Volatile Fatty Acids Production in the Rumen of Young Heifers Given Diets Containing a Large Proportion of Concentrate

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Abstract The rate of production of volatile fatty acids (VFA) in the rumen of animals on high concentrate feeding was studied with eighteen young heifers fitted with a permanent rumen fistula, using a single injection method of ^{14}C -acetate and polyethylene glycol (PEG) in order to get some basic informations of rumen fermentation on concentrate diets. The results obtained were as follows; 1) The pH value, total VFA concentration, and proportion of each acid on all-concentrate diets showed distinguished differences in comparison with those of the animals fed a large proportion of hay, but varied widely between days and heifers. 2) VFA proportions were significantly correlated with pH. At the pH value of about 5.2, acetic acid was minimum, and propionic acid and valeric acid were maximum in molar proportion. 3) It was suggested that, in the case of all-concentrate feeding for a long period, the VFA production in the rumen was depressed to 33.5-41% of digestible energy. In the animals fed hay and concentrate, the percentage was about 50%.

Abnormality of rumen fermentation and low growth rate have often been observed in heifers on common pasture during the early part of the grazing period. One of the causes is supposed to be the abrupt change from concentrate to forage, since the feeding regime in Japan is commonly based on the diets containing a large proportion of concentrate. The studies about rumen fermentation of the animals fed the concentrated diets have often been reported with respect to VFA concentration and proportion of each acid¹⁻¹⁰⁾. However, the production of VFA in the rumen on all-concentrate diet has not been reported except one by WHITEHEAD *et al.*¹¹⁾ on barley feeding with *in vitro* technique. As a part of studies of adaptive changes of rumen fermentation to various diets, this study was conducted to obtain some basic information about the VFA production in the rumen of heifers fed a concentrate alone.

Experimental Procedure

Animals and feeding regime: This study consisted of seven experiments, in which eighteen Holstein heifers equipped with rumen fistula were used. The number and weight of heifers and the diets used in each experiment were shown in Table 1. The heifers were kept in stanchions and offered the experimental diets at 9-10 AM and 4 PM in equal amounts daily. Water was available for them at all times in these experiments. The heifers used in Expt 1 had been fed hay and concentrate together for a month. The measurement of VFA production was carried out at

Table 1. Experimental design and diets used

Exp. No.	No. of heifers	Mean body weight (kg)	Diet/day (kg)	
1	9	124	concentrate A	1.0
			+ hay	1.5
2	3	127	concentrate B	4.0
3	3	127	"	3.0
4	2	136	"	3.0
5	3	179	"	5.0
6	3	97	"	3.0
7	3	98	"	2.0
			+ hay	0.8

the end of the period. Expts 2, 3, and 4 were conducted in series in order to investigate the adaptative change of rumen fermentation to a concentrate. The VFA production was measured on the 2nd, 5th, and 15th day after the commencement of feeding on the concentrate only. The animals in these experiments were three of the nine used in Expt 1. A heifer was removed from Expt 4 due to diarrhoea and anorexia. The heifers in Expt 5, which were not used in four previous experiments, had been fed the concentrate only for five weeks. VFA production was measured in the last week to investigate the stable condition of rumen fermentation on an all-concentrate diet. Expt 6 was carried out for the same objective as Expt 5. The VFA production was measured in the 6th week of on all-concentrate feeding. The animals in Expt 7 had been fed hay and concentrate for five weeks and were sampled for VFA production in the last week. Digestibility trials were carried out in Expts 4, 5, 6, and 7.

Feed constituents of experimental diets: The hay used in Expts 1 and 7 mainly consisted of orchard grass and partly white clover, Kentucky bluegrass, red top and meadow fescue.

Concentrate A consisted of 58% oats, 19.5% wheat bran, 19.5% soybean cake, 2% mineral mixture and 1% sodium chloride. Concentrate B consisted of 30% milo, 20% barley, 20% corn, 10% rice bran, 10% defatted rice bran, 6.5% soybean cake, 1.8% calcium carbonate, 1% sodium chloride, 0.5% calcium phosphate, 0.1% mineral mixture and 0.1% vitamin mixture. Chemical compositions of the concentrates were shown in Table 2.

