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Role of Omasum in the Control of Feed Intake and Rumen Digesta Outflow

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ABSTRACT

The objective of this study was to test whether the stimuli of osmotic pressure (OP), VFA or pH in the omasum would affect the passage of digesta from the rumen and feed intake in sheep. Five experements were carried out. Different solutions with specific, OP, VFA concentration and pH were infused into the omasal body. Rumen digesta volumes and outflow rates (liquid and solid) were measured by pulse dosing of liquid and solid marker into the rumen. Feed intake, solid and liquid outflow rates from the reticulo-rumen were (not always significant) reduced by increasing the (OP) of the infusate in the range of 400 to 2000 mOsmol/kg which gave calculated omasal OP up to 480 mOsmol/kg (perfect mixing with digesta was assumed). Feed intake and fractional ruminal liquid outflow rate were significantly increased by increasing VFA concentration of infusate in the range of 50 to 250 mMol/l or calculated omasal VFA concentrations up to 150 mOsmol/kg with the suggestion of a decrease above this range. pH in the range of 5.0 to 7.0 was without effect. Serum OP was not affected by any infusate. There was no or only a weak response to abomasal infusion compared with omasal infusion when the same infusate was used. The study demonstrated that omasum responds to changes in the composition of digesta. Increasing OP reduced DMI (dry matter intake) and reduced digesta outflow from the reticulo-rumen. Increasing VFA concentration increased DMI and liquid outflow, high VFA concentration decreased DMI and liquid outflow rate. It can be concluded that omasum has a role in the control of digesta outflow from the rumen.

Keywords: Feed intake; Omasum; Outflow rate; Osmotic pressure; VFA

INTRODUCTION

Animal production is firstly constrained by energy supply, and secondly by the nutrient balances which affect the efficiency of energy utilization. The optimum nutrient balance will be affected by climatic conditions, physiological state, level of production and physical activity. Ruminants adapted to grazing poor-quality forage have highly-developed forestomachs which appear to apply a tight control of the flow of digesta from the reticulo-rumen (Kennedy and Murphy, 1988). Intake is the most important contributor to utilisation of roughages, therefore, it is necessary to find ways of increasing the intake of roughage. Although feed characteristics such as digestibility can apparently determine the relative levels of intake, a large intake is the consequence either of rapid outflow or of increased rumen volume, or both (Pond *et al*, 1988). Through manipulation of dietary characteristics, it is sometimes possible to alter the outflow rates of digesta, and hence influence voluntary intake.

For understanding and predicting passage of digesta, it is essential to have some information, not only on the size and structure of the gastrointestinal tract (GIT) and its motor activity, but also on the physical and chemical properties of the feed and digesta (Uden and Van Soest, 1982). The highly digestible diets such as young spring grasses, high quality silages and cereal con-

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centrates are often associated with problems such as scour, acidosis and disturbances of digesta flow. A better understanding of all factors controlling digesta flow thus relates to many aspects of ruminant nutrition. The suggested functions for omasum include water, VFA and electrolyte absorption, (Engelhardt and Hauffe, 1975), and physically aiding digesta flow by pumping (Stevens *et al*, 1960) or valve action (Balch *et al.*, 1951). Moir, (1984) suggested that absorption of VFA and buffer would reduce the abomasal HCl secretion necessary to reduce digesta pH. Thus omasum might control the reticulo-omasal orifice and regulate digesta flow for abomasal protection. The objective of this work was to test whether the stimuli of osmotic pressure (OP), VFA or pH in the omasum would affect the passage of digesta from the reticulo-rumen and food intake or not.

MATERIALS AND METHODS

Animals, Surgical Preparation and Management

Four yearling and wether sheep weighing about 38 kg each were used in the experiments. Animals were fitted with cannula in the rumen wall (dorsal sac) (Polyvinylchloride ID 42 mm, OD 45 mm), and catheters to the omasal wall (greater curvature) (clear vinyl tube ID 1.0 mm, OD 2.5 mm or silicone tube ID 1.57 mm, OD 3.18 mm) and abomasal wall (fundus) (translucent vinyl tube ID 3.0 mm, OD 5.0 mm). The only novel procedure was the fitting of the omasal catheter. All animals recovered well from surgery. *Post mortem* examination showed the omasal leaves appeared normal in all sheep with no signs of any damage.

Sheep were housed individually before experiments and in individual metabolic cages during the experiments and were provided with *ad libitum* feed and water. The adaptation period to the metabolism crate was one week and the collection period varied between 12-24 days, depending upon the experimental design. Recovery between experiments was in individual pens for a period which was always greater than the time spent in metabolic cages. Sheep were fed with a diet containing chopped hay 50%, rolled barley 30%, molasses 10%, fishmeal 9%, minerals plus vitamins 1%, *ad libitum*, twice daily as two equal meal during the experiments at 08.30 a.m. and 4.30 p.m.. Daily feed refusals were collected before morning feeding. The amount fed was adjusted daily to allow refusals of 15-20% of the feed offered. Water was available at all times.

