Postprint: Absorption Mechanism of Volatile Fatty Acids in the Rumen of Ruminants

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Abstract

Rumen fermentation of carbohydrates produces volatile fatty acids (VFA), which are transported across the rumen epithelium via passive diffusion, anion exchange between volatile fatty acid anions (VFA-) and bicarbonate (HCO3-), nitrate-sensitive VFA absorption, proton-coupled VFA- transport, and electrogenic pathways, thereby providing energy for ruminants. Concurrently, VFA stimulates adaptive changes in the rumen epithelium, promoting rumen papillae growth and enhancing the expression of genes related to VFA absorption in the rumen epithelium. This review summarizes the absorption and transport mechanisms of VFA in the rumen epithelium and the associated genes, aiming to provide a theoretical foundation for further research on rumen nutritional regulation.

Full Text

Ruminal Absorption Mechanism of Volatile Fatty Acids in Ruminants

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Abstract: Volatile fatty acids (VFAs) produced by ruminal fermentation of dietary carbohydrates are translocated across the ruminal epithelium through multiple pathways including passive diffusion, anion exchange between VFA and bicarbonate (HCO), nitrate-sensitive VFA absorption, proton-coupled VFA transport, and electrogenic-mediated mechanisms, providing energy for ruminants. Simultaneously, VFAs stimulate adaptive changes in the ruminal epithelium, promoting papillae growth and upregulating gene expression associated

with VFA absorption. This review synthesizes current understanding of VFA absorption and transport mechanisms in the ruminal epithelium and examines the related gene expression patterns, aiming to provide a theoretical foundation for further research on ruminal nutritional regulation.

Keywords: ruminant; rumen volatile fatty acid; absorption mechanism; gene expression

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Ruminal absorption of volatile fatty acids (VFAs) represents a crucial energy source for animals, supplying approximately 75% of total metabolizable energy. VFAs produced through ruminal fermentation are partially absorbed by the ruminal epithelium, partially neutralized by saliva, and the remainder passes into the small intestine with digesta. The ruminal epithelium plays a pivotal role in VFA uptake, metabolism, and transport into the bloodstream. VFAs enter ruminal epithelial cells and associated tissues through various absorption mechanisms, a process that stimulates adaptive changes in the rumen and is essential for ruminant physiological functions across all life stages. As weak acids, VFAs dissociate hydrogen ions that affect ruminal pH. Under high-concentrate feeding conditions, elevated VFA concentrations cause ruminal pH to decline. If pH remains chronically low, it alters ruminal microbiota and fermentation patterns, potentially damaging ruminal epithelial barrier function and consequently impairing VFA absorption. Therefore, investigating the mechanisms of VFA absorption in the ruminal epithelium and the associated genes is critical for developing ruminal nutritional regulation systems in ruminants and holds significant practical implications for production.

1. Production of VFAs in the Rumen

Dietary carbohydrates fermented by rumen microbes produce VFAs as usable end products, as illustrated in [Figure 1: see original paper][2]. The primary VFAs—acetate, propionate, and butyrate—constitute 40–70%, 15–40%, and 10–20% of total VFAs (TVFAs), respectively, serving as the main energy source that provides over 75% of metabolizable energy for ruminants. Research indicates that differences in VFA concentration and composition in the rumen fundamentally stem from dietary composition variations, primarily neutral detergent fiber content, which affects microbial populations, species diversity, and the activity and proportions of various microbes, ultimately influencing intraruminal VFA concentrations. Kolver et al. reported that increasing dietary concentrate proportion elevates VFA concentration and improves ruminant performance metrics such as milk yield. However, as weak acids, most VFAs dissociate in the rumen, releasing H and lowering ruminal pH. When VFA concentrations exceed the rumen' s capacity for neutralization, subacute ruminal acidosis may occur.

The main metabolic pathways for carbohydrate fermentation to VFAs by rumen microbes are shown in [Figure 1: see original paper][2].

