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Goblet cell mucin distribution in the small intestine of newborn goat kids fed lyophilized bovine colostrum

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ABSTRACT

The number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, was investigated in the small intestine of goat kids fed with lyophilized bovine colostrum in the period of passive immunity acquisition. At 0, 7 and 14 h of life, 15 male newborns received 5% of body weight of lyophilized bovine colostrum (LBC) and 14 male newborns received goat colostrum (GC), both with 55 mg/mL of IgG. Three additional animals were sampled at birth, without colostrum intake. Duodenum, jejunum and ileum samples were collected at 18, 36 and 96 h of life. Histological stains, periodic acid-Schiff, 1% alcian blue pH 2.5 and 1% alcian blue pH 1.0 were used to identify neutral and acidic mucins and acidic sulphated mucins, respectively. The number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, does not differ in the duodenum ($P > 0.05$). In the jejunum, LBC showed a higher number of goblet cells containing sialomucins compared to GC ($P < 0.05$). The highest number of goblet cells containing acidic and neutral mucins and total number of goblet cells were observed at 96 h ($P < 0.05$). In this segment, vacuoles of colostrum were present at 18 and 36 h mainly in the upper region of the villi, while the goblet cells were located at the bottom. At 96 h, vacuoles of colostrum were not detected, only goblet cells distributed throughout the villi. In the ileum, the number of goblet cells containing sulphomucins was higher ($P < 0.05$) at 96 h than at 18 h. The LBC group showed higher ($P < 0.05$) number of goblet cells containing sulphomucins at 96 h and total number of goblet cells at 36 and 96 h than the 0-h group. The present work revealed that the greater the absorption of colostrum in the goat kids' jejunum epithelium, the smaller the number of goblet cells. Considering this segment, feeding newborns with heterologous colostrum caused alteration in the number of goblet cells containing sialomucin. This condition suggested a reaction of the intestinal epithelium with increasing secretion due to the presence of non-recognized substances from the lyophilized bovine colostrum.

1. Introduction

In small ruminants, the substitution of maternal colostrum with bovine colostrum has been used as an alternative to ensure appropriate acquisition of immunoglobulin by the newborns (Lima et al., 2009; Machado-Neto et al., 2011; Moretti et al., 2010, 2012b). The intake of this first mammary secretion with the potential presence of foreign elements and pathogens, hormones, bioactive factors and inflammatory mediators can stimulate exocytosis of secretory granules in goblet cells distributed in the intestinal epithelium (Antunović et al., 2005; Corfield et al., 2001; Deplancke and Gaskins, 2001).

The secretory granules contain glycoproteins, including mucins, which are classified into two types, neutral and acidic. The latter can be further differentiated in sulfated

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(sulphomucins) or non-sulfated (sialomucins) (Deplancke and Gaskins, 2001). The frequency of goblet cells containing neutral and acidic mucins in the epithelium is related to the gastrointestinal segment, the presence of harmful agents and the stage of development. The neutral mucin occurs in greater quantities in the gastric mucosa, whereas the acidic mucin predominates in the intestinal epithelium (Corfield et al., 2001; Deplancke and Gaskins, 2001). Acidic mucins are more resistant to degradation by bacterial glycosidases and host proteases and show higher viscosity and acidity compared with neutral mucins. Thus, the primary function of this mucin is associated with resistance to attack by microorganisms, justifying its greater presence in the large intestine (Deplancke and Gaskins, 2001; Fontaine et al., 1996).

The objective of this study was to evaluate the relationship between the number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in the small intestine of goat kids with the period of passive immunity acquisition and the supply of lyophilized bovine colostrum.

2. Materials and methods

2.1. Feed

Colostrum was collected from two Holstein cows and 14 goats from commercial dairy farms. The animals were milked manually and the lacteal secretions were homogenized to form a unique pool of bovine colostrum and goat colostrum, respectively. The colostrum pools were then stored at −20 °C. The frozen pool of bovine colostrum was lyophilized and the resulting powder was homogenized and stored in sealed containers at −20 °C.

Samples of each pool were collected to determine IgG concentration by radial immunodiffusion (Besser et al., 1985; Mancini et al., 1965). Antiserum to bovine immunoglobulin G was added to agarose solution 1% and standard bovine IgG or samples of the bovine colostrum (diluted 1:50 in phosphate-buffered solution) were placed in wells. The ring-shaped immunoprecipitates were measured after 24 h. The same procedure was repeated to evaluate the IgG concentration in goat colostrum using antiserum to goat immunoglobulin G.