Measurement of VFA production rate in the rumen: VFA production rate was measured with a single injection method of [$1-^{14}\text{C}$] acetate and polyethylene glycol (PEG). Within an hour after feeding 200 ml of very dilute solution, which included 40 g PEG (mol wt, 4000) and 10–15 μCi sodium acetate $1-^{14}\text{C}$, was infused into the rumen via the fistula through a polyethylene pipe of

Table 2. Chemical composition of the concentrates

	Dry matter (%)	based on dry matter (%)				
		Crude protein	Crude fiber	Ether extract	Ash	Nitrogen free extract
Concentrate A	86.3	21.7	2.3	1.3	4.9	69.8
Concentrate B	87.4	15.2	5.8	1.5	6.9	70.6

VFA Production on Concentrate Feeding

2 cm internal diameter, mixing with the rumen fluid as homogeneously as possible. Samples of rumen fluid were drawn through the polyethylene tube of 3 mm internal diameter fixed to the rumen fistula, with the intraruminal end covered with a nylon net. This was done immediately before morning feeding and 6–11 times after feeding. The samples of rumen fluid were stored at -20°C for analysis after measuring the pH values and mixing with mercuric chloride.

Analytical method: The pH values of rumen fluid were determined by glass electrode pH meter. After melting the stored samples, PEG concentration in a portion of rumen fluid sample was estimated by the method of HYDEN.¹²⁾ The residual samples were centrifuged at 3000 rpm for 15 minutes for the measurement of specific activity of ^{14}C -VFA and VFA analysis in the rumen fluid. The specific activity of ^{14}C -VFA in the rumen fluid was determined by liquid scintillation counting in a Packard Tricarb Liquid Scintillation Spectrometer Model 2003. The correction for quenching was made by using the external standardization. The scintillation mixture for radioactive counting comprised 7 g PPO (2,5-diphenyloxazole), 0.3 g POPOP [2,2-p-phenylenebis (5-phenyloxazole)] and 50 g naphthalene per a liter of dioxane. One ml of the supernatant of the sample was mixed with 10 ml of the scintillation mixture, centrifuged at 3000 rpm for 10 minutes, and was measured for the specific activity. VFA concentration and proportion of acid were measured on a Shimadzu GC-5A gas chromatograph, using a 150 cm column packed with Diasolid S, 60–80 mesh and 20% ethylene glycol sebacate with nitrogen as the carrier gas and column temperature at 150°C . One ml of rumen fluid sample was mixed and deproteinized with 0.2 ml of 20% metaphosphoric acid solution, the supernatant was used for VFA analysis by gas chromatography with crotonic acid as internal indicator. The concentrations of lactic acid and succinic acid in Expts 5, 6, and 7 were determined by gas chromatography with the same column as used for VFA analysis after being methylated with a boron trifluoride methanol complex. Malonic acid was used as the internal indicator.

Calculation of VFA production rate: The rate of production in the rumen, disappearance from the rumen, absorption from the rumen wall, and outflow to lower gut were calculated from the following equation;

$$\frac{dx}{dt} = -Kx, \text{ or } X = x_0 e^{-Kt}$$

x represents the specific activity of ^{14}C -VFA (dpm/mmol-VFA for production rate, dpm/ml-rumen fluid for disappearance rate, or dpm/mg-PEG for absorption rate) or PEG for outflow rate at time t . x_0 represents the x at the time of dosing. K is the constant rate that was calculated from the logarithmic regression of x on time. Rumen fluid volume was estimated from the PEG concentration at the time of dosing. As the rate of VFA production considerably changed according to the time after feeding, the disappearance rate was used for the production rate.

Results

Table 3 shows pH, total VFA, and proportion of each acid of rumen fluid in each experiment in mean value. The pH values changed diurnally as shown in Fig. 1. When hay was fed together with concentrate, the pH values fluctuated as Expt 1 in Fig. 1. In this case, the mean value was high and the range of variation was narrow. But, when the concentrate was fed, the patterns of the diurnal changes could be divided into two forms. One was a pattern shown in Expts 3 and 4 in Fig. 1. In such a pattern, the pH value was relatively high before feeding, but abruptly fell to a minimum in 2–4 hours after feeding, and then gradually rose until the next feeding. Expt 7, in which a small proportion of hay was given with a concentrate, also belonged

Table 3. Mean pH value, total VFA concentration and molar proportion of each acid on high concentrate feeding