2. Absorption of VFAs by the Rumen Epithelium

The rumen functions as an anaerobic fermentation vat, producing VFAs, carbon dioxide, and ammonia simultaneously. As the most important end products of carbohydrate fermentation, VFAs are primarily absorbed through the ruminal epithelium into the bloodstream, providing adequate energy substrates for ruminants. Studies show that 50–85% of rumen-produced VFAs are absorbed by the ruminal epithelium, with the remainder absorbed in the omasum and abomasum. Due to differences in VFA types and molecular sizes, absorption rates vary. When ruminal pH 7.0, absorption rates follow the order: acetate > propionate > butyrate; when pH < 7.0, this order reverses. Feng et al. directly infused goats with acetate solutions at low [0.5 g/(kg·d)], medium [1.0 g/(kg·d)], and high [2.0 g/(kg·d)] doses, measuring VFA concentrations 4 hours post-infusion. All three doses significantly increased ruminal acetate concentration. Low and medium doses did not significantly alter propionate or butyrate concentrations, whereas high-dose infusion caused a dramatic decrease in both. This occurred because all infusion doses exceeded the epithelium' s acetate absorption capacity, leading to acetate accumulation. The high acetate dose lowered ruminal pH, altering absorption kinetics such that the epithelium preferentially absorbed propionate and butyrate, thereby reducing their ruminal concentrations.

2.1 Possible Mechanisms of VFA Absorption in the Rumen Epithelium

Extensive research has investigated VFA absorption mechanisms, though the precise processes remain incompletely understood. [Figure 2: see original paper] illustrates current understanding of VFA absorption and ruminal pH stabilization mechanisms. Five potential mechanisms exist: First, passive diffusion allows lipophilic VFAs to directly cross ruminal walls into blood, with absorption extent and rate dependent on concentration gradients between ruminal fluid and blood. However, passive diffusion has limitations. VFAs can only diffuse through epithelial phospholipid bilayers in their undissociated state. When ruminal pH decreases, the proportion of undissociated VFAs increases, enhancing passive diffusion rates. However, under normal ruminal pH conditions, the undissociated fraction remains low. With a pKa of approximately 4.8, over 90% of VFAs remain dissociated even at pH 5.8, limiting passive diffusion to a small fraction. Additionally, while VFAs exhibit lipophilicity in the order butyrate > propionate > acetate, in vitro studies show similar absorption rates when concentrations are equal. Increasing TVFA concentration from 10 to 50 mmol/L only increased acetate and butyrate absorption rates by 2.1-fold and 2.4-fold, respectively, indicating passive diffusion plays only a modest role.

Second, anion exchange between VFA and HCO occurs because most VFAs exist in dissociated form (VFA) in the rumen. VFA absorption proceeds through electroneutral processes mediated by multiple potential anion exchangers, providing HCO to neutralize H via carbonic anhydrase reactions producing CO and water. HCO -dependent VFA absorption increases with both intraruminal

VFA concentration and decreasing pH.

Third, nitrate-sensitive VFA absorption involves nitrate (NO) interacting with anion exchange mechanisms in the ruminal epithelium, including VFA /HCO and chloride (Cl)/HCO exchangers on the apical membrane. Dengler et al. validated this mechanism using Ussing chambers by adding NO to the serosal side to increase VFA flux from mucosa to serosa, supporting the hypothesis that HCO -dependent transport mechanisms receive VFA (rather than HCO) at the basolateral membrane. Aschenbach et al. reported this process occurs with or without bicarbonate present. Laarman et al. found that increased HCO inhibited acetate absorption but not butyrate, consistent with Kramer et al., and also observed inhibited propionate and Cl absorption with increasing HCO concentration. However, the specific transporter proteins involved remain unidentified and require further investigation.

Fourth, proton-coupled VFA transport: passive diffusion removes one H from ruminal contents, but VFAs rapidly dissociate once in the cytosol, releasing H that must be expelled to maintain intracellular pH and tissue integrity. Monocarboxylate transporters (MCTs) and Na /H exchangers (NHEs) involved in intracellular pH regulation transport H back to the rumen or into extracellular space while facilitating removal of VFA metabolites such as ketone bodies and lactate. The direction of H export is therefore critical for determining whether passive diffusion contributes to ruminal pH stabilization.

Finally, electrogenic VFA transport is thought to be mediated by large anion channels, though its contribution to VFA transport remains unclear.

Limited research exists on the relative proportions of these transport processes. Available data suggest that for acetate, HCO -dependent transport, nitrate-sensitive transport, and passive diffusion account for 0–14%, 42–57%, and 29–59%, respectively. For butyrate, these proportions are 24–46%, 0–4%, and 25–76%, respectively.

