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The Metabolism of Volatile Fatty Acids by Portal-Drained Viscera and Liver of Goats Fed Diets with Different Forage to Concentrate Ratio

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Abstract.- Six non-lactating Chinese goats (average weight 40±2 kg) fed low forage (LF) or high forage (HF) diets were used in a randomized crossover trial to determine the net flux of VFA across portal-drained viscera and liver for 8 h from initial feeding. Chronic catheters were established in mesenteric, portal, and hepatic veins, and femoral artery to measure the plasma flow by using *p*-aminogippurric acid. The concentrations of acetate, propionate, butyrate, isobutyrate, isovalerate and TVFA were higher ($P<0.05$) and a ratio of acetate to propionate lower ($P<0.05$) in the portal, hepatic vein and artery in the LF diet compared with HF diets, but not for butyrate in portal vein and artery. The plasma flux of acetate, propionate, butyrate and TVFA in the portal, acetate and TVFA in artery were not affected by diets. The hepatic VFAs fluxes were higher ($P<0.05$) in LF than HF diet. Net acetate was produced and net propionate, butyrate, isobutyrate and isovalerate were absorbed by the liver in LF or HF diet. Net gut plus hepatic output of acetate, propionate and TVFA were greater ($P<0.05$) in LF than HF diet. VFAs concentrations reached at peak after feeding and then decreased in the portal, hepatic vein and artery in both diets. Net portal appearance and net gut plus hepatic output of VFAs reached peak at 2 to 6 h post-feeding and the maximum hepatic absorption of propionate, butyrate and output of acetate were observed at 2 to 6 h post-feeding. The results suggested that the plasma concentration and net fluxes of VFAs were increased in LF diet.

Key words: Chinese goats, forage to concentrate ratio, liver, volatile fatty acids, metabolism.

INTRODUCTION

Ruminants depend on volatile fatty acids (VFAs) for up to 80% of their maintenance energy requirements (Tagang *et al.,* 2011). Ruminal absorption of VFAs is quantitatively the most important nutrient flux in ruminants (Strom *et al.*, 2012). In addition to their involvement as the major source of energy, the VFAs also serve as building blocks for milk synthesis; acetate is an essential component in the formation of milk fat, while propionate is used for glucose production, which is needed for synthesis of lactose (Tagang *et al.*, 2011). VFAs, produced by microbial fermentation of organic matter in rumen, are absorbed mainly through the rumen wall into the portal blood and are an important source of energy for ruminants (Masson and Phillipson, 1951). The relative proportion and quantity of VFAs produced in rumen are influenced by a number of factors, including substrate composition, availability and rate of depolymerization and presence of microbial species (Cantalapiedra-Hijar *et al.*, 2009; Liu *et al*., 2012; Wu *et al*., 2011; Yang *et al*., 2009).

VFAs represented 69% of net energy absorption by portal-drained viscera (PDV) (Baird *et al*., 1975) and acetate and propionate are the predominant VFAs absorbed; each represents 30% of net PDV energy absorption in lactating Holstein cows (Reynolds and Huntington, 1988). Although the tissues of the gastrointestinal tract (GIT) and liver represent only 6 to 10% of body weight (Burrin *et al*., 1991), liver is an important organ in VFA metabolism. VFAs derived from the gut are metabolized and removed by the liver. About 93% of propionate absorbed by PDV is removed by hepatic tissues in the lactating dairy cows (Lomax and Baird, 1983), and acetate that is an important precursor for lipid synthesis is metabolized in the liver. Previous studies have reported the net metabolism of VFAs by PDV and liver (Reynolds and Huntington, 1988; Reynolds *et al*., 1988a), and the prediction of net portal appearance of VFAs and glucose in ruminants (Loncke *et al*., 2009). However, in recent years few researches has been conducted on the influence of the diet containing

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different proportion of forage and concentrate and its effects on the metabolism of VFAs in splanchnic tissue in goat. The objective of this study was to evaluate the effects of forage to concentrate ratio, on net metabolism of VFAs by PDV and liver in nonlactating goats.

