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The Partial Efficiency of Acetate Utilization in Sheep

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ABSTRACT: The experiment was undertaken to estimate the partial efficiency of acetate utilization in sheep by increasing exogenous acetate through the rumen and glucose load through the jugular vein. Three Merino wethers were fed a diet chosen to provide intake above maintenance with low propionate. Polyvinyl chloride catheters were surgically implanted into rumen, an iliac artery, portal and jagular veins. In this experiment sheep were administered with saline as control (T1), i mole/d acetate infusion (T2), 2 moles/d acetate infusion and 2 moles/d acetate plus 0.3 mole/d glucose infusion (T4). Dry matter intake (DMI) of T2 and T3 was greater than in T4 (P<.05). The acetate plus glucose (T4) had a higher (P<.05) digestibility of energy than a control group (T1). Substantial differences in mean values in particular acetate infusion without glucose tended to an increase in 02 uptake and infusion of glucose and acetate together appeared to decrease rate of methane production. Proportion of Metabolizable energy (ME) intake retained (PR) ranged from 17 to 51%, indicating that throughout the measurement period of the sheep were in positive energy balance. The partial efficiency of acetate utilization (PE) for body tissue gain varied from 47 to 78% while glucose did not significantly improve PE of acetate utilization at 2 moles/d of acetate infusion use.

Key Words : Efficiency, Acecate, Sheep

Introduction

The early reports by Armstrong and Blaxter (1957) showed convincing evidence that the energy from acetate infused into the rumen of sheep fed dried grass was used less efficiently than the energy from either propionate or butyrate. However, several experiments have shown equally convincingly that acetate may be used with a relatively high partial efficiency (Rook et al., 1963; Elliot et al., 1965; Ørskov et al., 1966., 1979, 1989; Bull et al., 1967, 1970; Poole and Allen, 1970; Roob and Reid, 1972; Johnson, 1972; Johnson et al., 1974). These conflicting results were explained by Tyrrell et al. (1979), which suggested that acetate utilization was influenced by the type of diet fed, it was use more efficiently when given to cattle consuming a hay-and-concentrate diet than hay alone. Later MacRae and Lobley (1982) tried to rationalize these contradictory findings and argued that those diet in which acetate infusion resulted in a relatively high efficiency of utilization had a ready supply of either glucose or glucose precursors (propionate and amino acids) to provide sufficient nicotinamide adenine dinucleotide phosphate (NADPH) for the synthesis of fatty acid from acetate.

Therefore this experiment was undertaken to estimate efficiency of acetate utilization in sheep by increasing exogenous acetate through the rumen and glucose load through te jugular vein.

Materials and Methods

Sheep and ration

Three Merino wethers (approximately 2 months of ages) were brought indoors. The wethers were fed chopped phalaris hay (90%) chopped lucerne (10%) and urea 2% *ad libitum*. The diet was chosen to provide intake above maintenance with low propionate. Sheep were fed continously with an automatic belt feeder. Amounts of feed offered were monitored everyday and water was provide at all times. Molar proportion of rumen VFA (volatile fatty acids) and body weight changes were shown in Table 1. Sheep were adapted to the experimental conditions and fed at least 2 weeks prior to the experiment begin. Acetate and glucose infused were included in the energy utilization calculation as a diet component contributing energy.

This experiment was done in Dairy Research Unit of Sydney University at Camden, New South Wales (NSW) Australia for 4 (four) months.

Surgical and experimental procedures

Polyvinyl chloride catheters (Dural Plastics, Sydney) were surgically implanted into rumen, an aliac artery, portal and jugular veins as mentioned by Katz and Bergman (1969). Correct final placement of these catheres were confirmed at postpartum examination. All catheters were kept patent by flushing 2 times a week with sterile heparinized saline (10^6 IU heparin and 9 g sodium chloride per litre of distilled water).