Experimental Design and Statistical Analysis

The sheep were allowed up to seven days adaptation to the mtabolism crate, and then measurements were made over one day at three day intervals. The 4×4 Graeco-Latin squares were used in Experiment1 and Latin squares (4×4 or 3×3) were used in the rest of the experiments except Experiment 4 in which a balanced Change-over design was used. The data from the experiments were analysed and the correlations between variables were performed on the Genstat 5 statistical program (Genstat 5 Release 3.1, 1994, Lawes Agricultural Trust, Rothamsted Experimental Station). The differences between treatment means were compared using t-tests.

Preparation and Infusion of Hypertonic Solution

In the experiments (Experiment 1 to 5) with four or three sheep, a solution of sodium salts of VFA (0.65 acetate, 0.25 propionate and 0.10 butyrate) was used with NaCl and HCl to bring the pH to 6.5 and pH 5.0 (Experiment 5) to make solutions with specific osmolality and VFA concentrations. The solutions were infused into the omasum or abomasum at the rate of 2 ml / min, (Tables, 1and 2). Water was infused into the abomasum during the omasal infusion, and

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into the omasum during abomasal infusion calculated at a rate sufficient (in amounts related to the amounts of salts infused) to allow for the dilution of the infusate to an osmolality of 300 mOsmol/kg (similar to plasma). This was done so as to ensure that no additional water was drunk by the sheep during infusion days (Possibly confounding outflow measurements from the reticulo-rumen). The solutions or water were infused with a peristaltic pump (Belmont Instruments, Watson Marlow Ltd.Model 502 S). The infusion started at about 08.30, before the morning feeding and continued for 24 hours. The rate of pumping was checked every two hours by weighing the solution or water.

Analytical Methods

Measurement were taken of matter oven dried at 105^{o}C for 24 hours, ash Produced by a muffle fumace at 550^{o}C for 24 hours, pH using pH meter (Pye Unicam Model 292 Ltd Cambrige), Osmotic pressure using an os-mometer (Osmette Model 2007 percision system Inc), VFA concentration according, (Ottensteion and Baertley, 1971), nitrogen by the kejedal method, chromium according, (Mathieson, 1970) and cobalt by atomic ab-sorption spectrophotometer (Hart and Polan, 1984).

Table1. Experiment, 1 to 4. The composition of solutions infused into the omasum or abomasum, (at 2 ml/min).

Solution	VFA Salt (g /l) [a]	NaCl (g /l)	VFA concentration (mMol/l)	Osmotic pressure (mOsmol/kg)
Experiment1				
1	4.5	8.6	50	400
2	9	5.9	100	400
3	13.5	2.9	150	400
4	18	Nil	200	400
5	4.5	14.6	50	600
6	9	11.7	100	600
7	13.5	8.8	150	600
8	18	5.85	200	600
9	4.5	20.5	50	800
10	9	17.6	100	800
11	13.5	14.6	150	800
12	18	11.7	200	800
13	4.5	26.3	50	1000
14	9	23.4	100	1000
15	13.5	20.5	150	1000
16	18	17.6	200	1000
Experiment2				
	9	26	100	1000
Experiment3				
1	nil	32.5	nil	1000
2	11.25	24.38	125	1000
3	22.5	16.25	250	1000
4	45.0	nil	500	1000
Experiment4				
1	31.5	0	350	700
2	63	0	700	1400

[a] Na salts to give proportions (0.65 acetate, 0.25 propionate and 0.10 butyrate).

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Table 2. Experiment 5. Composition of solutions with pH=5 and pH=7 infused into the omasum (at 2 ml/min).

Solution	VFA salt (g /l) [a]	Hco_3Na (g/l)	HCO_3K (g/l)	Na_2HPO_4 (g/l)	VFA concentration (mMol/l)	Osmotic Pressure (mOsmol/kg)
	13.5	4.2	5.05	7.1	150	800

[a] Na salts to given proportions (0.65 acetate: 0.25 propionate: 0.10 butyrate

Measurements and Calculation

During the infusion periods, rumen digesta volumes and outflow rates were measured by pulse dosing 40-50 ml Co-EDTA as a liquid marker, 40 g chromium-mordanted hay (Cr-hay) with about 5% - 11% Cr in all experiments as a solid marker. Samples were collected from the reticulo-rumen during 24 hours at 2 hour intervals. The natural log markers concentration then regressed with time, gave fractional outflow rates. Rumen pH and osmolality were measured immediately after sampling and the VFA concentration on a bulked sample later. Daily urine output, urine pH and osmolality, daily feed and water intake were measured throughout the experiment. Feed intake was measured at 2 hour intervals on rumen sampling days and extended for 8 hours into the following day. Diet digestibility was determined by the collection of all faeces over the whole experiment (12-17 days). Blood samples were taken in Experiments 2 and Experiment 3 before morning feeding on infusion days and before morning feeding the following day. With the information of ruminal osmotic pressure, VFA concentration, liquid outflow rate, rumen liquid volume and osmotic pressure, VFA concentration of infusate and rate of infusion, the osmotic pressure and VFA concentration at the site of infusion (omasum or abomasum) were calculated by assuming a complete mixing of infusate with the digesta leaving the rumen, and no absorption of the infusate or rumen liquid composition at the site of infusion.