MATERIALS AND METHODS

Animals and diet

Six nonlactating and nonpregnant three years old Guanzhong (Chinese breed) dairy goats (average body weight 40±2 kg) were used in a randomized crossover trial designed to determine the effects of different proportion of forage and concentrate, on the metabolism of VFA by PDV and liver. Animals were housed in individual metabolic pens in an environmentally controlled intensive housing system. They were fed low (40% hay and 60% concentrate, LF) or high (60% hay and 40% concentrate, HF) forage diets (Table I), to meet the nutrients requirements of Chinese dairy goat. The equal amount of diet (0.39 kg DM/goat) was fed twice daily (at 08:00 am morning and 08:00 pm evening), and water was available *ad libitum*. After 15 days of adaptation period, the blood samples were collected on three consecutive days.

Catheterization and blood collection

Catheters were installed surgically in the mesenteric, portal, and hepatic veins and a femoral artery to measure blood flow and net flow across the PDV, liver and splanchnic tissues (PDV + liver). After surgery, the goats were allowed for two weeks to recover before returning to normal feed consumption. The Institutional Animal Care and Use Committee of Nanjing Agricultural University (Nanjing, People's Republic of China) approved all of the procedures (surgical procedures and care of goats).

The goats were infused with a sterile aqueous solution (pH 7.4) of *para*- aminohippurric acid (PAH, 1%, wt/vol, Alfa Aesar, CAS 94-16-6, from Alfa Aesar China (Tianjin) Co., Ltd) into mesenteric vein by using the syringe pump((SN-50F6, Sino Medical-Device Technology Co., Ltd., Shenzhen, China). The initial rate was at 3 ml/min for 5 min followed by a regular rate of 0.8 ml/min for at least 30 min before collecting blood and the same rate was used until the end of sampling. The blood samples were obtained simultaneously from the portal, hepatic and arterial catheters at 0 h (before feeding), and at 2, 4, 6 and 8 h (after feeding). After blood collection, immediately all the samples were transferred from the syringe to heparinized (3.6 U heparin/ml blood) tubes placed on ice and transported to the laboratory. The blood samples were centrifuged at 1,469×*g* for 20 min at 4°C to separate the plasma. The PAH was immediately analyzed and the remaining plasma was stored at -20°C for analyses of VFAs.

Table I.- Chemical composition and nutrient level of diets.

Ingredient	% of diet (air dry mater)	
	Low forage (LF)	High forage (HF)
Chinese wildrye hay	32.00	48.00
Alfalfa hay	8.00	12.00
Corn	43.17	28.78
Soybean meal	12.68	8.45
Limestone	1.15	0.77
Calcium phosphate dibasic	1.65	1.10
Salt	0.60	0.40
Premix [a]	0.75	0.50
Nutrient level		
Dry mater, %	88.60	88.90
Net energy, MJ/kg	5.89	5.40
CP, %	13.45	12.24
NDF, %	27.69	36.55
ADF, %	17.54	24.04

[a] Premix provided: 3000, 1250, and 40 IU/kg of diet of vitamin A, D and E, and 6.25, 62.5, 62.5, 50, 0.25, 0.125, 0.125 mg/kg of diet of Cu, Fe, Zn, Mn, I, Se, Co, respectively. CP, crude protein; NDF, neutral detergent fiber; ADF, acid detergent fiber.

Laboratory analyses

The plasma samples were deproteinized by an addition of 0.5 mol/l trichloroacetic acid, then centrifuged at 2,296×*g* for 20 min at 4°C. The supernatant was analyzed for PAH concentration according to the procedures described by Katz and Bergman (1969a). A portion of plasma was deproteinized with 5% 5-Sulfosalicylic acid dehydrate and kept at -20°C for 12 h, then centrifuged at 20,664×*g* for 30 min and the supernatant aliquots were analyzed for VFAs.