In this experiment sheep were administered with saline infusion as control (T1). 1 mole/d acetate infusion (T2), 2 moles/d acetate infusion (T3) and 2 moles/d acetate plus 0.3 mole/d glucose infusion (T4). This experiment was designed as an in complete Latin Square with 4 treatments and 3 sheep. The sheep had 8 days between treatments to return to basal state. Each treatment period consisted of infusion of either saline (9 g of sodium chloride plus 1 litre of distilled water) or acetate solution (potassium acetate : sodium acetate = 2:1, 500 g Ajax Chemical, Sydney) into the rumen for 5 days. In treatment 4, glucose solution (0.3 mole/d, 50% w:v, Abbott Australia Pty. Ltd.) was also infused via the jugular vein for 5 days.

An attempt was made to introduce acetate into the abomasum, but feed intake fell and sheep developed diarrhea. When acetate infusion was pH 3, feed intake reduced substantially. This was not due to pH for when acetate was infused at pH 7, the sheep suffered severe diarrhea. It was concluded that infusion of acetate into the duodenum of sheep was not an appropriate alternative to rumen infusion, therefore the procedure was abandoned.

On the day 4 of infusion, sheep was put in a ventilated hood (modified by Nutrition and Feeds Evaluation Unit. Dept. of Agruculture Glenfield, NSW as calorimetry measurement) and 02 uptake (Oxygen Analyser Beckman, USA), CO2 output (Infared Analyzer 303, Lira MSA, USA), and CH4 output (Horiba PIR 2000, USA) measured.

Samples of feed offered, feed refusals, feces and urine were collected for 5 days during each treatment group and pooled daily samples for each sheep for measuring gross energy and nitrogen content, respectively.

Statistical analysis

This experiment was designed an Incomplete Latin Square and Tukey's studentized range test (TSRT 5% or 1%) was used to evalutate the significance of differences between mean values (John and Quenouille, 1977).

Calculation

a. Heat production (HP) using ventilated hood (Brouwer, 1965) = [(0.3833 X O2 uptake in moles) + (0.1125 X CO2 output in moles) - (0.03954 X CH4 output in L)] X [1440: T (running time)] - [0.0059 X N in urine, g/d] Mj/d.

   Metabolizable Energy (ME) =
   Gross energy (GE) of feed ingested + GE of acetate and glucose infused - GE (feces + urine + methane).

   Energy retention (ER) = ME - HP

   Nitrogen balance (NB) =
   Nitrogen intake (NI) - Fecal nitrogen (FN) - Urine nitrogen (UN).

   ME, ER, and NB were calculated based on Van Es and Boek holt (1987). Where it was not possible to measure urine energy directly. It was calculated from urine N using the following equation (V.H. Oddy, personal communication) :
   UE = 0.62 (± 0.0131) UN - 0.0129 (± 0.6336).
   r^2 = 0.981; P<.01; n = 45

b. Proportion of ME retained (PR) = $\frac{ER}{ME}$ X 100%

c. Partial efficiency of acetate utilization (PE) =

$$\frac{\text{(ER treatment - ER control)}}{\text{(ME treatment - ME control)}} \text{ X } 100\%$$

PE was calculated based on Tyrrell et al. (1979)

Results

Feed DM intake (DMI) and feed OM intake (OMI) are shown in table 2. There were differences between treatments, DMI of T2 and T3 was greater than in T4 (P<.o5). The acetate plus glucose (T4) had a higher (P<.05) digestibility of energy than a control group (T1). DMI shown in this Table does not include the weight of acetate infused into the rumen.