RESULTS AND DISCUSSION

Feed Intake

There was a clear response to the omasal infusion of infusate with high osmotic pressure. In most of cases there was a reduction in feed intake when omasal osmotic pressure was increased (Table 3). Though the effects appeared to be insignificant, the trend was consistent. The results of Experiment1 showed a significant ($P<0.05$) negative and linear correlation -0.413 ± s.e. 0.184 between osmotic pressure of the infusate (at400 to 1000 mOsmo/kg or -1.809 ± s.e. 0.805 between calculated omasal osmotic pressure 340 to 477 mOsmo/kg) and feed intake. The level of feed intake, the rumen the liquid volume and liquid outflow rate would have affected dilution of the infusate and hence osmolality at the site of infusion. The calculated omasal osmotic pressure which assumed no absorption at the site of infusion and a complete mixing of infusate with the digesta leaving the rumen would, therefore, have overestimated the mean osmotic pressure in the omasum. However, the calculated omasal osmotic pressure indicated that with a calculated omasal osmolality higher than about 480 mOsmol/kg feed intake reduced significantly ($P<0.05$) or close to significant (t-test, $P<0.07$), (Experiments 1 to 4). The same trend was present at lower osmotic pressures, but not statistically significant (Table 3). These decreases in feed intake were associated with a decreasing rumen solid outflow rate and, at times both of solid and liquid outflow rate as the result of an infusion of hypertonic solution into the

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Table 3. Effect of infusates on feed intake, solid and liquid outflow rates (Experiments1 to 5).

Experiment Number	Infusate OP (mOsmol/kg)	Infusate VFA (mMol/l)	Site of Infusion OP (mOsmol/kg)	site of infusion VFA (mMol/l) [a]	DMI (g/d)	ks (\ h)	kl (\ h)
1	400		340a	119	1096[a b]	0.0797 [a]	0.1311 [a]
1	600		386b	125	1013 [ab]	0.0706 [ab]	0.1231 [ab]
1	800		431c	130	931 [ab]	0.0615 [bc]	0.1152 [bc]
1	1000		477d	135	848 [b]	0.0524[c]	0.1072 [c]
SED			7	8	102	0.0065	0.0052
1		50	419a	100a	817 [a]	0.0614	0.1055 [a]
1		100	411a	118b	920 [ab]	0.0645	0.1146 [ab]
1		150	404ab	136c	1024 [ab]	0.0676	0.1237 [bc]
1		200	396b	155d	1127 [b]	0.0707	0.1328 [c]
SED			7	8	102	0.0065	0.0052
2	Control	100	298a	141	1291	0.0864	0.1509
2	1000(Oms)	100	420b	130	1140	0.0691	0.1471
2	1000(Abom)		432b	137	1250	0.0822	0.1527
SED			11	6	75	0.0099	0.0094
3	1000	0	410	111a	1728	0.0746	0.1326
3	1000	125	404	135b	1873	0.0712	0.1357
3	1000	250	402	153c	1922	0.0805	0.1327
3	1000	500	414	196d	1620	0.0719	0.1267
SED			10	3	138	0.0098	0.0048
4	700(Oms)	350	370b	170b	1858	0.0752	0.1148 [ab]
4	700(Abom)	350	370b	171b	2087	0.0770	0.1171 [ab]
4	Control		306a	139a	2093	0.0784	0.1323 [a]
4	1400(Omas)	700	514c	239c	1660	0.0650	0.1011 [b]
4	1400(Abom)	700	512c	249c	1833	0.0729	0.1068 [b]
SED			11	7	211	0.0082	0.0085
5	Control		309a	142	2101	0.0567	0.1228
5	800(pH=7)	150	366b	144	2196	0.0627	0.1180
5	800(pH=5)	150	374b	144	2215	0.0572	0.1252
SED			4	4	82	0.0037	0.0067

[a] Calculated by assuming perfect mixing with the rumen digesta and no absorption in the site of infusion.
[b] Means with the same superscripts are not significantly different (P< 0.05) .
DMI: Dry mater intake ks: Solid outflow rate kl: Liquid outflow rate

omasum. The change (reduction) in faecal output in the day of infusion or the following day was also associated with a decreasing rumen digesta outflow rate and feed intake due to the infusion of hypertonic solution into the omasum.