2.2 Genes Related to VFA Absorption in the Rumen Epithelium

Three major classes of carrier proteins involved in VFA absorption have been identified in the ruminal epithelium: (1) VFA /H exchange carriers including downregulated in adenoma (DRA), putative anion transporter 1 (PAT1), and anion exchanger (AE); (2) VFA /H cotransport carriers including monocarboxylate transporter 1 (MCT1) and MCT4; and (3) cellular homeostasis regulatory proteins including NHE, vH -ATPase pump, and Na /K -ATPase. The following sections focus on DRA, AE, MCT, NHE, and Na /K -ATPase.

2.2.1 DRA DRA was initially identified during hybrid cloning for colonic adenoma pathological genes and later characterized as a gastrointestinal-specific anion exchanger functioning as a Cl /HCO exchanger. DRA expression is primarily found in intestinal villus cells and colonic surface absorptive cells. Studies report that DRA functionally couples with apical NHE2 and NHE3 to

mediate electroneutral NaCl absorption, regulated by carbonic anhydrase, and functionally couples with cystic fibrosis transmembrane conductance regulator (CFTR) to mediate Cl and HCO secretion.

DRA, PAT1, and AE2 are the primary VFA /HCO exchange carriers, with apical VFA absorption capacity depending largely on these exchangers. Acetate is predominantly absorbed via HCO -dependent mechanisms, with DRA playing a crucial role in epithelial membrane VFA uptake. Yan and Connor et al. demonstrated synergistic effects between DRA and MCT1, suggesting that increased dietary concentrate levels enhance ruminal epithelial VFA absorption capacity through regulation of transporters including MCT1, MCT4, DRA, PAT1, and AE2.

2.2.2 AE Four AE isoforms (AE1–AE4) exist in the ruminal epithelium, with AE2 located on the basolateral membrane exchanging VFA for HCO and playing an important role in regulating homeostasis. Würmli et al. first confirmed proteins directly regulating HCO secretion in ruminal epithelial cells. Bilk et al. reported that the ruminal epithelium exchanges HCO and Cl through AE in processes related to VFA absorption and transport. HCO secretion is influenced by intraruminal VFA concentration. Yan et al. showed that increasing dietary concentrate-to-forage ratio from 4:6 to 7:3 in dairy cows downregulated AE2 expression by 30% while upregulating DRA and NHE3 by 140% and 60%, respectively. In vitro cell culture studies revealed that pH 6.6 reduced AE2 expression, while VFA concentration had no effect, suggesting AE2 expression may be closely related to ruminal fluid pH.

2.2.3 MCT MCTs belong to the solute carrier family 16 (SLC16) and function as proton-coupled transporters on the basolateral membrane, transporting intracellular VFA and metabolites including ketone bodies and lactate. Only MCT1, MCT2, and MCT4 are confirmed to function in VFA transport, with MCT1 and MCT4 requiring the auxiliary protein CD147 for normal function. Koho et al. detected MCT1 and MCT4 expression in sika deer ruminal epithelium. Kirat et al. and Graham et al. identified MCT1, MCT2, and MCT3 expression in cattle and goat ruminal epithelium, with MCT1 distributed at basal and spinous cell margins transporting acetate and propionate into blood and directly facilitating VFA efflux. Weng et al. found that low-concentrate diets significantly upregulated MCT1 expression in dairy cow ruminal papillae compared to high-concentrate diets, while MCT2 and MCT3 expression remained unchanged, suggesting they may not directly participate in VFA transport. However, Yan found that with constant rumen-degradable protein (RDP) but varying NDF/non-fibrous carbohydrate (NFC) ratios, MCT1 expression was unaffected while MCT4 expression decreased with lower NDF/NFC ratios, with highest MCT1 and MCT4 expression occurring when both NDF/NFC and RDP were relatively high.

2.2.4 NHE NHEs located on apical and basolateral membranes exchange intracellular H for extracellular Na in a 1:1 ratio, regulating Na transport and cytoplasmic pH. Multiple NHE family members are expressed in ruminal epithelium, including NHE1, NHE2, and NHE3, whose activity influences VFA absorption. VFA absorption is a key mechanism for stabilizing ruminal pH; when VFAs enter epithelial cells in acidic form, they rapidly dissociate into H and VFA , increasing intracellular H concentration and activating NHE to regulate intracellular pH. Enhanced NHE levels and activity therefore help maintain epithelial cell stability. Graham et al. demonstrated NHE1, NHE2, NHE3, and NHE8 presence in ruminal epithelial cells, with NHE1 and NHE3 at the apical membrane importing Na and exporting H to the rumen, while NHE2 imports Na but exports H to extracellular space, making NHE activity a key driver for pH neutralization.

