References
Human milk	1	24	220	313	Buts et al. (1995)
	1	33.8	224.4	276.2	Pollack et al. (1992)
	1	145.83	443.5	435.17	Romain et al. (1992)
Goat milk	1	29.8	334	232.4	Galitsopoulou et al. (2015)
Sheep milk	1	51	177.4	198	Galitsopoulou et al. (2015)
Cow milk	4		470	400	Motyl et al. (1995)
		100	100–300	100–300	Bardócz et al. (1993)

[a] 1 = 1st week of lactation; 4 = 1st month of lactation.