In the osmolality of ruminal fluid after the consumption of alfalfa chaff mixed with wheaten chaff or oats, ruminal fluid tonicities have been reported approaching 500 mOsmol/kg (Warner and Stacy, 1968). Thus the osmolalities infused in this experiment

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were within, or close to, the range of values which could occur normally. In some cases of acidosis, where the osmolality of rumen liquid is very high due to the fermentation of high concentrate diets, Britton and Stock, (1986) suggested that the high osmolality of the rumen liquid decreases or inhibits feed intake. The increased feed intake may be related to rumen fluid with high osmolality passing to the omasum and this influences digesta outflow rate from the reticulo-rumen. Possible mechanisms could be changing omasal motility, or the reticulo-omasal orifice size, which consequently affect feed intake. In the goat, Engelhardt and Hauffe, (1974) reported much smaller differences, with mean tonicity values for the reticulum, omasum and abomasum at 268 ±11, 256 ± 9 and 282 ± 6 mOsmol/kg, respectively. With sheep, the osmolality of omasum (229 ± 19) was lower and abomasum (282 ± 11) was higher than rumen digesta (247 ± 37) mOsmol/kg, due to the absorption of rumen soluble digesta components, particularly VFA and buffered components, by the rumen and omasum. The higher osmolality of the abomasum could be due to HCl secretion by the abomasum and to pepsin hydrolysed protein.

There was a significant ($P<0.05$) positive and linear correlation 2.07± s.e. 0.80 between VFA concentration of infusate (50 to 200 mMol/l) with feed intake and a, positive and linear correlation 5.64 ± s.e 1.81 between calculated omasal VFA concentration (99 to 155 mMol/l) with feed intake. Food intake increased as VFA concentration increased. The impact of omasal infusion to infusate with 50 to 200 and 125 to 250 mMol/l VFA concentrations on feed intake was positive in Experiments1 and 3 and at those higher VFA concentrations (350 to 700 mMol/l) was negative in Experiments 3 and 4 (Table 3). In most cases where there were affects on feed intake by osmotic pressure or VFA concentration of infusate, normal intakes were resumed the following day and animals compensated their feed intake, especially in the 2 to 8 hours after the infusion stopped (Experiments 1, 2, 3 and 4).

The feed intake increase was related to the VFA concentration of the infusate. Again, the level of feed intake, rumen liquid volume and liquid outflow rate would have caused dilution of VFA concentration of the infusate at the site of infusion (calculated omasal VFA concentration assumed no absorption in the site of infusion and a complete mixing of infusate with the digesta leaving the rumen). The calculated omasal VFA concentration indicated that, with a VFA concentration of about 130 to 150 mMol/l, feed intake increased, but when lower than about 100 and higher than about 170 mMol/l, feed intake decreased (Table 3). This implies that the effect of omasal VFA concentration on feed intake could be quadratic (Experiments 3 and 4), although the data do not have the sensitivity to confirm this. The lowest calculated omasal VFA concentration was 100 mMol/l in Experiment 1 with the infusate with a 50 mMol/l VFA concentration. The highest calculated omasal and abomasal VFA concentrations were 239 and 249 mMol/l respectively in Experiment 4. These changes in feed intake were associated with changes in the rumen solid outflow rate and some time both the solid and liquid outflow rates as a result of an infusion of solution with a varying VFA concentration into the omasum.

About 50% of VFA that enters the omasum (with the rumen digesta) was reported as disappearing during passage through the omasum. Usually, the VFA concentrations of omasum and abomasum are lower than rumen digesta (Badawy *et al*, 1958: Gray *et al.*, 1994). The results of Gray *et al.*, (1994) indicted that omasal VFA disappearance is some three-to four- fold greater than abomasal disappearances. In this study, it was not known how much VFA and buffer were absorbed by the omasum or abomasum, and perfect mixing of the infusate with rumen digesta with no absorption from the site of infusion were assumed. Therefore, the real calculated omasal osmotic pressures and VFA concentrations should be lower than that calculated. The calculated abomasal osmotic pressure should possibly be higher and VFA concentration lower than calculated, due to the absorption of VFA and the

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secretion of digestive juices. However local effects with osmotic pressures and VFA concentrations closer to those of the infusate may have occurred.

There was no or little response to abomasal infusion on feed intake compared with omasal infusion in Experiments 2 and 4. It could be that some part of the water infused into the omasum passed from the omasum to the abomasum during the abomasal infusion of hypertonic solutions and diluted the abomasum contents (Experiment 2). However, in Experiment 4, with an abomasal infusion of 700 mOsmol/kg, no water was infused into the omasum, and the response as feed intake to abomasal infusion was again small compared with the control (2087 vs 2093 g-DM). In both omasal infusions at 1000 mOsmol/kg and 700 mOsmol/kg in Experiments 2 and 4, feed intake decreased (12 %) compared with the control.