Plasma acetate, propionate, butyrate, isobutyrate and isovalerate concentrations were determined by using gas chromatography (Agilent Technologies 7890A, GC system) with flam ionization detector, based on the method of (Bjorkman and Forslund, 1986; Reynold *et al.*, 1986) with some modifications. Briefly, the gas chromatography was performed using a 30 m×0.25 mm i.d. fused silica capillary column (Catalog No: 24107, Supelco) with a 0.25 µm film. Nitrogen was used as the carrier gas and hydrogen as a fuel gas at the flow rate of 30 ml/min, respectively. The pressure was 260 kPa and air was a combustion-supporting gas. The temperature of the column, the flame ionization detector and the injector were 125°C, 210°C and 220°C, respectively. The split ratio was 40:1 and 1 µl was injected. Portal and hepatic plasma flow were calculated from the plasma *p*-aminohippureate concentrations as described by Katz and Bergman (1969b). The portal appearance and net hepatic release of blood metabolites were calculated as reported by Wieghart *et al.* (1986).

Statistical analysis

All statistical computations were conducted in MIXED procedure of SAS (version 9.0; SAS Institute Inc., Cary, NC). Goats were used as the random factor, diet and time were used as main effect factor, and diet×time was used as interaction. Means were compared by least squares. Treatment means within diets at different time were compared using a Tukey's adjustment multiple range test. Significance was declared at $P<0.05$.

RESULTS

The volatile fatty acid (VFA) concentration

The plasma VFA concentrations of portal, hepatic veins and femoral artery are given in the Table II. The concentrations of acetate, propionate, butyrate, isobutyrate, isovalerate and total volatile fatty acids (TVFA) were markedly higher ($P<0.05$) (except butyrate concentration for portal vein and artery), while the ratio of acetate to propionate lower ($P<0.01$) in the portal, hepatic vein and artery in goats fed LF diets as compared with HF diets. Acetate, propionate, butyrate, isobutyrate, isovalerate and TVFA concentration were increased by 11.9%, 40.1%, 19.5%, 83.3%, 33.3% and 17.0% in portal, 9.5%, 101.4%, 45.3%, 328.6%, 117.6%, and 14.6% in hepatic vein, and 12.0%, 90.6%, 16.4%, 187.5%, 55.6%, and 15.8% in artery, respectively, in LF diets than that of HF diets. The interaction between diet and time was not observed.

The VFA flux

There were no differences ($P>0.05$) in portal and hepatic plasma flow between diets (Table III). Although the portal vein fluxes of isobutyrate and isovalerate were significantly ($P<0.05$) higher in the goats fed with LF diet, while the acetate, propionate, butyrate and TVFA were not statistical different ($P>0.05$) between both diets, but the high values were obtained in goats fed with LF diets. Results revealed highly significant increase ($P<0.05$) in hepatic and arterial fluxes of acetate, propionate, butyrate, isobutyrate, isovalerate and TVFA in LF diets compared with HF diets, except acetate and TVFA in arterial flux. There was no interaction of diet and time ($P>0.05$) between both diets.

The venous-arterial concentration differences of VFAs

The results for venous-arterial concentration differences of VFAs are summarized in Table IV. The portal-arterial (P-A) concentration, the hepatic-portal (H-P) concentration and the hepatic-arterial (H-A) concentration differences of acetate, butyrate and isobutyrate were not significantly different ($P>0.05$) between diets, while P-A, H-P and H-A concentrations of propionate, isovalerate and TVFA were higher ($P<0.05$) in goats fed LF diets than HF diets, except TVFA in H-P. There was no interaction between diet and time ($P>0.05$) in both diets.

The net flux of VFA across splanchnic tissues

Net portal appearances and net hepatic release of VFAs were not significantly different ($P>0.05$) between the diets (Table V). On a net basis, hepatic tissues produced acetate and removed other VFAs for both LF and HF diets. Net hepatic removal accounted for 86.3%, 52.4%, 59.6%, 55.8%, 18.8% and 92.4%, 83.8%, 106.1%, 117.8%, 19.3% of net PDV appearance of propionate, butyrate, isobutyrate, isovalerate and TVFA for LF and HF

Table II.- Mean portal, hepatic and arterial VFA concentrations in goats fed LF and HF diets.