Exp. No.	pH mean $\pm$ SD	Total VFA (mM)	molar proportion of VFA (%)							
			Acet	Pro	Isobut	But	Isoval	Val	Cap	
1	6.70 $\pm$ 0.28	93.4 $\pm$ 23.1	61.9	25.1	1.4	8.4	0.8	2.3	0.1	
2	5.65 $\pm$ 0.54	127.4 $\pm$ 36.8	51.4	28.5	1.4	12.7	1.5	4.0	0.5	
3	5.20 $\pm$ 0.59	167.3 $\pm$ 43.2	41.1	42.7	1.2	9.4	1.2	3.3	1.1	
4	5.33 $\pm$ 0.67	101.5 $\pm$ 18.4	42.4	33.9	1.6	12.5	1.1	8.0	0.5	
5	5.34 $\pm$ 0.27	141.1 $\pm$ 24.8	49.6	27.5	0.5	14.0	0.6	6.0	1.9	
6	5.07 $\pm$ 0.69	132.6 $\pm$ 50.9	52.3	28.4	0.6	12.4	0.5	4.1	1.7	
7	5.71 $\pm$ 0.79	141.6 $\pm$ 56.1	52.7	29.8	0.7	10.7	1.1	4.5	0.5	

to this pattern. The other was shown in Expts 2, 5 and 6 in Fig. 1. The pH values were relatively low even before feeding and fell in a small range after feeding. The diurnal fluctuation was relatively narrow. All of the mean daily pH values on all-concentrate feeding were below 6 in contrast to the high level of pH values in Expt 1. The diurnal changes of VFA concentration were shown in Fig. 2. The concentration in Expt 1, which was the group given hay and concentrate, was lower and varied in a smaller range compared with the group fed the concentrate only. Though the VFA concentration on all-concentrate feeding was high, the fluctuation was not

Fig. 1. The diurnal changes of pH in the rumen on high concentrate feeding

Fig. 2. The diurnal changes of total VFA on high concentrate feeding

VFA Production on Concentrate Feeding

Table 4. A extreme difference between the heifers fed same concentrate diet in Expt 5

animal No.	pH	Total VFA (mM)	Molar proportion of VFA (%)							Lac-tate	Suc-cinate (mM)
			Acet	Pro	Isobut	But	Isoval	Val	Cap		
50	5.41	116.8	41.1	18.7	0.5	25.5	0.8	10.7	2.7	NE	15.9
45	5.21	159.6	45.4	42.3	0.6	6.7	0.5	4.1	0.3	NE	NE

NE; negligible

so wide except in Expts 3 and 6. But the concentration in Expt 7, that was the group given a small proportion of hay, changed at high level with wide fluctuation.

In the diurnal changes of VFA proportions, acetic acid, isobutyric acid, and isovaleric acid had a tendency to decrease after feeding. On the other hand, propionic acid increased after feeding. However, butyric acid, valeric acid, and caproic acid had no regular tendency. The mean daily proportions of each acid in these experiments were shown in Table 3. Acetic acid was the lowest and propionic acid was the highest in molar proportion in Expt 3 that was on 5th day after the commencement of all-concentrate feeding. However, there were great differences in the proportion of each acid between days and the heifers on all-concentrate feeding. Table 4 showed a large difference in the proportions of VFA and succinic acid between heifers in Expt 5. In No. 50 heifer, the proportion of propionic acid was very low. But the proportions of butyric acid, valeric acid, and caproic acid were very high. Succinic acid was also observed at high level in contrast with a trace of lactic acid, although both of succinic acid and lactic acid were negligible in other heifers in Expts 5, 6, and 7.

The relationships between pH and VFA proportions were shown in Fig. 3. The increase of

Fig. 3. The relationships between pH and VFA proportions on high concentrate feeding

Table 5. VFA production in the rumen on high concentrate feeding

Exp. No.	rate constant (%/hr)			produc- tion rate (mole/hr)	rumen volume per 100 kg wt (l)	VFA/ DE (%)
	out- flow	absorp- tion	produc- tion			
1	13.1	22.8	35.8	424	10.9	—
2	11.0	21.9	33.9	923	17.6	49.3
3	10.0	27.2	37.2	848	10.7	63.0
4	10.3	26.6	36.9	525	10.3	41.0
5	7.7	21.6	29.3	696	9.4	38.0
6	18.0	32.0	50.0	479	7.8	33.5
7	13.1	19.6	32.7	564	13.2	49.8

acetic acid and the decrease of propionic acid in molar proportion were observed at the pH value below about 5.2. At the mean daily pH value above about 5.2, propionic acid, valeric acid and caproic acid had significant tendencies to increase in molar proportion as pH value went down ($P < 0.01$). On the other hand, acetic acid and isobutyric acid significantly decreased as pH value went down ($P < 0.01$). Total VFA concentration was negatively correlated with pH ($r = -0.83$, $P < 0.01$) and the regression equation was expressed as follows;

$$Y = 380.2 - 44.1X \quad Y = \text{VFA concentration, mM} \quad X = \text{pH value}$$