Carter and Grovum, (1990b) reported that, when loading the abomasum with 14.3 g NaCl and the equivalent osmotic load as PEG (molecular weight 200) in 200 ml solution, the osmolality of abomasal contents was elevated to 606 (SE±29) mOsmol/kg with no effect on food intake from 0 to 10 min after feeding. However, 28.6 g NaCl which raised abomasal osmolality to 1012 (SE±61) mOsmol/kg depressed intake in the first minute after feeding. This abomasal tonicity is well beyond the physiological range and greater than those used in the work reported here. They (Carter and Grovum, 1990) concluded that any increase in tonicity of abomasal digesta in the physiological range was not responsible for intake depression. Carter and Grovum do not appear to have infused salt into the omasum. The calculated abomasal osmolality in the experiments reported here was not higher than about 520 mOsmol/kg. This is lower than the abomasal osmolality of 606 mOsmol/kg after salt dosing reported by Carter and Grovum, (1990b), and substantially lower than their 1012 mOsmol/kg which depressed intake in the first minute after feeding. Due to the differing objectives of this study, feed intake was not measured from 0 to 10 min after feeding as it noted in the study of Carter and Grovum, (1990b). In Experiment 4 with an abomasal osmolality of about 520 mOsmol/kg (treatment 1400 mOsmol/kg), the daily feed intake decreased slightly but not significantly and by as much energy as the supply of the total VFA infused. Taken together, this implies that there is no significant abomasal effect on feed intake due to digesta osmotic pressure or VFA concentration in the physiological range.

The effect of pH on the omasal response and feed intake was not significant within the range of pH=5 to 7. Due to the inaccessiblity of omasal digesta and an unknown buffering capacity of digesta inside the omasum, it was impossible to measure or calculate the pH of digesta at the site of infusion. Owing to the absorption, excretion and exchange of cations and anions by omasum, and preferential absorption of buffer, the pH of the omasum is generally the same or lower than rumen digesta (Engelhard and Hauffe, 1975. However, with the information concerning the liquid outflow rate and liquid volume of rumen as well as the rate of infusion, the quantity and proportion of rumen liquid to infusate passed throughout the omasum was calculated. So that, when it was mixed, rumen liquid with infusate at a proportion of (5: 1) the pH of rumen liquid dropped by about 0.2 and increased by about 0.2 degrees, respectively for infusates with pH= 5 and pH= 7. Therefore, with reference to a rumen pH about 6.2 on control day, it is possible to estimate the pH of omasum between the range of 5.5 to 6.0, that is in the normal range of a concentrated diet as reported by (Carter and Grovum, 1990).

There were other questions, which were raised about the effects of infusate on feed intake reduction, such as those related to the following cases:

a) Increased osmotic pressure or VFA concentration of plasma.

b) Feed intake decreased due to energy supplied by VFA in the infusate.

Water was infused into the abomasum at the same time as the omasal infusion and into the omasum by abomasal infusion at a

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sufficient rate to allow for the dilution of the infusate to an osmolality of 300 mOsmol /kg (about that of plasma). However, it was impossible to measure or estimate how rapidly, or how much of these hypertonic solutions were absorbed from the omasum or abomasum. So it is not known how much of infusate components contributed to plasma osmotic pressure. In Experiment 2, the effect of omasal and abomasal infusion of solutions with the same osmolality and VFA concentration (1000 mOsmol/kg & 100 mmolar VFA) on serum osmotic pressure was not significant ($P< 0.05$). In Experiment 3, the effect of omasal infusion of solutions with same osmolality and varying VFA concentration on serum osmotic pressure was not significant either ($P< 0.05$). All of the serum osmolalities were in the normal range as reported by Carter and Grovum, (1990). The tonicity of jugular plasma rose by 2 to 4 mOsmol/kg within five minutes after sheep started to eat a 1 kg meal of alfalfa chaff following a fiften hour fast. Plasma tonicity continued to increase by 18 mOsmol/kg (289 to 307 mOsmol/kg) after three hours, then declined over the next two to three hours, but remained above prefeeding levels for ten hours after feed was offered (Carr and Titchen, 1978). The increase in the tonicity of jugular and portal plasma may not only be due largely to the loss of water into saliva and other secretions, but also to the presence of VFA and other nutrients in the blood (Carter and Grovum, 1990; Carr and Titchen, 1978). The results of Carter and Grovum, (1990) showed that there was no consistent relationship between feed intake and the change in the tonicity of jugular plasma following abomasal solute loading with 14.3, 28.6 g NaCl and an equivalent osmotic load to PEG-200 in 200 ml solution. The increases in plasma osmolality were 3.9 and 7 mOsmol/kg after 10 minutes of feeding for 14.3 g and 28.6 g NaCl treatments respectively. The plasma tonicity at 60 minutes was already 15 mOsmol/kg higher (312 mOsmol/kg) than pre-injection values (297 mOsmol/kg) for the 28.6 g NaCl treatment, yet the sheep consumed as much feed as controls from 60 to 90 minutes, which implies that daily and two hourly feed intake were not affected in spite of high and rapid rises on plasma tonicity.

This could have been mediated either by elevation of serum VFA, or by compensation for the energy contribution of the VFA. With respect to serum VFA, in spite of the fact that it is not known whether serum VFA changed in these experiments, the two hourly feed intake was not affected significantly ($P< 0.05$) by any infusate with different VFA concentrations. This implies that there was no direct or indirect effect from the two hourly feed intake or changed serum VFA concentrations on either the two hourly or total feed intake and any possible rapid rise of serum VFA concentration due to infusion or absorption did not affect feed intake. The results of de Jong *et al.* (1981); Bail and Mayer, (1968) showed that infusion of a mixture of the sodium salts of VFAs with concentrations not exceeding 0.5 mol/l into the hepatic portal vein and of sodium salts of acetate with concentrations of 0.5, 1 and 2 mol/l intravenously into goats at a rate of 4 mmol/min, no change in feed intake was observed despite a doubling of plasma levels of VFAs. This implies that infusion of sodium salts of VFAs at the rate of 0.1 to 1.4 mmol/min with concentrations of 50 mmol/l to 0.7 mol/l into the omasum in this study could not affect feed intake.