At the time of meal offering, the pool of goat colostrum was diluted with whole milk until reaching a concentration of 55 mg/mL of IgG. Bovine colostrum powder, however, was resuspended in water until it reached the original chemical composition of colostrum taken to the lyophilization process and, subsequently, diluted with whole milk until reaching a concentration of 55 mg/mL of IgG. Samples of final meals were collected for the analysis of chemical composition, Table 1.

2.2. Experimental procedures

In this study, 32 Saanen × Boer male goat kids were used. The animals were kept, maintained and treated according to accepted standards for the humane treatment of animals (authorized by the ESALQ/USP ethics committee).

Table 1
Chemical composition (mean ± standard deviation) of lyophilized bovine and goat colostrum fed to newborn goat kids.

Composition	Lyophilized bovine colostrum	Goat colostrum
Humidity and volatile (%)	81.11 ± 0.19	79.88 ± 0.18
Dry matter (%)	18.9 ± 0.2	20.1 ± 0.2
Crude protein (%)	9.4 ± 0.1	9.8 ± 0.1
Fat (%)	4.0 ± 0.1	7.8 ± 0.1

The newborn goat kids were separated from their mothers immediately after birth, without any maternal colostrum intake. Fifteen animals received 5% of body weight of lyophilized bovine colostrum (LBC group) and 14 animals received goat colostrum (GC group) at 0, 7 and 14 h of life. Three goat kids did not receive colostrum and were sampled just after birth (0-h group).

Goat kids from LBC and GC were randomly slaughtered at 18, 36 and 96 h of life with anesthesia (0.3 mg/Kg of xylazine and 20 mg/Kg of ketamine) and bled from the carotid arteries. Three animals were sampled immediately after birth without colostrum ingestion, constituting a 0-h group. After slaughter, the abdominal cavity was opened, and the gastrointestinal tract was removed within 5–10 min. The small intestine was separated into the duodenum, middle jejunum and ileum and samples were collected for histochemical analysis of goblet cells.

2.3. Histochemistry

The intestinal segments were fixed in buffered (0.1 M; pH 7.2), 4% p-formaldehyde solution, and subdivided into 5-mm sections, which were washed in phosphate-buffered saline (PBS; 0.1 M, pH 7.2) four consecutive times. The washed material was dehydrated by immersion in increasing ethanol concentrations (30%, 50%, 70%, 90% and 100%). The dehydrated material was blocked in glycolmethacrylate resin (JB-4; Polysciences, Inc., Warrington, PA, USA), and transverse non-sequential, 5-μm sections were obtained. For each animal and segment, oriented villi were taken (magnification, × 10) and used to characterize and quantify different mucins in the goblet cells (Mashimo et al., 1996).

Sections were stained with 1% Alcian blue (Ab, pH = 2.5)/periodic acid-Schiff (PAS) to detect neutral (pink) and acidic (blue) mucins. For identification of the subtypes of acidic mucins (sulphomucins and sialomucins), the tissue sections were stained with 1% Ab pH = 1.0 (only strong sulphated mucins were stained) and the goblets cells containing sulphomucins were counted. Thereafter, the same slides were counterstained with 1% Ab pH = 2.5 and the total number of acidic goblet cells were counted. The number of goblet cells containing sialomucins was obtained by determining the difference between the total number of acidic mucin and the number of sulphomucins (Kleessen et al., 2003).

Goblet cells in 20 oriented villi were counted using a light microscope (Top Light B2, BEL Engineering srl)

Table 2
Number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in 20 villi from the duodenum of goat kids fed with lyophilized bovine and goat colostrums.

Mucin	Treatment[b]	Time (h)				Effect[a]		
		0 h[c]	18 h	36 h	96 h	T	ST	T × ST
Neutral mucin	LBC		135 ± 14	105 ± 14	91 ± 14	NS	NS	NS
	GC		120 ± 16	112 ± 16	85 ± 16			
	Overall mean	168 ± 23	127 ± 17	108 ± 11	88 ± 11			
Acidic mucin	LBC		235 ± 34	232 ± 35	163 ± 34	NS	NS	NS
	GC		187 ± 39	189 ± 38	174 ± 40			
	Overall mean	214 ± 54	211 ± 26	211 ± 26	169 ± 27			
Sulphomucin	LBC		194 ± 25	95 ± 25	118 ± 25	NS	NS	NS
	GC		111 ± 28	103 ± 27	97 ± 29			
	Overall mean	152 ± 75	153 ± 19	99 ± 18	108 ± 20			
Sialomucin	LBC		85 ± 32	88 ± 30	75 ± 29	NS	NS	NS
	GC		101 ± 33	91 ± 32	51 ± 34			
	Overall mean	83 ± 38	93 ± 23	90 ± 22	63 ± 23			
Total[d]	LBC		370 ± 42	337 ± 44	254 ± 43	NS	NS	NS
	GC		307 ± 49	300 ± 47	260 ± 50			
	Overall mean	373 ± 51	338 ± 32	319 ± 32	257 ± 34			