Laarman et al. found that feed restriction upregulated NHE3 expression, providing evidence for its pH-regulating function. Increased NHE3 expression during fermentation may enhance H export from epithelial cells, helping regulate pH. Recent studies support these findings, showing enhanced NHE expression and activity in goats fed high-concentrate diets, with NHE1, NHE2, and NHE3 expression increasing with dietary concentrate levels.

2.2.5 Na /K -ATPase Na /K -ATPase located on the basolateral membrane regulates Na efflux from cells and is essential for maintaining electrochemical gradients. This transporter is ubiquitous in eukaryotic cell membranes, using energy from one ATP molecule to pump three Na ions out and two K ions in, maintaining ionic balance, regulating membrane potential, and preserving cell volume. The Na gradient generated by Na /K -ATPase is necessary for Na absorption and indirectly related to Na /H exchange transport. Yan et al. reported highest Na /K -ATPase expression at dietary NFC/NDF ratio of 0.66, with lower expression at both lower and higher ratios. Metzler-Zebeli et al. showed that goats fed 60% grain diets had significantly higher Na /K -ATPase expression than those fed 30% grain, with regression analysis revealing negative correlations between Na /K -ATPase expression and ruminal stratum corneum thickness and ruminal pH. McLeod et al. also found that increasing dietary concentrate levels enhanced Na /K -ATPase activity.

3. Factors Influencing VFA Absorption

3.1 Ruminal Fluid pH

Based on VFA absorption mechanisms, elevated ruminal pH is not conducive to VFA absorption. Li investigated pH effects on VFA absorption, finding that low ruminal pH favors VFA absorption only within the rumen' s tolerable pH range; excessively high or low pH impairs absorption capacity, and overly acidic conditions damage epithelial integrity. Melo et al. demonstrated that high pH (pH $>$ 7.0) inhibits VFA absorption, while low pH ($4.9 <$ pH < 7.0) enhances absorption by increasing protonated VFA concentrations, favoring passive diffusion.

Ruminal pH can influence absorption capacity by regulating gene transcription; under in vitro conditions, pH 6.8 increased MCT1 expression while decreasing AE2 expression in goat ruminal epithelial cells compared to pH 7.4.

3.2 Rumen Epithelial Morphology

The ruminal epithelium maintains a dynamic equilibrium that adjusts according to digestive and metabolic conditions. Jia found that high-concentrate diets significantly increased ruminal papillae projections in dairy cows, which expand the effective absorption surface area and enhance VFA absorption capacity. Yan et al. controlled for rumen-reticulum epithelial surface area and found VFA absorption affected by epithelial permeability and blood flow. VFA absorption is also linked to barrier function; subacute ruminal acidosis damages the epithelial barrier, increasing permeability and enhancing VFA absorption.

3.3 Dietary Composition

Diet type is a fundamental factor influencing VFA concentration, composition, and absorption. Increasing dietary concentrate levels upregulates VFA absorption-related gene expression in goat ruminal epithelium, enhancing absorption capacity, likely related to increased VFA concentrations and decreased pH. Reports indicate that adding readily fermentable carbohydrates to diets enhances VFA absorption capacity by up to 1.7-fold. Schurmann et al. showed that continuously increasing dietary carbohydrate content reduces ruminal epithelial barrier function while enhancing Na and VFA absorption, with passive diffusion being the primary VFA absorption pathway. However, Weng found that low-concentrate diets (MF group) promoted acetate fermentation patterns while high-concentrate diets (CS group) favored propionate patterns, yet dietary concentrate levels did not affect VFA absorption rates (15.9% in MF group vs. 13.7% in CS group), consistent with Júnior et al.

4. Summary

Dietary carbohydrates fermented by rumen microbes produce VFAs that enter ruminal epithelial cells or other metabolic tissues through various absorption mechanisms to provide energy. While substantial research has investigated VFA absorption mechanisms, studies on interactions between different mechanisms, among various VFAs (acetate, propionate, and butyrate), and effects of factors such as diet type and physiological morphological changes remain limited. The application of molecular biology techniques in ruminant nutrition has identified key genes related to VFA absorption, significantly advancing mechanistic understanding. Future research should explore deeper connections between VFA absorption/metabolism genes and various signaling pathways to achieve efficient VFA utilization and improve ruminant production efficiency.