	LF	HF	SEM	P-value		
				Diet	Time	D×T
Portal concentration (mmol/L)						
Acetate	3.09	2.76	0.32	0.04	<0.001	0.66
Propionate	0.69	0.49	0.10	<0.001	<0.001	0.56
Butyrate	0.19	0.16	0.02	0.22	<0.001	0.28
Isobutyrate	0.05	0.03	0.01	0.01	0.19	0.27
Isovalerate	0.06	0.04	0.00	0.00	0.01	0.06
TVFA	4.07	3.48	0.43	0.00	<0.001	0.59
A:P	4.51	5.98	0.22	0.01	<0.001	0.57
Hepatic concentration (mmol/L)						
Acetate	2.70	2.46	0.27	0.03	<0.001	0.60
Propionate	0.15	0.07	0.01	<0.001	0.04	0.45
Butyrate	0.11	0.07	0.08	<0.001	0.06	0.54
Isobutyrate	0.03	0.01	0.01	0.01	0.56	0.18
Isovalerate	0.04	0.02	0.00	<0.001	0.59	0.16
TVFA	3.03	2.64	0.27	0.00	<0.001	0.49
A:P	20.41	33.59	1.12	<0.001	0.18	0.99
Arterial concentration (mmol/L)						
Acetate	1.78	1.59	0.11	0.00	0.00	0.39
Propionate	0.10	0.05	0.01	0.01	0.14	0.44
Butyrate	0.08	0.07	0.01	0.22	0.31	0.54
Isobutyrate	0.02	0.01	0.00	<0.001	0.31	0.54
Isovalerate	0.03	0.02	0.00	0.01	0.40	0.05
TVFA	2.01	1.72	0.11	0.00	0.00	0.49
A:P	20.55	30.17	0.85	<0.001	0.00	0.12

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean; D×T, Diet×Time; TVFA, total volatile fatty acids; A; P, acetate: propionate.

diets, respectively. Net gut plus hepatic output of acetate, propionate and TVFA were higher (P<0.05) in LF diets than in HF diets. The negative values of the net gut plus hepatic output of isobutyrate (-0.001 mmol/h/kg of LW) indicated that there was a little net removed by total viscera in goats fed HF diets.

The concentrations of VFA across splanchnic tissues in relation to feeding time

The concentration of acetate was significantly affected (P<0.05) by feeding time in portal, hepatic and arterial in goats fed LF or HF diets, except arterial acetate concentration in LF diets, the peak of acetate was recorded at 2 h post feeding, and then declined gradually to the pre-feeding levels. The portal propionate concentration was significantly (P<0.05) effected for both diets, highest was obtained after 2 h post feeding and then progressively decreased in time dependent manner, while hepatic and arterial propionate concentrations were also non significantly increased after feeding, then decreased gradually as the time progressed towards the initial feeding. The portal concentration of butyrate reached a plateau at 2 h (P<0.05) for LF diets (Table VI). However it was not significant in case of hepatic and arterial for both diets.

The net flux of VFAs across splanchnic tissues in relation to feeding time

Net portal appearance for acetate was at highest levels at 4 h (P<0.05) post feeding in goats fed LF diet and at 2 h (P>0.05) in HF diet, while for propionate it was higher (P<0.05) at 6 h for LF diet and (P>0.05) at 2 h post feeding for HF diet. The net portal appearance for butyrate was at peak after 4 h (P<0.05) in LF diet and at 2 h in HF diet, respectively. There was a net hepatic absorption for propionate and butyrate, and a net hepatic output for

Table III.- Mean portal, hepatic and arterial VFA flux in goats fed LF and HF diets.