NS = non significant ($P > 0.05$).
[a] T = treatment; ST = sampling time; T × ST = interaction between treatment and sampling time.
[b] LBC = goat kids that received lyophilized bovine colostrum; GC = goat kids that received goat colostrum.
[c] Comparisons between the 0-h group mean and the mean of each treatment were performed by orthogonal contrasts.
[d] Sum of neutral and acidic mucins.

coupled to a BEL Micro Image Explorer analysis system (BEL Engineering srl).

2.4. Statistical analysis

The statistical analysis was performed using the SAS (v 9.1) program package (SAS Institute, Cary, USA). The number of goblet cells in each segment was analyzed based on a 2 × 3 completely randomized factorial design. The treatments (LBC and GC) and sampling time (18, 36 and 96 h of life) were considered the main effects. After the data were confirmed for normal distribution with the Shapiro–Wilk test, analysis of variance was performed using the PROC MIXED (SAS Institute Inc., 1999). If the *F* value was significant, the Tukey test was used for multiple comparisons between pairs of means at 5% probability. The values are presented as least-square means and root means square errors.

Furthermore, the effect of 0-h group versus the other groups was tested by orthogonal contrasts using general linear model (SAS Institute Inc., 1999). If the *F* value was significant, multiple comparisons between the 0-h group and each treatment (LBC 18 h, LBC 36 h, LBC 96 h, GC 18 h, GC 36 h and GC 96 h) were performed at 5% probability. The values are presented as least-square means and root means standard errors.

3. Results

3.1. Duodenum

The number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in the duodenum of goat kids is presented in Table 2. The number of goblet cells containing acidic and neutral mucins and sialomucins and sulphomucins was not affected by treatment and sampling times. There was also no interaction between treatment and sampling time ($P > 0.05$). In this segment, the 0-h group did not show difference in the number of goblet cells containing neutral mucins, acidic mucins, sulphomucins and sialomucins and in the total number of goblet cells compared to each treatment (LBC 18 h, LBC 36 h, LBC 96 h, GC 18 h, GC 36 h and GC 96 h), $P > 0.05$.

3.2. Jejunum

The number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in the jejunum of goat kids is presented in Table 3. The number of goblet cells containing acidic and neutral mucins and the total number of goblet cells was affected only by sampling times ($P < 0.05$), with the highest number observed at 96 h. The number of goblet cells containing sialomucins was affected by treatment ($P < 0.05$) with LBC group showing a higher number than the GC group. In this segment, the 0-h group did not show difference in the number of goblet cells containing neutral mucins, acidic mucins and sialomucins compared to each treatment (LBC 18 h, LBC 36 h, LBC 96 h, GC 18 h, GC 36 h and GC 96 h), $P > 0.05$. The number of goblet cells containing sulphomucins in the jejunum of GC 96 h (163 ± 55) was higher than in the 0-h group (76 ± 37), $P < 0.05$, and the total number of goblet cells of the LBC 18 h (167 ± 34) was lower than in the 0-h group (360 ± 76), $P < 0.05$.

3.3. Ileum

The number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins,

Table 3
Number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in 20 villi from the jejunum of goat kids fed with lyophilized bovine and goat colostrums.