References

[1] BERGMAN E N. Energy contributions of volatile fatty acids from the gastrointestinal tract in various species[J]. Physiological Reviews, 1990, 70(2): 567-590.
[2] 杨红建. 不同碳水化合物和蛋白质水平日粮瘤胃 VFA 产生及微生物蛋白合成规律研究 [D]. 博士学位论文. 北京: 中国农业大学, 2000.
[3] 袁庆启, 姜发彬, 王亚琼, 等. 不同精粗比日粮对奶牛瘤胃发酵与肝脏 VFA 代谢及产奶性能的影响 [J]. 家畜生态学报, 2016, 37(7): 36-43.
[4] KOLVER E S, DE VETH M J. Prediction of ruminal pH from pasture-based diets[J]. Journal of Dairy Science, 2002, 85(5): 1255-1266.
[5] 李伟忠, 单安山. 挥发性脂肪酸在动物体内的作用 [J]. 饲料博览, 2003(10): 5-7.
[6] 封贵. 瘤胃内灌注乙酸对山羊瘤胃内环境及真胃壁 M2、M3 和 eNOS 的基因表达影响 [D]. 硕士学位论文. 扬州: 扬州大学, 2016.
[7] ASCHENBACH J R, PENNER G B, STUMPFF F, et al. Ruminant Nutrition Symposium: role of fermentation acid absorption in the regulation of ruminal pH[J]. Journal of Animal Science, 2011, 89(4): 1092-1107.
[8] LIDE D R. CRC Handbook of chemistry and physics[M]. 88th ed. Boca Raton, FL: CRC Press, 2007: 8-40.
[9] ZAHER U, BOUVIER J C, STEYER J P, et al. Titrimetric monitoring of anaerobic digestion: VFA, alkalinities and more[C]//Proceedings of 10th World Congress on Anaerobic Digestion (AD10). [S.l.]: [s.n.], 2004: 330-336.
[10] SCHWAIGER T, BEAUCHEMIN K A, PENNER G B. The duration of time that beef cattle are fed a high-grain diet affects the recovery from a bout of ruminal acidosis: dry matter intake and ruminal fermentation[J]. Journal of Animal Science, 2013, 91(12): 5729-5742.
[11] ASCHENBACH R, BILK S, TADESSE G, et al. Bicarbonate-dependent and bicarbonate-independent mechanisms contribute to nondiffusive uptake of acetate in the ruminal epithelium of sheep[J]. American Journal of Physiology Gastrointestinal and Liver Physiology, 2009, 296(5): G1098-G1107.
[12] SEIFTER J L, ARONSON P S. Cl transport via anion exchange in Necturus renal microvillus membranes[J]. American Journal of Physiology, 1984, 247(2): F888-F895.
[13] WÜRMLI R, WOLFFRAM S, SCHARRER E. Inhibition of chloride absorption from the sheep rumen by nitrate[J]. Transboundary and Emerging Diseases, 2010, 34(1-10): 476-479.
[14] KRAMER T, MICHELBERGER T, GÜRTLER H, et al. Absorption of short-chain fatty acids across ruminal epithelium of sheep[J]. Journal of Comparative Physiology B, 1996, 166(4): 262-269.
[15] DENGLER F, RACKWITZ R, BENESCH F, et al. Bicarbonate-dependent transport of acetate and butyrate across basolateral membrane of sheep rumen epithelium[J]. Acta Physiologica, 2013, 210(2): 403-414.
[16] LAARMAN A H, PEDERZOLLI R A, WOOD K M, et al. Effects of subacute ruminal acidosis and low feed intake on short-chain fatty acid transporters and flux pathways in Holstein steers[J]. Journal of Animal Science, 2016, 94(9): 3729-3737.