In these experiments, the VFA concentration of infusates varied from 50 to 750 mmol/l. The response of omasal and abomasal infusion of solutions with varying VFA concentration on feed intake were not consistent. If we assume all of the infusate VFA was absorbed from the omasum, abomasum or lower tract, the effect on feed intake due to energy supply by the total infusion of VFAs, would be expected to have the same trend and effect on feed intake, but it did not. The response of omasal infusion to infusate with 50 to 200 mmol/l and 125 to 250 mmol/l VFA concentrations on feed intake was positive in Experiments 1 and 3 and with the higher VFA concentration (500 to 700 mmol/l) was negative in Experiments 3

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Table 4. Feed equivalent as energy supply from total VFAs infused on changes in feed intake (compared with control, except in Experiment 3 which compared with 0 VFA concentration).

Experiment No.	Treatment VFA Concentration (mMol/ l)	Treatment Osmotic Pressure (mOsmol/kg)	Total VFA infused (mMol/l)	Feed equivalent (g-DM)	Changing in feed intake (g-DM)
2	100 VFA (Omas)	1000	288	31	-151
	100 VFA (Abom)	1000	288	31	-41
3	125 VFA(Omas)	1000	351	39	+109
	250 VFA(Omas)	1000	705	79	+194
	500 VFA(Omas)	1000	1408	168	-108
4	350 VFA (Omas)	700	1025	110	-229
	350 VFA (Abom)	700	1014	109	+6
	700 VFA (Omas)	1400	2026	218	-427
	700 VFA (Abom)	1400	2141	230	-254
5	150 VFA (Omas)	800	427	46	+95

and 4. The impact of abomasal infusion on feed intake in spite of the same energy supply was very weak compared with the same omasal infusion in Experiments 5 and 7 with an omasal infusion with an osmolality of 700 mOsmol/kg. The gross energy of digestible organic matter (DOM) was taken as 19 MJ/ kg, and ME as 0.82 DOM energy (ARC, 1984), and the digestibility of organic matter, given a diet with ME values of 8.10, 9.85, 10.8, and 10.9 MJ/kg respectively. Thus the results relating to energy supply by infusion in Experiments 2, 3, 4 and 5 and their feed equivalent compared with feed changing are summarized in Table. 4. This demonstrates that there was little relationship between any changes in feed intake and the energy contribution of the VFA infused.

The infusate in Experiment 2 was equivalent to about 31 g of the diet. The depression in feed intake was 151 g DM about five times of the energy value of the infusate. The infusates in Experiment 3 were equivalent to about 39, 179, and 168 g DM of the diet for treatments with 125, 250 and 500 mmol/l VFA concentrations. The changes in feed intake were +109, +194, -108 g DM respectively and thus feed intake effectively increased in spite of energy supply by total VFA (351 and 705 mmol) of infusate in Experiment 3, compared with 0 mmol/l VFA concentration. The infusates in Experiment 4 were equivalent to about 110 and 220 g DM of the diet for treatments with low and high VFA concentration. The depression in intake was 229 g DM for omasal low concentration (about two times the energy value of the infusate for a low omasal concentration) and the increase was +6 g DM for a low abomasal concentration infusion. There was no response from the low abomasal concentration infusion, which would be expected to decrease feed intake by 110 g DM. The feed intake depressions were 427 g for high omasal concentration and 254 g DM for a high abomasal concentration, about two times the energy value of the infusate for a high omasal concentration, all compared with the Control. This implies that the response to omasal infusion was twice that of abomasal infusion. There was no reduction in feed intake in spite of the total VFA of infusate, which was equivalent to about 46 g DM of the diet in Experiment 5. These results imply that energy supply from the infusate infused either into the omasum or abomasum on feed intake reduction, were not consistent. Indeed, low levels of VFA concentration infused into the omasum were associated

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with increases in feed intake (Experiments 1 and 3).