	LF	HF	SEM	P-value		
				Diet	Time	D×T
Plasma flow (l/h)						
Portal	57.62	59.17	2.28	0.38	0.01	0.18
Hepatic	93.87	92.18	2.56	0.94	<0.001	0.61
Portal flux (mmol/h/kg of LW)						
Acetate	4.57	4.16	0.39	0.16	<0.001	0.22
Propionate	0.99	0.74	0.17	0.11	<0.001	0.04
Butyrate	0.28	0.24	0.03	0.33	<0.001	0.16
Isobutyrate	0.08	0.04	0.10	0.03	0.03	0.08
Isovalerate	0.08	0.06	0.01	0.00	0.00	0.00
TVFA	6.01	5.25	0.57	0.11	<0.001	0.11
Hepatic flux (mmol/h/kg of LW)						
Acetate	6.53	5.81	0.60	0.05	<0.001	0.53
Propionate	0.36	0.17	0.04	0.00	0.01	0.36
Butyrate	0.27	0.18	0.03	0.00	0.01	0.49
Isobutyrate	0.07	0.02	0.02	0.03	0.37	0.09
Isovalerate	0.09	0.04	0.10	0.00	0.16	0.09
TVFA	7.32	6.22	0.62	0.03	<0.001	0.42
Arterial flux (mmol/h/kg of LW)						
Acetate	1.67	1.36	0.15	0.11	<0.001	0.70
Propionate	0.09	0.05	0.02	0.03	0.02	0.49
Butyrate	0.07	0.06	0.01	0.01	0.01	0.22
Isobutyrate	0.02	0.01	0.00	<0.001	0.10	0.06
Isovalerate	0.03	0.02	0.00	0.00	0.02	0.01
TVFA	1.89	1.48	0.16	0.09	<0.001	0.71

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean; D×T, Diet×Time; TVFA, total volatile fatty acids; LW, live weight.

acetate during pre and post feeding time in both diets. The maximum propionate absorption was 1.08 mmol/h/kg of LW at 6 h ($P<0.05$) post feeding in LF diet and 0.94 mmol/h/kg of LW at 2 h ($P<0.05$) post feeding in HF diet, respectively. Net gut plus hepatic output of acetate increased after feeding and reached to the highest level at 4 h ($P<0.05$) in LF and at 2 h ($P>0.05$) in HF diet. The maximum total splanchnic output was at 2 h post feeding in both diets for propionate, at 4 h in LF diet and at 2 h in HF diet for butyrate, respectively (Table VII).

DISCUSSION

Volatile fatty acids, mainly acetate, propionate and butyrate, are mainly absorbed through the rumen wall into the portal blood (Masson and Phillipson, 1951). The type of digested carbohydrate is a decisive factor in determining the ratio and quantity of the resultant rumen VFAs (Cantalapiedra-Hijar *et al*., 2009; Huntington *et al*., 2006). The net production of total VFAs were increased in cows fed low roughage diets (Liu *et al*., 2012; Sutton *et al.*, 2003; Wu *et al*., 2011). Similarly, Annison *et al.* (1974) found the increased portal concentration and molar proportion of propionic acid in the rumen of adult dairy cows fed high concentrate diet. The similar results were obtained in non-lactating cows (Wiltrout and Satter, 1972). The results of the present study showed that VFA concentrations were higher in goats fed LF diets than HF diets, furthermore, acetate, propionate, and butyrate concentration in portal plasma accounted for 75.8%, 16.8% and 4.7% of total VFA in LF diet, and 79.3%, 14.1% and 4.6% of total VFA in HF diet, respectively. The ratio of acetate to

Table IV.- The venous-arterial concentration differences of VFA in goats fed LF and HF diets.

	LF	HF	SEM	P-value		
				Diet	Time	D×T
Portal-arterial difference (P-A) (mmol/L)						
Acetate	1.30	1.17	0.21	0.20	0.00	0.49
Propionate	0.58	0.44	0.10	0.01	<0.001	0.67
Butyrate	0.11	0.09	0.02	0.46	<0.001	0.39
Isobutyrate	0.03	0.02	0.01	0.13	0.13	0.22
Isovalerate	0.03	0.02	0.00	0.03	0.05	0.00
TVFA	2.06	1.74	0.33	0.01	<0.001	0.49
Hepatic-portal difference (H-P) (mmol/L)						
Acetate	-0.39	-0.30	0.08	0.44	0.01	0.82
Propionate	-0.54	-0.42	0.10	0.02	<0.001	0.68
Butyrate	-0.08	-0.08	0.02	0.82	0.08	0.95
Isobutyrate	-0.03	-0.02	0.00	0.06	0.03	0.38
Isovalerate	-0.02	-0.03	0.00	0.01	0.64	0.62
TVFA	-1.05	-0.84	0.17	0.19	<0.001	0.95
Hepatic-arterial difference (H-A) (mmol/L)						
Acetate	0.92	0.87	0.17	0.48	0.01	0.42
Propionate	0.05	0.02	0.00	<0.001	0.00	0.39
Butyrate	0.03	0.01	0.01	0.05	0.25	0.68
Isobutyrate	0.01	0.00	0.00	0.22	0.61	0.08
Isovalerate	0.01	-0.00	0.00	0.01	0.49	0.51
TVFA	1.01	0.90	0.17	0.02	0.01	0.38