[17] MÜLLER F, HUBER K, PFANNKUCHE H, et al. Transport of ketone bodies and lactate in the sheep ruminal epithelium by monocarboxylate transporter 1[J]. American Journal of Physiology: Gastrointestinal and Liver Physiology, 2002, 283(5): 1139-1146.
[18] KIRAT D, MASUOKA J, HAYASHI H, et al. Monocarboxylate transporter 1 (MCT1) plays a direct role in short-chain fatty acids absorption in caprine rumen[J]. The Journal of Physiology, 2006, 576(2): 635-647.
[19] PENNER G B, ASCHENBACH J R, GÄBEL G, et al. Epithelial capacity for apical uptake of short chain fatty acids is a key determinant for intraruminal pH and the susceptibility to subacute ruminal acidosis in sheep[J]. The Journal of Nutrition, 2009, 139(9): 1714-1720.
[20] WALPOLE M E, SCHURMANN B L, GÓRKA P, et al. Functional roles of aquaporins and urea transporters in urea flux across ruminal epithelium[C]//OLTJEN J W, KEBREAB E, LAPIERRE H. Energy and protein metabolism and nutrition in sustainable animal production. Wageningen: Wageningen Academic Publishers, 2013.
[21] MOSELEY R H, HÖGLUND P, WU G D, et al. Downregulated in adenoma gene encodes a chloride transporter defective in congenital chloride diarrhea[J]. American Journal of Physiology, 1999, 276(1): G185-G192.
[22] ALREFAI W A, WEN X M, JIANG W, et al. Molecular cloning and promoter analysis of downregulated in adenoma (DRA)[J]. American Journal of Physiology: Gastrointestinal and Liver Physiology, 2007, 293(5): G923-G934.
[23] MUSCH M W, ARVANS D L, WU G D, et al. Functional coupling of the downregulated in adenoma Cl /base exchanger DRA and apical Na /H exchangers NHE2 and NHE3[J]. American Journal of Physiology: Gastrointestinal and Liver Physiology, 2009, 296(2): G202-G210.
[24] JACOB P, ROSSMANN H, LAMPRECHT G, et al. Down-regulated in adenoma mediates apical Cl /HCO exchange in rabbit, rat, and human duodenum[J]. Gastroenterology, 2002, 122(3): 709-724.
[25] PENNER G B, OBA M, GÄBEL G, et al. A single mild episode of subacute ruminal acidosis affects ruminal barrier function short term[J]. Journal of Dairy Science, 2010, 93(10): 4838-4845.
[26] 艳城. 日粮对细毛羊瘤胃上皮的 SCFA 吸收相关基因及氮素转运的调控 [D]. 硕士学位论文. 呼和浩特: 内蒙古农业大学, 2015.
[27] CONNOR E E, LI R W, BALDWIN R L, et al. Gene expression in the digestive tissues of ruminants and their relationships with feeding and digestive processes[J]. Animal, 2010, 4(7): 993-1007.
[28] BILK S, HUHN K, HONSCHA K U, et al. Bicarbonate exporting transporters in the ovine ruminal epithelium[J]. Journal of Comparative Physiology B, 2005, 175(5): 365-374.
[29] GÄBEL G, ASCHENBACH J R, MÜLLER F. Transfer of energy substrates across the ruminal epithelium: implications and limitations[J]. Animal Health Research Reviews, 2002, 3(1): 15-30.
[30] 闫磊, 沈赞明. 日粮精粗比对奶牛瘤胃上皮 VFA 吸收相关基因表达的影响 [J]. 畜牧与兽医, 2012, 44(Suppl. 1): 125.