Rumen Kinetics

In some cases, the effect of infusates on the reduction of solid outflow rate and, in some cases both of solid and liquid outflow rates, was significant (P<0.05) (Experiments 1, and 4). The results of Experiment 1 showed a significant (P<0.05) negative and linear correlation -0.04± s.e. 0.01 and -0.046 ± s.e. 0.012 between osmotic pressure of the infusate (0.4 to 1.0 Osmo/kg) and the solid and liquid outflow rates or a negative and linear correlation -0.1996 ± s.e 0.051 and -0.175 ± s.e 0.04 between calculated omasal osmotic pressure (340 to 477 mOsmo/kg) and the solid and liquid outflow rates. Compared with the control, when the calculated omasal osmolality was higher than about 480 mOsmol/kg, solid or liquid outflow rates or both solid and liquid outflow rates decreased either significantly (P<0.05) or nearly significantly (t-test P<0.07) (Experiments 1, and 4) as summarised in Table 3

The levels of these solid and liquid outflow rate reductions were related to the osmolality of infusate. The level of feed intake, rumen liquid volume and liquid outflow rate, would all have affected the dilution of infusate at the site of infusion (calculated omasal osmotic pressure assuming no absorption in the site of infusion and a complete mixing of infusate with the digesta leaving the rumen). When the calculated omasal osmolality was higher than about 480 mOsmol/kg, the solid or liquid outflow rate or both the solid and liquid outflow rates were reduced significantly (P<0.05) or nearly significantly (t-test P<0.07) compared with the control (Experiments 1 and 4) as summarised in Table 4. The infusion of the solution with a high osmolality into the omasum may have caused a reduction of motility of the omasum and /or a partial closure of the omasal orifice, and consequently reduced the digesta outflow rate. This is consistent with the results of Lopez *et al*, (1994) who showed that there was a significant linear effect of osmotic pressure on rumen volume which increased (P<0.01), with rumen osmolality. A rumen osmolality of 490 mOsmol/kg which was associated with increases in the rumen liquid contents of about 10-20% compared with a rumen osmolality of 290 mOsmol/kg, implies that possible changes of the omasal motility, or some closing of the reticulo-omasal orifice occurred and were responsible for regulating digesta outflow rate from the rumen. The results of Lopez *et al*, (1994) are interesting since their animals were maintained by intra-gastric infusion, and the rumen contents were 100% liquid. The calculated omasal osmotic pressure of about 480 mOsmol/kg in this study, was compared with the result of Lopez *et al.,* (1994) which had an osmolality of 490 mOsmol/kg.

There was a significant (P<0.05) positive and linear correlation of 0.18 ± s.e. 0.041 between VFA concentration of infusate (0.05 to 0.2 Mol/l) and the liquid outflow rate or of 0.49 ± s.e 0.11 between calculated omasal VFA concentration (0.099 to 0.155 Mol/l) and the liquid outflow rate. Liquid outflow rate was increased significantly when the VFA concentration of the infusate was increased from 50 to 200 mMolar in Experimen 1 and, although the effect on solid outflow rate was not statistically significant, there was a trend for the solid outflow rate to increase as VFA concentration increased (Table 3). In Experiment 3 an increased VFA concentration from 0 to 500 mMol/l was without any effect on either the solid or liquid outflow rates (there was a trend to increase the solid outflow rate particularly with the treatment of 250 mMolar VFA concentration, see Table 3.).

The liquid outflow rate and feed intake increased significantly when VFA concentration of the infusate was increased from 50 to 200 mMolar in Expereiment 1 and, although the effect on solid outflow rate was not statistically significant, there was a trend for the solid outflow rate to increase as the VFA concentration increased, (Table 3), presumably due to changes in omasal leaf mo-

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tility or the omasal orifice. Faichney (1983) and Uden (1988) pointed out that there is a positive correlation between liquid outflow and feed intake. Feed intake increased when the VFA concentration of infusate increased from 125 to 250 mMol/l and decreased (not significantly) with 500 mMolar VFA in Experiment 3, without any effect on solid or liquid outflow rate (there was trend for the solid outflow rate to increase particularly with a treatment of 250 mMolar VFA concentration, see Table 3). This was possibly due to changes in omasal body, leaf motility or the omasal orifice size.

Bueno and Ruckebusch, (1974) reported that an infusion of 50 ml of a 75 mM solution at pH 5.6 of buffered fatty acid directly into the lumen of the omasum increased the motility of leaves by 40-60% over a period of 10-15 minutes. This implies that the increasing omasal VFA concentration in Experiment 1 up to about 155 mMol/l (calculated) increased the motility of omasal leaves and therefore increased solid and liquid outflow rates from the reticulo-rumen. Calculated omasal VFA concentrations higher than this decreased outflow, although not significantly as in Experiment 3, and significantly decreased liquid outflow ($P< 0.05$) when calculated VFA concentration of omasal digesta was higher than about 240 mMol/l (Experiment 4 shown in Table 3). This could be due to decreasing the motility of omasal leaves or changes in the omasal orifice size. The experimental results suggested that the effect of a high VFA concentration on digesta outflow rate may be quadratic.

There was little or no response to abomasal infusion on solid and liquid outflow rates compared with omasal infusion in Experiments 2 and 4. When the same solution (1000 mOsmol/kg) was infused into the omasum or abomasum giving the same calculated omasal and abomasal osmolality (about 425 mOsmol/kg) in Experiment 2, the response in terms of solid outflow rate to the omasal infusion was stronger than to the abomasal infusion. With omasal infusion, the solid outflow rate decreased by about 20%, whereas there was no response to the abomasal infusion. In Experiment 4 with the same omasal and abomasal infusions (1400 mOsmol/kg) and with the same calculated omasal and abomasal osmolalities (about 520 mOsmol/kg), the response to omasal infusion on solid outflow rate was stronger (double, t-test $P<0.075$) than to abomasal infusion. With this high concentration, omasal and abomasal infusion solid outflow rate decreased by 17% and 7% respectively compared with the control. The liquid outflow rate was significantly ($P<0.05$) affected by high concentration omasal and abomasal infusion (Table 3).