The rate constants of outflow, absorption, and production, production rate, rumen volume per 100 kg body weight and percentage of VFA in ingested digestible energy in each experiment were shown in Table 5. Outflow rate constant was 13%/hr on an average in the heifers given hay and concentrate together. In the case of all-concentrate feeding, the mean daily outflow rate constants ranged from 4.1%/hr to 18%/hr among heifers. However, the mean value except Expt 6 was 9.7%/hr that was significantly lower than those in the heifers fed on hay and concentrate diet in Expts 1 and 7. Absorption rate constants ranged from 21.6%/hr to 32%/hr among the animals on the concentrate diet only. In comparison with those on hay and concentrate diet that indicated 22%/hr in mean value, the absorption rate constants had a higher value. The rumen volume on all-concentrate feeding except Expt 2 was 9.6 l per 100 kg live weight on an average, and was significantly smaller than that on hay and concentrate feeding in these experiments ($P < 0.05$). The percentage of energy produced from VFA in ingested digestible energy in Expts 2 and 7 was about 50%. The highest value, 63%, was shown in Expt 3. However, the percentage after third week after commencement of all-concentrate feeding decreased to below 41%.

Discussion

It was observed in these experiments that, in the groups on all-concentrate feeding compared with those on hay concentrate feeding, pH, and the proportions of acetic acid and isovaleric acid tended to be low, and the total VFA and proportions of propionic acid, valeric acid, and caproic acid were high. However, the proportion of individual VFA changed very widely in the groups on all-concentrate feeding. Though the reason why the great difference in the proportions of VFA between the heifers on the same concentrate and between days was not obvious, it seems to be attributable to the instability of the types and functions of microorganisms involved in rumen metabolism. These may have been changed by physiological condition of host animal or quan-

tity of feed intake.

There were high positive correlations among the concentrations of butyric acid, valeric acid and caproic acid, particularly between butyric acid and valeric acid ($r=0.76$). But the high correlations could not be easily explained because the metabolic pathways of valeric acid and caproic acid were not informed. However, it was considered that bacteria, such as *Megasphaera elsderii*¹³⁾ which produce higher acids from lactic acid, participated in the production of butyric acid, valeric acid and caproic acid. Furthermore, it is interesting that high concentration of succinic acid in contrast with a trace of lactic acid was detected in a heifer in Expt 5. In our knowledge, such a phenomenon has not been informed yet. In the same heifer, the proportion of propionic acid was much lower than those in other heifers in Expt 5. On that account, this may suggest that the metabolic pathway from succinic acid to propionic acid is sometimes inhibited during a long term feeding of a concentrate only though succinic acid was known as a important precursor of propionic acid¹⁴⁻¹⁶⁾.

The relationships between pH and VFA proportions were reported by several workers^{2,17-19)}. Also in these experiments, some significant relationships between pH and VFA proportions were observed. REID *et al.*²⁾ suggested the increase of acetic acid and the decrease of propionic acid in molar proportion at low pH level from the diurnal changes of pH and VFA proportions. SUTTON and JOHNSON¹⁹⁾ also showed that such relationships were seen when the mean daily pH was 4.7-5.1 with two cows on two rations. The present results also confirmed such phenomena. Although the proportion of butyric acid had a tendency to increase with large variation as pH fell, it may be affected more greatly by other factors than with pH. The relationship between pH and valeric acid was similar to that between pH and propionic acid. The similarity may be caused by the same pH requirement of bacteria or of enzymes responsible for the production of propionic acid and valeric acid and interconversion between them. Though it was reported²⁰⁻²²⁾ that the concentration of caproic acid was fairly high in the rumen fluid on high concentrate diet, the relationship with pH has not been reported. The concentration of caproic acid had a significant negative correlation with pH in these experiments ($P<0.01$). It is generally accepted that fatty acids with branched chains are produced from decomposition of amino acid or protein. However, ORSKOV *et al.*²¹⁾ and PRADHAN and HEMKEN²²⁾ reported that isovaleric acid increased by the intra-ruminal infusion of ethanol. Therefore, the interpretation of the role of fatty acids with branched chains is difficult. The present result showed the relationships of the concentrations of isobutyric acid and isovaleric acid with pH were not significant ($P>0.05$). On that account, the production of isobutyric and isovaleric acid seems not to be affected by pH.