Mucin	Treatment[b]	Time (h)				Effect[a]		
		0 h[c]	18 h	36 h	96 h	T	ST	T × ST
Neutral mucin	LBC		90.0 ± 23	92 ± 24	190 ± 24	NS	*	NS
	GC		71 ± 27	106 ± 23	139 ± 27			
	Overall mean	149 ± 31	80 ± 18*b*	99 ± 17*b*	164 ± 18*a*			
Acidic mucin	LBC		106 ± 25	125 ± 23	170 ± 23	NS	*	NS
	GC		108 ± 26	147 ± 22	210 ± 26			
	Overall mean	187 ± 32	107 ± 18*b*	136 ± 16*ab*	190 ± 18*a*			
Sulphomucin	LBC		55 ± 22	81 ± 21	98 ± 20	NS	NS	NS
	GC		85 ± 23	96 ± 20	126 ± 29*y*			
	Overall mean	76 ± 37*x*	70 ± 16	88 ± 14	112 ± 18			
Sialomucin	LBC		78 ± 13	50 ± 14	57 ± 14	*	NS	NS
	GC		8 ± 15	36 ± 13	50 ± 16			
	Overall mean	56 ± 18	43 ± 10	43 ± 10	53 ± 11			
Total[d]	LBC		169 ± 45*y*	223 ± 42	354 ± 41	NS	*	NS
	GC		208 ± 40	251 ± 40	340 ± 46			
	Overall mean	360 ± 76*x*	188 ± 30*b*	237 ± 29*b*	347 ± 31*a*			

NS=non significant ($P > 0.05$); means within rows without common letters (*a*,*b*) differ ($P < 0.05$); means without common letters (*x*,*y*) differ from 0-h ($P < 0.05$).
* Significant ($P < 0.05$).
[a] *T*=treatment; ST=sampling time; T × ST=interaction between treatment and sampling time.
[b] LBC=goat kids that received lyophilized bovine colostrum; GC=goat kids that received goat colostrum.
[c] Comparisons between the 0-h group mean and the mean of each treatment were performed by orthogonal contrasts.
[d] Sum of neutral and acidic mucins.

Table 4
Number of goblet cells containing neutral and acidic mucins, including sulphomucins and sialomucins, in 20 villi from the ileum of goat kids fed with lyophilized bovine and goat colostrums.

Mucin	Treatment[b]	Time (h)				Effect[a]		
		0 h[c]	18 h	36 h	96 h	T	ST	T x ST
Neutral mucin	LBC		220 ± 59	273 ± 61	287 ± 60	NS	NS	NS
	GC		245 ± 68	222 ± 59	279 ± 78			
	Overall mean	223 ± 93	232 ± 45	248 ± 42	283 ± 50			
Acidic mucin	LBC		307 ± 41	457 ± 42	457 ± 42	NS	NS	NS
	GC		366 ± 47	365 ± 41	448 ± 64			
	Overall mean	296 ± 63	336 ± 31	411 ± 29	453 ± 38			
Sulphomucin	LBC		312 ± 30	412 ± 31	494 ± 31*y*	NS	*	NS
	GC		350 ± 35	398 ± 30	436 ± 48			
	Overall mean	371 ± 12*x*	331 ± 23*b*	405 ± 22*ab*	465 ± 29*a*			
Sialomucin	LBC		106 ± 23	69 ± 24	42 ± 24	NS	NS	NS
	GC		79 ± 27	61 ± 30	63 ± 31			
	Overall mean	54 ± 12	92 ± 17	65 ± 19	53 ± 20			
Total[d]	LBC		521 ± 94	712 ± 97*y*	744 ± 95*y*	NS	NS	NS
	GC		591 ± 94	581 ± 94	619 ± 123			
	Overall mean	364 ± 184*x*	556 ± 66	646 ± 68	682 ± 79			

NS=non significant ($P > 0.05$); means within rows without common letters (a,b) differ ($P < 0.05$); means without common letters (x,y) differ from 0-h ($P < 0.05$).
* Significant ($P < 0.05$).
[a] T=treatment; ST=sampling time; T × ST=interaction between treatment and sampling time.
[b] LBC=goat kids that received lyophilized bovine colostrum; GC=goat kids that received goat colostrum.
[c] Comparisons between the 0-h group mean and the mean of each treatment were performed by orthogonal contrasts.
[d] Sum of neutral and acidic mucins.

in the ileum of goat kids is presented in Table 4. The number of goblet cells containing sulphomucins was affected by sampling times ($P < 0.05$). At 96 h, the number was higher than at 18 h. In this segment, the 0-h group did not show difference in the number of goblet cells containing neutral mucins, acidic mucins and sialomucins compared to each treatment (LBC 18 h, LBC 36 h, LBC 96 h, GC 18 h, GC 36 h and GC 96 h), $P > 0.05$. The number of goblet cells containing sulphomucins in the ileum of LBC 96 h (475 ± 45) was higher than in the 0-h group