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean; D×T, Diet×Time; TVFA, total volatile fatty acids.

propionate was lower ($P<0.05$) and TVFA higher ($P<0.05$) in portal, hepatic vein and artery in LF than in HF diet. This might be due to the fact that low forage diet provided more net energy (+9.07%) and less NDF (-24.2%) than did high forage diets for animals, and which increased more digestible matter to produce more VFAs in rumen and finally increased portal VFAs quantity although goats fed the same feed intake (0.88 kg/d). Results of the present study were in accordance to the previous studies reported by various researchers (Lomax and Baird, 1983; Nasrullah *et al*., 2013; Reynolds *et al.*, 1988b).

There were no significant difference for mean portal and hepatic plasma flows between both diets (Table III), which was in agreement with previous results (Burrin *et al.,* 1991). The positive values of the net hepatic release of acetate indicated there was a net output of acetate in the present study in both diets, consistent with previous *in vivo* measurements dairy cows (Snoswell *et al.,* 1978; Lomax and Baird, 1983). The liver takes up the majority of VFAs absorbed into the portal vein. However, acetate was simultaneously produced and utilized by all tissues (Bergman and Wolff, 1971; Pethick *et al.*, 1981) while, the endogenous acetate was produced mainly by liver.

Propionate and n-butyrate are almost completely removed from portal blood by the hepatic tissue as found in studies on sheep (Bergman and Wolff, 1971) and dairy cattle (Lomax and Baird, 1983). Within the liver, propionate serves as a major substrate for gluconeogenesis, which is absolutely critical to the ruminant because almost no glucose reaches the small intestine for absorption.

Propionate is not only an important glucose precursor in ruminant hepatic tissue (Danfær *et al.*, 1995), but also may enter the tricarboxylic acid cycle, be oxidized, or be incorporated into amino acids, and conversion into glucose accounts for 95% of propionate metabolism in sheep liver (Reynolds *et al*., 1988a). In the present study, the plasma propionate concentration was high, which indicated that more propionate was absorbed by PDV tissues

Table V.- Net flux of VFA across splanchnic tissues of goats fed LF and HF diets

	LF	HF	SEM	P-value		
				Diet	Time	D×T
Net portal appearance (mmol/h/kg of LW)						
Acetate	1.95	1.74	0.23	0.26	0.00	0.47
Propionate	0.85	0.66	0.16	0.21	<0.001	0.10
Butyrate	0.16	0.14	0.03	0.60	<0.001	0.15
Isobutyrate	0.05	0.03	0.01	0.23	0.04	0.04
Isovalerate	0.04	0.03	0.00	0.53	0.86	0.76
TVFA	3.05	2.62	0.41	0.19	<0.001	0.46
Net hepatic release (mmol/h/kg of LW)						
Acetate	0.29	0.29	0.11	0.95	0.51	0.53
Propionate	-0.73	-0.61	0.15	0.38	<0.001	0.04
Butyrate	-0.09	-0.12	0.02	0.06	0.45	0.90
Isobutyrate	-0.03	-0.04	0.07	0.45	0.08	0.45
Isovalerate	-0.02	-0.03	0.02	0.14	0.49	0.54
TVFA	-0.57	-0.51	0.12	0.68	0.49	0.31
Net gut plus hepatic output (mmol/h/kg of LW)						
Acetate	2.28	2.04	0.36	0.02	<0.001	0.58
Propionate	0.12	0.05	0.01	<0.001	0.04	0.56
Butyrate	0.08	0.00	0.00	0.09	0.22	0.63
Isobutyrate	0.02	0.00	0.01	0.24	0.46	0.05
Isovalerate	0.02	0.00	0.00	0.28	0.58	0.46
TVFA	2.47	2.11	0.38	0.01	<0.001	0.47