Margan, (1988) reported that the abomasal infusion of sodium salts of VFA at rate of 1 ml/min and with a concentration of (1170 to 1760 meq / l) increased rates of flow of liquid and chloride from the abomasum to the small intestine compared with VFA acid, but had little or no effect on rumen or omasal liquid outflow under restricted feeding. The results of Experiments 2 and 4 are consistent with the results of Margan, (1988) at low concentration solutions. However, in Experiment 7, omasal and abomasal infusions with the high concentration solution (1400 mOsmol/kg) affected rumen liquid outflow rate which decreased significantly compared with the control.

CONCLUSION

The digesta outflow rate can define the feed intake and extent of digestion of feed by animals. With ruminants this is particularly the case, due to their dependence on bulky diets often of low digestibility. With very highly digestible diets such as cereal concentrates, there are often associated problems of scour, acidosis and disturbances of digesta outflow and feed intake. The high digestibility of these types of diet is due to rapid degradation within the reticulo-rumen, producing digesta giving high VFA concentrations, low pHs and high osmolalities. The results reported here show that both osmo-

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lality and VFA concentration affect digesta outflow rate and feed intake.

The results of these experiments indicate that:

i. The omasum responds to changes in the composition of digesta.
ii. In most cases, increasing omasal osmotic pressure reduced liquid and solid outflow rates from the reticulo-rumen and daily feed intake.
iii. Rumen outflow rates increased with the omasal infusion of VFA solutions of increasing concentrations, in the range of 50 to 250 mMol/l, and decreased above this range. Feed intake reflected these changes.
iv. Omasal and abomasal comparison showed that there was no (or low) abomasal response to hypertonic solutions or to VFA concentration. Feed intake and digesta outflow rate did not change compared with the control (no infusion), whereas feed intake and solid outflow rate decreased with the omasal infusion.
v. There was no visible damage on the omasal or abomasal tissue *post mortem*.

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نقش هزارلا در کنترل مصرف خوراک و عبور مواد هضمی از شکمبه

ا. افضل زاده و د. ب. هاوول

چکیده

هدف از این تحقیق بررسی تاثیر فشار اسمزی، غلظت اسیدهای چرب فرار و اسیدیته محلول‌های مختلف تزریق شده بداخل هزارلا بر روی مصرف خورک و عبور مواد هضمی از شکمبه در گوسفند بود. با انجام پنج آزمایش محلولهایی با فشار اسمزی، غلظت اسیدهای چرب فرار و اسیدیته مختلف، بداخل هزارلا تزریق شد. حجم مواد هضمی شکمبه و نرخ عبور مواد جامد و مایع از شگمبه بوسیله مارکر جامد و مایع اندازه‌گیری شد. مصرف خوراک و نرخ عبور مواد جامد و مایع از شکمبه با افزایش فشار اسمزی محلول تزریقی در دامنه ٤٠٠ تا ٢٠٠٠ میلی اسمز در کیلو گرم، در اکثر موارد بطور معنی داری کاهش یافت. مصرف خوراک و نرخ عبور مواد مایع بطور معنی داری با افزایش غلظت اسیدهای چرب فرار محلول تزریقی در دامنه ٥٠ تا ٢٥٠ میلی مول در لیتر، افزایش یافت، ولی بالاتر از دامنه فوق مصرف خوراک و نرخ عبور مواد هضمی کاهش یافت.تزریق محلول‌هائی با اسیدیته ٥ تا ٧ بداخل هزارلا هیچگونه تاثیری برمصرف خوراک و نرخ عبور مواد هضمی از شکمبه نداشت. فشار اسمزی پلاسما تحت تاثیر محلول‌های تزریقی قرار نگرفت. عکس‌العمل شیردان در مقایسه با هزارلا به محلولهای تزریقی مشابه بداخل هزارلا بسیار ضعیف بود. نتایج این آزمایش نشان داد که هزارلا در برابر تغییرات شیمیائی مواد هضمی که از آن عبور میکنند عکس العمل نشان میدهد. با افزایش فشار اسمزی محلول تزریقی بداخل هزارلا خوراک مصرفی و نرخ عبور مواد هضمی از شکمبه کاهش یافت. با افزایش غلظت اسیدهای چرب فرار محلول تزریقی بداخل هزارلا در دامنه مشخص خوراک مصرفی و نرخ عبور مواد مایع از شکمبه افزایش و فراتر از آن غلظت، کاهش یافت. لذا میتوان نتیجه گرفت که هزارلا در کنترل عبور مواد هضمی از شکمبه نقش دارد.

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