There was no significant effect of acetate or acetate plus glucose infusion on O2 consumption,

Table 1. Sheep Weighta and Molar Proportion Of Rumen VFA

Parameter	Before Experiment	After Experiment
Sheep weights (kg)		
Sheep no. 07	43.0	45.0
Sheep no. 08	44.0	46.5
Sheep no. 75	37.0	40.0
Molar proportion of rumen VFA (%)		
Acetate	75.5	76.3
Propionate	15.8	16.2
Butyrate	8.7	7.5

Table 2. Dry Matter (DM), Organic Matter (OM) and Energy Digestibilities and Intakes of Dry Matter and Organic Mater

Parameter	Treatment (T) [a]			
	1	2	3	4
	Mean1SEM, n=3			
Feed DM intake (g/d)	718±77bc	768±59c	740±78c	624±65b
Feces DM output (g/d)	349±20	334±40	328±38	260±33
DM digestibility (%)	52±0	56±9	56±1	59±2
Feed DM intake (g/d)	658±40bc	704±54c	678±72c	571±595b
Feces DM output (g/d)	314±170	298±36	289±30	234±31
DM digestibility (%)	52±1	58±5	57±1	60±1
Energy digestibility(%)	50±1b	59±4bc	60±1bc	65±1c

[a] T1 = control; T2 = acetate infused at 1 mole/d; T3 = acetate infused at 2 moles/d; T4 = acetate infused at 2 moles/d + glucose 0.3 mole/d.

[b,c]; values with different superscript differed significantly

CO_2 and CH_4 output (Table 3). There were, however substantial differences in mean values in particular acetate infusion without glucose tended to an increase in O2 uptake and infusion of glucose and acetate together appeared to decrease rate of methane production.

Nitrogen intake, excretion and balance are shown in Table 4. Nitrogen intake (NI) at T4 was different significantly (P<.05) with T2 and T3. There were no significant differences (P>.05) in fecal nitrogen (FN), urine nitrogen (UN) and nitrogen balance (NB). Urinary N excretion tended to be greater in those sheep infused with acetate alone, but because of large errors inherent in this measurement were not significantly different to control.

The energy partition of energy between intake and various excretory nutrients is shown in Table 5. The gross energy intake in this Table includes the energy provided as acetate and acetate plus glucose. GE intake of T4 was less (P<.05) than T2 and T3. Similar differences also occured in DE and ME

Table 3. Measurement of O2 uptake, CO2 Output and CH4 Output by Sheep in Ventilated Hood (Head Box). Measurements Were Made Over a Period of 3 Hours

Parameter	Treatment (T)			
	1	2	3	4
	Mean1SEM, n=3			
O2 Uptak (mole/d)	9.6010.71	11.312.14	10.610.80	8.510.96
CO2 Output (mole/d)	15.910.27	16.512.02	16.211.87	15.412.63
CH4 Output (L/d)	21.011.49	18.613.03	21.614.94	11.615.21

Table 4. Nitrogen Utilization

Parameter	Treatment (T)[a]			
	1	2	3	4
	Mean1SEM, n=3			
Nitrogen intake (g/d)	15.210.94^{bc}	16.311.25^{c}	15.711.65^{c}	13.211.36^{b}
Fecal nitrogen (g/d)	3.410.27	3.510.54	3.510.54	2.510.59
Urine netrogen (%)	6.511.54	8.311.95	8.412.11	7.011.02
Nitrogen balance(g/d)	5.310.88	4.512.69	3.811.75	3.710.63

[a] T1 = control; T2 = acetate infused at 1 mole/d; T3 = acetate infused at 2 moles/d; T4 = acetate infused at 2 moles/d + glucose 0.3 mole/d.

b,c, values with different superscript differed significantly (P<.05).

Table 5. Partition of Energy Consumed as Diet or infused into Rumen as Acetatic Acid or into Jugular Vein (T4) as Glucose (MJ/d).