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean; D×T, Diet×Time; TVFA, total volatile fatty acids; LW, live weight.

in goats fed LF diets, it might be due to the increase in net splanchnic flux of propionate with increased propionate absorption to the portal vein (Berthelot *et al*., 2002; Majdoub *et al.,* 2003). Net hepatic releases of propionate showed a negative value in both diets, which suggested that much propionate absorbed from gastrointestinal tract was removed. In the present study, the liver received 86.3% and 92.4% of the net PDV appearance of propionate in goats fed LF diets and HF diets, respectively. These results are in accordance with previous in vive study in dairy cows (Kristensent, 2005). The propionate absorbed by liver would be used to synthesize glucose in liver tissues (Table V) so that net hepatic releases of glucose were positive (35.50 vs 30.49 mmol/h for LF diets and HF diets, respectively, unpublished), while the net portal appearances of glucose were negative (-16.18 vs -8.99 mmol/h, unpublished) for LF diets vs HF diets, respectively. Besides propionate, there was a net hepatic uptake of butyrate, isobutyrate and isovalerate in both diets, findings similar to those observed by others researchers (Lomax and Baird, 1983; Reynolds *et al*., 1988b; Danfær, 1994). In ruminant tissues, particularly in liver, much butyrate is removed to β-hydroxybutyrate (BOHB) (Katz and Bergman, 1969b), which was confirmed by our other experiment (unpublished) which showed that net hepatic release of BOHB was higher compared with net portal appearance (9.99 vs 5.05, and 14.18 vs 5.51 mmol/h, for LF diets and HF diets, respectively).

The net absorption of VFAs increased after morning feeding (Huntington and Reynolds, 1983). There was a positive relationship between metabolizable energy intake and the rates of net portal appearance of VFAs, hydroxybutyrate and lactate in fed and fasted cows and sheep. Fasting caused a rapid decrease but re-feeding rapid increases in the blood concentration of the VFA (Lomax and Baird, 1983). In present study, the portal concentration and net splanchnic flux of

Table VI.- VFA concentrations in goats fed different diets in relation to feeding time.

		Post feeding time (h)					
		0	**2**	**4**	**6**	**8**	**SEM**
Acetate concentration (mmol/L)							
Portal	LF	2.39^{b}	3.96^{a}	3.59^{ab}	3.03^{ab}	2.46^{b}	0.39
	HF	1.99^{b}	3.48^{a}	3.00^{ab}	2.80^{ab}	2.56^{ab}	0.39
Hepatic	LF	2.20^{b}	3.52^{a}	2.99^{ab}	2.71^{ab}	2.08^{b}	0.33
	HF	1.88^{b}	3.05^{a}	2.65^{ab}	2.49^{ab}	2.25^{ab}	0.33
Arterial	LF	1.76	2.19	1.73	1.76	1.48	0.17
	HF	1.25^{b}	2.04^{a}	1.71^{ab}	1.47^{ab}	1.49^{ab}	0.17
Propionate concentration (mmol/L)							
Portal	LF	0.39^{c}	0.94^{a}	0.72^{abc}	0.83^{ab}	0.55^{bc}	0.12
	HF	0.27^{b}	0.66^{a}	0.54^{ab}	0.53^{ab}	0.45^{ab}	0.12
Hepatic	LF	0.12	0.20	0.18	0.16	0.09	0.02
	HF	0.06	0.09	0.08	0.08	0.06	0.02
Arterial	LF	0.09	0.11	0.14	0.11	0.06	0.02
	HF	0.05	0.06	0.06	0.05	0.04	0.02
Butyrate concentration (mmol/L)							
Portal	LF	0.14^{bc}	0.26^{a}	0.24^{ab}	0.19^{ab}	0.12^{c}	0.03
	HF	0.11	0.21	0.16	0.16	0.15	0.03
Hepatic	LF	0.09	0.15	0.13	0.11	0.07	0.02
	HF	0.06	0.10	0.72	0.07	0.07	0.02
Arterial	LF	0.08	0.10	0.08	0.07	0.06	0.01
	HF	0.07	0.07	0.07	0.06	0.06	0.01

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean.
The different superscript letter in row mean significant difference at 0.05 levels for LF diet or HF diet, respectively.