[31] HALESTRAP A P, MEREDITH D. The SLC16 gene family—from monocarboxylate transporters (MCTs) to aromatic amino acid transporters and beyond[J]. Pflügers Archiv, 2004, 447(5): 619-628.
[32] 曾军英, 韩雪峰, 谭支良. 单羧酸转运蛋白家族及其生物学功能 [J]. 生命的化学, 2008, 28(4): 404-407.
[33] KOHO N, MAIJALA V, NORBERG H, et al. Expression of MCT1, MCT2 and MCT4 in the rumen, small intestine and liver of reindeer (Rangifer tarandus tarandus L.)[J]. Comparative Biochemistry and Physiology Part A, Molecular & Integrative Physiology, 2005, 141(1): 29-34.
[34] GRAHAM C, GATHERAR I, HASLAM I, et al. Expression and localization of monocarboxylate transporters and sodium/proton exchangers in bovine rumen epithelium[J]. American Journal of Physiology: Regulatory, Integrative and Comparative Physiology, 2007, 292(2): R997-R1007.
[35] 翁秀秀. 饲喂不同日粮奶牛瘤胃发酵和 VFA 吸收特性及其相关基因表达的研究 [D]. 博士学位论文. 兰州: 甘肃农业大学, 2013.
[36] RØJEN B A, POULSEN S B, THEIL P K, et al. Short communication: Effects of dietary nitrogen concentration on messenger RNA expression and protein abundance of urea transporter-B and aquaporins in ruminal papillae from lactating Holstein cows[J]. Journal of Dairy Science, 2011, 94(5): 2587-2591.
[37] YANG W, MARTENS H, SHEN Z M. Effects of energy intake and ruminal SCFA on mRNA expression of Na /H exchangers in rumen epithelium of goats[C]//Proceedings of the 11th International Symposium on Ruminant Physiology. Clermont-Ferrand: [s.n.], 2009.
[38] SCHÜRMANN N, TRABUCO L G, BENDER C, et al. Molecular dissection of human argonaute proteins and shuffling[J]. Nature Structural & Molecular Biology, 2013, 20(7): 818-826.
[39] YAN L, ZHANG B, SHEN Z M. Dietary modulation of the expression of genes involved in short-chain fatty acid absorption in the rumen epithelium is related to short-chain fatty acid concentration and pH in the rumen of goats[J]. Journal of Dairy Science, 2014, 97(9): 5668-5675.
[40] LEONHARD-MAREK S, STUMPFF F, MARTENS H. Transport of cations and anions across forestomach epithelia: conclusions from in vitro studies[J]. Animal, 2010, 4(7): 1037-1056.
[41] ZOUZOULAS A, DUNHAM P B, BLOSTEIN R. The effect of the gamma modulator on Na/K pump activity in intact Mammalian cells[J]. The Journal of Membrane Biology, 2005, 204(1): 49-56.
[42] ALBRECHT E, KOLISEK M, VIERGUTZ T, et al. Molecular identification, immunolocalization, and functional activity of a vacuolar-type H -ATPase in bovine rumen epithelium[J]. Journal of Comparative Physiology B, 2008, 178(3): 285-295.
[43] METZLER-ZEBELI B U, HOLLMANN M, SABITZER S, et al. Epithelial response to high-grain diets involves alteration in nutrient transporters and Na /K -ATPase mRNA expression in rumen and colon of goats[J]. Journal of Animal Science, 2013, 91(9): 4256-4266.
[44] MCLEOD K R, BALDWIN R L. Effects of diet forage:concentrate ratio

and metabolizable energy intake on visceral organ growth and in vitro oxidative capacity of gut tissues in sheep[J]. Journal of Animal Science, 2000, 78(3): 760-770.
[45] 李文. 瘤胃液 pH 值、渗透压、挥发性脂肪酸 (VFAs) 浓度对绵羊瘤胃上皮 VFAs 吸收影响的研究 [D]. 硕士学位论文. 泰安: 山东农业大学, 2014.
[46] MELO L Q, COSTA S F, LOPES F, et al. Rumen morphometrics and the effect of digesta pH and volume on volatile fatty acid absorption[J]. Journal of Animal Science, 2013, 91(4): 1775-1783.
[47] 闫磊. 日粮精料水平对瘤胃上皮 SCFA 吸收相关载体表达的影响及其机理研究 [D]. 博士学位论文. 南京: 南京农业大学, 2014.
[48] 贾玉东. 日粮精粗比对奶牛瘤胃厌氧细菌和挥发性脂肪酸及血液指标的影响 [D]. 硕士学位论文. 泰安: 山东农业大学, 2008.
[49] 杨淑青. 亚急性瘤胃酸中毒对奶山羊瘤胃上皮屏障功能影响机制的研究 [D]. 硕士学位论文. 呼和浩特: 内蒙古农业大学, 2014.
[50] ETSCHMANN B, SUPLIE A, MARTENS H. Change of ruminal sodium transport in sheep during dietary adaptation[J]. Archives of Animal Nutrition, 2009, 63(1): 26-38.
[51] SCHURMANN B L, WALPOLE M E, GÓRKA P, et al. Short-term adaptation of the ruminal epithelium involves abrupt changes in sodium and short-chain fatty acid transport[J]. American Journal of Physiology: Regulatory, Integrative and Comparative Physiology, 2014, 307(7): R802-R816.
[52] JÚNIOR J C R, PEREIRA M N, BÔER H, et al. Comparison of techniques to determine the clearance of ruminal volatile fatty acids[J]. Journal of Dairy Science, 2006, 89(8): 3096-3106.

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