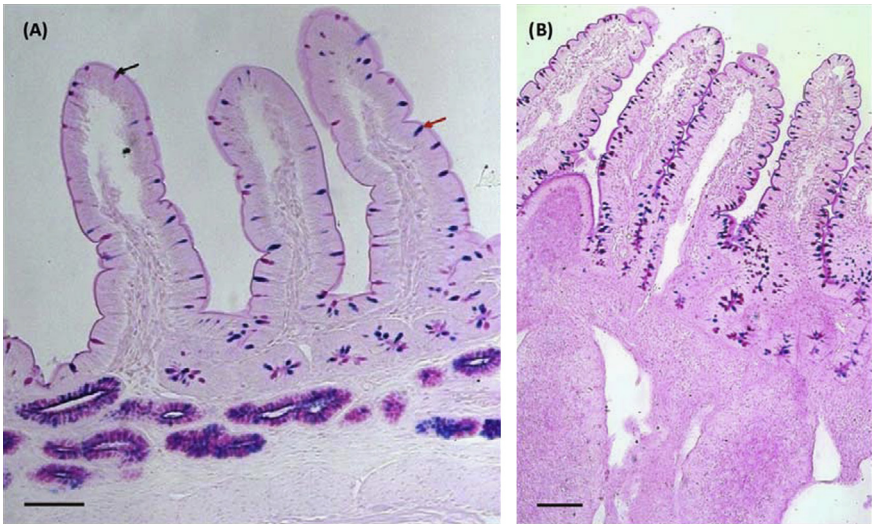

Fig. 1. Longitudinal section of the small intestine of the goat kids; (A) duodenum segment; (B) ileum segment; black arrow: goblet cell containing neutral mucin; red arrow: goblet cell containing acidic mucin; bar = 100 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(371 ± 12), $P < 0.05$. The total number of goblet cells of the LBC 36 h (766 ± 75) and LBC 96 h (712 ± 126) was also higher than in the 0-h group (364 ± 184), $P < 0.05$.

3.4. Small intestine

The duodenum, jejunum and ileum showed a higher percentage of goblet cells containing acidic mucins, 63%, 55% and 68%, respectively, compared to neutral mucins. Between the two acidic mucins, there was a higher percentage of goblet cells containing sulphomucins, 61%, 64% and 85%, respectively, compared to sialomucins. The analysis of histological sections revealed brush border with a predominance of neutral mucins and higher presence of goblet cells in the ileum segment compared to other segments (Fig. 1). In the jejunum, vacuoles of colostrum were observed at 18 and 36 h in the absorptive cells (Fig. 2). These vacuoles of colostrum were found mainly in the upper region of the villi while the goblet cells were located at the bottom. At 96 h, sampling time without vacuoles of colostrum, there was a high number of goblet cells distributed throughout the villi.

4. Discussion

The frequency of goblet cells in the epithelium may vary according to the postnatal phase, challenging substances, development, diet and mucosal microflora (Balan et al., 2011a; Corfield et al., 2001; Deplancke and Gaskins, 2001; Masanetz et al., 2010). Although the mucins have a binding ability to microflora bacterial cells, adherence of a number of pathogens can also occur (Ascencio et al., 1998). A variety of intestininal diseases are also accompanied by changes in the mucin composition, resulting in susceptibility of the intestinal epithelium (Corfield et al., 2001; Deplancke and Gaskins, 2001; Rhodes, 1997). In the present study, the predominance of neutral mucins in the goblet cells revealed a physical barrier function. However, a greater number of goblet cells filled with acidic mucins, especially sulphomucins, were distributed in the villi. It has been suggested that acidic mucins protect against bacterial translocation because sulfated mucins, in particular, appear less degradable by bacterial glycosidases and host proteases (Fontaine et al., 1996). Enss et al. (1992) suggests that the shift to more acidic mucins after bacterial colonization is a result of stimulated secretion as well as from a selective bacterial