Parameter	Treatment (T)[a]			
	1	2	3	4
	Mean1SEM, n=3			
Gross energy (GE)	12.60±0.78^{cd}	13.8±0.9d	13.0±1.37d	11.1±1.14^{c}
GE plus extra energy [b]	12.6±0.78c	14.6±0.94d	14.6±1.38d	13.5±1.13^{cd}
Fecal Energy (FE)	6.3±0.43	6.0±0.74	5.9±0.70	4.8±0.56
Digestible energy(DE)	6.3±0.36c	8.6±0.73e	8.7±0.68e	8.7±0.58^{e}
Urine Energy (UE)	0.4±0.09	0.5±0.12	0.5±0.13	0.4±0.06
Methane energy (CH4E)	0.8±0.06	0.7±0.12	0.8±0.57	0.4±0.18
Metabolizable energy (ME)	5.0±0.29c	7.1±0.80e	7.6±0.57e	7.9±0.44^{e}
Heat production (HP)	4.3±0.22df	5.5±0.64e	4.8±0.28ed	3.9±0.47^{f}
Energy retention(ER)	0.8±0.09c	1.9±0.23de	2.7±0.22e	4.0±0.45^{f}
Proportion of MEI retained (%)	16.6±1.00c	25.6±2.00cd	35.0±2.00d	50.8±5.00^{e}

c,d,e,f; different superscripts differed significantly :

c-d; df-e; e-f; ed-f (p<.05)

c-e; c-f; cd-e; de-f (p<.01)

[a] Saline infused (T1); acetate infused 1 mole/d (T2); acetate infused 2 moles/d (T3); Acetate infused 2 moles/d + glucose infused 0.3 mole/d (T4)

[b] Additional GE introduced based on 1 mole of acetate (heat of combustion = 816 KJ) and 1 mole of glucose (heat of combustion = 2816 KJ).

Table 6. Increment of Energy Consumed and Partial Efficiency of Acetate Utilization

Parameter	Treatment (T)		
	(T2 - T1)	(T3 - T1)	(T4 - T1)
	Mean1SEM, n=3		
Increment of GE + acet. /gluc. (MJ/d)	2.1210.26a	2.1510.69a	1.1710.52a
Increment of FE (Mj/d)	-0.2010.69	-0.2210.36	-1.1510.29a
Increment of DE (Mj/d)	2.3210.51a	2.3710.34a	2.6810.27a
Increment of UE (Mj/d)	0.1610.13	0.1510.12	0.0310.09
Increment ofCH4E(Mj/d)	-0.0110.12	0.0610.20	-0.3010.24
Increment of ME (Mj/d)	2.1710.62a	2.2910.28a	2.9510.18a
Increment of HP (Mj/d)	1.2810.53a	0.4110.17	-0.1710.08
Increment of ER (Mj/d)	0.8910.15a	1.7510.17a	3.1210.41a
Partial efficiency of acetate utilization(PE)[c]	0.4710.01b	0.7810.09bd	1.0510.10de

[a] T-test to zero significantly differed (P<.05). Value eith different superscripts (b,d) differed significantly (P<.01).
[e] Increase of glucose plus acetate infusion, figure shown is PE of acetate and glucose combined.

intakes, sheep in T1 having less (P<.01) than all treated groups. The changes in DE and ME were followed by differences in energy retention (ER) and proportion of ME intake retained (PR). ER was greatest in T4 followed by T3, T2, and T1, respectively.PR ranged from 17% (T1) to 51% (T4) indicating that throughout the measurement period of the sheep were in positive energy balance and this is con-firmed by increase in weight of the sheep over the period of the experiement (Table 1). There were also difference (P<.05) in heat production (HP) measured. HP of T1 was less (P<.05) then (p<.05) than T2, whereas T2 and T3 were significantly different (P<.05) than T4.

Increment of energy to illustrate the calculation of partial efficiency of acetate and glucose infusion are shown in Table 6. Partial efficiency of acetate utilization (PE) was 47% at 1 mole/d acetate infused (T2), 78% at 2 moles/d acetate infused (T3) and 105% at 2 moles/d acetate plus 0.3 mole/d glucose infused (T4), respectively.