VFAs reached to maximum values at 2, 4 and 6 h post-feeding, and then gradually declined to the pre-feeding level in both diets. Similarly, Evans *et al.* (1975) reported that the values obtained between 1.5 to 5.5 h post-feeding were greater than 0.5 h pre-feeding and 7.5 h post-feeding values. It was also observed that the peaks of net portal appearance of VFAs delayed for LF diet as compared with HF diets. The reason may be that the LF diet supplied more digestible matter, increased VFAs concentration and also kept high level for long time in rumen, which resulted in high concentration of VFAs in portal vein (Tables II and VI). On the other hand, the portal plasma flow reached to peak at 2 h in HF diet and 6 h in LF diets, therefore which caused net portal appearance delay in LF diets. The mean net gut plus hepatic output of TVFA was higher ($P<0.05$) in LF diet as compared to HF diets, it might be due to production of the more VFAs in rumen when goats fed LF diets.

CONCLUSIONS

Based on present results, it was concluded that the plasma VFA concentration and flux were increased, whereas ratio of acetate to propionate was decreased in portal, hepatic vein and femoral artery of goats fed low forage diets compared with high forage diets. Net acetate output was produced and net propionate, butyrate, isobutyrate and isovalerate were removed by goat liver. Net gut plus hepatic outputs of acetate, propionate and TVFA were greater in LF diet than HF diet. The concentration and net flux of VFAs were increased in after feeding then gradually declined and close to pre-feeding levels.

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Table VII.- Net flux of VFA across splanchnic tissues in relation to feeding time.

		Post feeding time (h)					
		0	**2**	**4**	**6**	**8**	**SEM**
Net portal appearance (mmol/h/kg of LW)							
Acetate	LF	0.83^{b}	2.27^{ab}	3.20^{a}	2.18^{ab}	1.26^{ab}	0.46
	HF	0.89	2.47	2.13	1.72	1.50	0.46
Propionate	LF	0.41^{b}	1.07^{ac}	0.98^{abc}	1.21^{a}	0.57^{bc}	0.19
	HF	0.27	1.02	0.79	0.61	0.61	0.19
Butyrate	LF	0.08^{b}	0.19^{ab}	0.27^{a}	0.21^{ab}	0.07^{b}	0.04
	HF	0.04^{b}	0.27^{a}	0.15^{ab}	0.13^{ab}	0.12^{ab}	0.04
Net hepatic release (mmol/h/kg of LW)							
Acetate	LF	0.10	0.74	0.34	0.27	0.01	0.25
	HF	0.38	0.18	0.36	0.59	0.06	0.25
Propionate	LF	-0.33^{c}	-0.85^{ab}	-0.88^{ab}	-1.08^{a}	-0.51^{bc}	0.17
	HF	-0.24^{b}	0.94^{a}	-0.74^{ab}	-0.55^{ab}	-0.55^{ab}	0.17
Butyrate	LF	-0.04	-0.09	-0.13	-0.11	-0.06	0.05
	HF	-0.06	-0.18	-0.15	-0.09	-0.11	0.05
Net gut plus hepatic output (mmol/h/kg of LW)							
Acetate	LF	0.93^{c}	3.01^{abc}	3.54^{a}	2.45^{abc}	1.25^{bc}	0.55
	HF	1.28	2.65	2.49	2.22	1.57	0.55
Propionate	LF	0.08	0.21	0.10	0.12	0.06	0.03
	HF	0.03	0.08	0.05	0.06	0.04	0.03
Butyrate	LF	0.04	0.11	0.13	0.09	0.01	0.00
	HF	-0.03	0.09	0.00	0.04	0.01	0.00

LF, low forage diet; HF, high forage diet; SEM, standard error of the mean.
The different superscript letter in row mean significant difference at 0.05 levels for LF diet or HF diet, respectively.

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