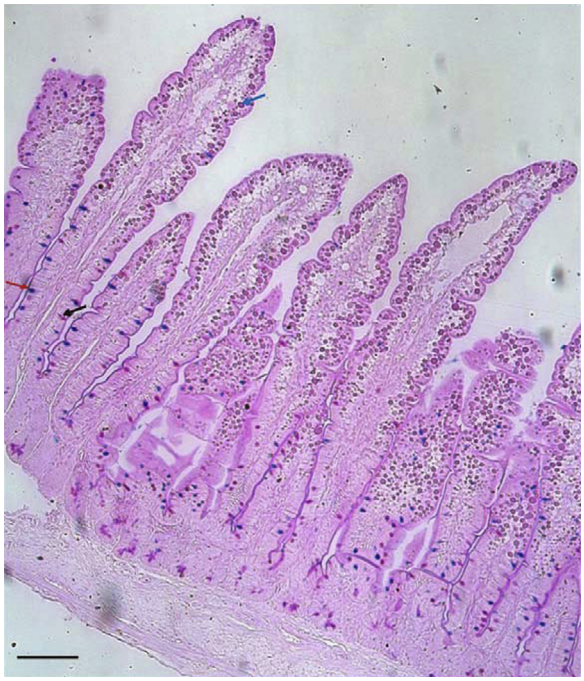

Fig. 2. Longitudinal section of the jejunum at 18 hours of life; black arrow: goblet cell containing neutral mucin; red arrow: goblet cell containing acidic mucin; blue arrow: vacuoles of colostrum absorption; bar = 100 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

degradation of neutral mucin components. As found by Deplancke and Gaskins (2001), the higher frequency of acidic mucins during the fetal period is related to an innate defense barrier, since the immune system in this phase is not fully functional, which could also explain the results observed in the present study.

According to Kleessen et al. (2003), changes in the mucin content, or composition, in the jejunal mucosa might be involved in modifications of small intestinal nutrient absorption. In small ruminants, the jejunum has significant importance to newborn animals, since absorption of immunoglobulins in the first hours of life occurs primarily in cells of this segment (Clark and Hardy, 1971; Machado-Neto et al., 2011; Nordi et al., 2012). Frequent vacuoles of absorption containing colostrum can be verified in jejunum enterocytes of goat kids in the first hours of life, a period of intense macromolecules internalization activity (Clark and Hardy, 1971; Machado-Neto et al., 2011; Moretti et al., 2012a; Nordi et al., 2012). After 24 to 36 h, the membranes of enterocytes are altered and lose their ability to absorb macromolecules, resulting in intestinal closure (Smeaton and Simpson-Morgan, 1985). In the jejunum, the reduced presence of goblet cells at 18 h, compared to 96 h, suggests that the greater the absorption of colostrum, the smaller the number of goblet cells. In these sampling times, the vacuoles of colostrum were found mainly in the upper region of the villi and the goblet cells were located at the bottom, indicating that exocytosis of granules may have occurred in the goblet cells in the apical region of villi due to the intense absorption of colostrum.

The number of sialomucins in the jejunum epithelium of goat kids fed with lyophilized bovine colostrum was higher than in goat kids fed with goat colostrum. Tsubokawa et al. (2009) observed a rapid increase of the sialomucin in the jejunal mucosa of rats inoculated with intestinal parasitic nematode, suggesting that this change may contribute to rapid worm expulsion. Therefore, changes of sialomucins found in the present work indicate a possible adverse effect of the bovine lacteal secretion on the intestinal epithelium of newborn goat kids.

In the ileum, the greatest number of goblet cells containing acidic and neutral mucins compared to the other segments may be related to the nearness of segment to the large intestine. The greatest number of goblet cells in the large intestine, a region densely populated by microorganisms, shows the importance of the mucin secretion for the intestinal epithelium protection (Deplancke and Gaskins, 2001). Kleessen et al. (2003) suggest that the mucin content or composition at the distal intestine mucosa might reflect different responses to specific bacterial populations or metabolite. In this segment, the LBC group showed a higher number of goblet cells containing sulphomucins at 96 h and a total number of goblet cells at 36 and 96 h than the 0-h group, corroborating that the consumption of bovine colostrum stimulated the production of this mucin. Balan et al. (2011b), working with rats in a 21-day study, observed that an orally administered diet containing freeze-dried ovine immunoglobulin influenced gut mucins in the growing rat, evidenced by increases of mucin gene expression and goblet cell count.

In conclusion, the present work shows that the greater the absorption of colostrum in the jejunum epithelium of goat kids, the smaller the number of goblet cells. Considering this segment, feeding newborns with heterologous colostrum caused alteration in the number of goblet cells containing sialomucin. This condition suggested a reaction of the intestinal epithelium with increasing secretion due to the presence of non-recognized substances from the lyophilized bovine colostrum.

Conflict of interest statement

The authors declare that there are no conflicts of interest.

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