Discussion

The Partial or incremental efficiency of acetate utilization (PE) for body tissue gain observed in this study where sheep were fed a low quality roughage diet varied from 47% to 78%. Glucose did not significantly improve PE of acetate utilization at 2 moles/d of acetate infusion use, because PE of acetate utilization 78% is already very high (Table 6). It is concluded that the variabel partial efficiency of acetate utilization for body tissue deposition is a general phenomenon in the ruminant.

The earlier suggestion (Blaxter, 1962) that the poor efficiency of utilization of metabolizable energy (ME) above maintenance (kf) by ruminant given certain forage diets is related to the amounts of acetate produced during rumen fermentation and the subsequent poor utilization of this substrate when compared to propionate and butyrate (Armstrong and Blaxter, 1957 a,b) has been challenged over the last 20 years by a series of experiments which have indicated that in growing lambs (Ørskov and Alan, 1966) and calves (Rook et al., 1963) acetate supplementation (given either as the acid or sodium salt) are utilized as efficiently as propionate or butyrate supplements. Indeed when lambs sustained by intragastric infusion of VFA into the rumen and casein into the abomasum were given different rations of acetate : propionate their efficiency of utilization of the ME was virtually identical independent of the molar proportions of acetate : propionate infused (Ørskov et al., 1979).

Later MacRae and Lobley (1982) clarified these contradictory findings and used the argument that the anabolism of acetate to fat has a obligatory requirement for NADPH and glycerol 3-phosphate. In ruminants the generations of these intermediates relies on the availability of either propionate or

glucogenic amino acids and in most experiments where high efficiencies of acetate utilization have been demonstrated on or other of 3 precursors are inplentiful supply. The metabolic consequence of diet composition was shown by Tyrrel et al. (1979) who observed that the efficiency of rumen supplied exogenous acetate was high (0.69) on a concentrate based ration (30% lucerne, 70% corn) but much lower (0.27) on a whole forage feed (100%).

The hypothesis predicts that the differences in efficiency of utilization of ME between forage diets should be related to differences in either the ration of acetate : propionate absorbed from the rumen or in the amounts of amino acid absorbed from the small intestine. MacRae et al. (1985) have indicated that where sheep were given grasses harvested from the same sward at different seasons of the year they had different kf values (spring harvested grass/SHG kf between M and 2 M 0.54; Autumn harvested grass/AHG kf 0.43). Sheep absorbed twice the amount of amino acid from their small intestine per unit of ME intake on SHG as on AHG. Furthermore when casein was infused into the abomasum of sheep given AHG the efficiency of utilization of AHG increased from 0.45 to 0.57.

In the present study, feed plus infused nutrients ranged from 5.14 to 8.09 MJ/d. It is possible therefore that the extent of inefficiency of acetate utilization may not have been apparent in the present study.

In the present study heat production (HP) associated with various levels of acetate infused was changed particularly during 1 mole/d acetate infused (Table 5). Increment of GE plus additional acetate and glucose was high during 1 mole/d acetate infusion (Table 6), therefore significant change ($P<.05$) in HP was detected. The error in measuring HP with the head box was typically 15% CV (9-20%). The short time animals were in the box could also have contributed to range in values obtained, given the minute changes in O2 uptake seen. In the present study heat increment ranged from 25% to 156% of acetate infused uncorrected for additional intake of blood feed, but no increment at all when glucose was added, suggesting this extra energy went to body tissue rather loss as heat. As comparison, Tyrrell et al. (1979) who used additional energy in the form of acetic acid to the rumen of cows fed a hay diet resulted an increase in heat production, which is equivalent to 73% of the energy infused as acetic acid, where as Armstrong and Blaxter (1957 b) reported as much as 67% when acetic acid was infused into rumen of mature wether sheep fed a diet of dried gras. The measurements of energy retention (ER) were significantly different because they were obtained by difference between HP and MP intake over a longer time.

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