Outflow rate constants on all-concentrate feeding except in Expt 6 were significantly lower than those on hay and concentrate diet ($P<0.01$), and agreed with the result of BAUMAN *et al.*²³⁾ that was $9.6\pm2.8\%/hr$ with the cows fed on a high grain, low fiber diet. However, the high outflow rate constant in Expt 6 was considered to be induced by underdeveloped small rumen volume. The production rate constants in the present experiments were above $29\%/hr$, higher than that of KNOX *et al.*²⁴⁾ with lactating cows, and lower than those by GRAY *et al.*²⁵⁾ with sheep and by DAVIS²⁶⁾ with lactating cows on high grain diets. The rumen volume on all-concentrate feeding except Expt 2 was significantly smaller than that on hay and concentration feeding in these experiments. But the rumen volume in Expt 2 was much larger than those in other periods on all-concentrate feeding, which may have been caused by a sudden change to concentrate and also retention of diets fed up to two days before.

The relationship between VFA production rate and pool size in the rumen was reported by

WESTON and HOGAN²⁷⁾ who showed the correlation was 0.81 with sheep on dried ryegrass and forage oats. The relationship in the present experiments also indicated similar high correlation ($r=0.81$).

The adaptative changes of VFA production in the rumen to all-concentrate diet were noteworthy. The percentage of energy produced from VFA in ingested digestible energy was 49.8% in Expt 7, in which animals had been fed hay and concentrate, and 49.3% in Expt 2 on the 2nd day after commencement of all-concentrate feeding. These were little less than 54% by GRAY *et al.*²⁸⁾ on lucerne hay and 52% by LENG *et al.*²⁹⁾ on pasture. However, the VFA production in Expt 3 on the 5th day after commencement of all-concentrate feeding increased to 63% of digestible energy with parallel increase of VFA concentrations. The percentage decreased to 41% in Expt 4 and, furthermore, indicated lower values in Expts 5 and 6 measured in 5-6th week after starting all-concentrate feeding. The highest concentration of total VFA from the first week to the second week after commencement of all-concentrate feeding and the decline of total VFA concentration after that were observed also by BIGHAM *et al.*³⁰⁾, TREMERE *et al.*³¹⁾, and SUTTON and JOHNSON¹⁹⁾, who discussed the phenomena as adaptative changes. Though BIGHAM *et al.*³⁰⁾ suggested that the decline of VFA level was likely to be due to one of two major factors, namely, decreased rates of production or increased disappearance rates of VFA out of the rumen. They could not determine which was more important from their results. However, from the present result, the decline of VFA level on a long term feeding of an all-concentrate diet could be explained by decreased rate of production because of decreased percentage of VFA in digestible energy. The measurement of the percentage of VFA in digestible energy on all-concentrate diet has been done only by WHITELAW *et al.*¹¹⁾ with cattle on barley feeding with *in vitro* technique. They showed 36.5% of digestible energy was produced as VFA but considered the low production rate to be a discrepancy of technique. However, the percentage of VFA in digestible energy on a long term feeding of a concentrate alone in these experiments was significantly lower than those on a hay and concentrate diet.

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濃厚飼料多給時における第一胃内 VFA 生産について

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濃厚飼料を多給した際の第一胃内 VFA 生産についての知見は非常に少ないので，第一胃フィステルを装着したホルスタイン種育成雌牛を用い，ポリエチレン・グリコールと ^{14}C -酢酸ソーダの1回投与法により，濃厚飼料のみ，あるいは一部乾草を給与した場合の第一胃内で生産される VFA について測定を行った。1) 濃厚飼料のみを給与した場合には，乾草を同時に与えた場合に比べて，pH は著しく低下し，最低 4.5 を示した。VFA 濃度は日内変動が大きい，最高 200 mM 以上の値を示し，VFA 組成は日間変動，個体差が大きく不安定であ

った。2) pH と VFA 組成との間に有意な関係が認められ，pH が 5.2~5.4 付近で酢酸割合が最低になり，プロピオン酸，吉草酸割合は最高値を示した。カブロン酸は pH が低下するに従って増加する傾向にあったが，酪酸割合は有意な関係が認められなかった。3) 乾草と濃厚飼料を同時に与えた場合には，摂取された可消化エネルギーの約 50% が第一胃内で VFA に変換されるのに対し，濃厚飼料のみを長期間給与した場合には，33.5~41% に抑制されることが示唆された。