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Glucose Metabolism in Steers Receiving High Fibre Diets and Glucose Infusion Into Abomasum

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ABSTRACT: Glucose has been the subject of a number of studies due to its important role in ruminant metabolism. Nevertheless, there is paucity in the literature dealing with glucose metabolism when ruminants are offerred a low-quality roughages. Eight Brahman steers approximately two years old and weighing 238 ± 23 kg were alloted randomly into an individual metabolism cage. Each steer received barley straw ad lib., 150 g/d mineral mix and 75 g/d urea which was infused continously into the rumen. In addition to that, two steers were infused continously per abomasum with 1500 ml water/head/d, whilst the remainders were infused with 50, 100, 150, 200, 250 and 300 g/1500 ml/d anhydrous glucose during which the following parameters were observed : feed consumption, rumen metabolites, nitrogen balance (NB), and metabolism of glucose. The last parameter was studied using a radio isotope technique. The results showed that abomasal infusion of glucose significantly improved ($P<0.01$) the consumption of dry matter and organic matter as well as NB. The latter was associated with a significant reduction of urinary N excretion suggesting that there was a competition of glucose requirement on the expense of amino acid catabolism. There was no significant alteration ($P>0.1$) on the rumen metabolites attributable to glucose infusion. Pool size of glucose was not altered by infusion but glucose entry rate (GER) and T 1/2 were linearly increased as the level of glucose infusion increased. The implication of this study is discussed in relation to practical application with particular emphasis given to enhancement of ruminant productivity on low-quality roughage.

Key Words : Glucose, Metabolism, Barley Straw, Nitrogen Balance

Introduction

Results from previous sheep experiments reported by Soetanto et al. (1990) suggested that the supply of exogenous glucose in the form either abomasal glucose or rumen propionate infusion improved nitrogen balance. This improvement may be associated with the so-called N sparing effect of glucose (Asplund et al., 1985) and hence supports the hypothesis that glucose is a limiting metabolite in ruminants on low-quality forages (Preston and Leng, 1987). If this is the case, it thus seems likely that optimum ruminant production from low-quality forages could be achieved through supplementation with glucogenic compounds.

However, as a carry over effect was evidenced in those studies resulting in increased nitrogen retention in the control animals following a period of exogenous glucose supply, and together with the existence of some conflicting results in the literature reporting that glucose infusion had no significant effect on nitrogen balance (e.g. Clark et al., 1977; Ranawana and Kellaway, 1977) more direct proof is required.

The following experiments were carried out to ascertain whether the suggested important role of glucose in the utilization of low-quality roughage such as barley straw can be demonstrated in cattle. The studies aimed at obtaining a response curve in terms of digestion and nutrient utilization in steers on straw diets as affected by graded levels of abomasal glucose infusion.

Material and Method

Animals and their management. Eight steers weighing on average 238 ± 23 kg (approximately two years old) were allotted

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randomly into metabolism cages. All steers had both rumen and abomasal cannulae which were inserted two months before the commencement of the study. A two week adaptation was allowed to accustom the animals with the basal diet when the animals were still in the cattle yard. This was followed by another three week adaptation period where all animals received the respective experimental treatments in the metabolism cages. The following two weeks were used to collect the data for nitrogen balance, glucose metabolism, and acetate flux rates and other related metabolites.

Diets. The basal diet consisted of ad libitum hammer milled barley straw, 150 g/head /d mineral premix and 500 ml/head/d molasses. In addition, all animals received continuous urea infusion (@ 75 g/head/d) into their rumen calculated to meet the RDN requirement. The straw was offered ad libitum and delivered at hourly interval by the automatic feeder whilst minerals and molasses were offered once a day in the morning at 10.00 h and placed directly into the feed bin. Throughout the experimental period the mineral mix and molasses were usually consumed completely within an hour.

Infusion and data collection. Two steers were sustained on the basal diet and infused with an equal volume of water (1500 ml/d) into their abomasum while the other six animals received intra-abomasal infusion containing anhydrous glucose (g/1500 ml), respectively, 50, 100, 150, 200, 250 and 300 per day in addition to the basal diet, with one animal allocated to each level.

Following the adaptation period, a seven day total faecal and urine collection was performed to allow subsequent calculation for nitrogen balance. On the day after the completion of nitrogen balance study, samples of rumen fluid were withdrawn before and two hours after the morning feeding. The samples were then stored at - 15°C pending NH_3 and VFA analyses.

Upon the completion of this collection day, plastic catheters (internal diameter 1 mm) were inserted into both jugular veins (Chapter 3) of all animals at least 18 h prior to the commencement of isotope studies. To study the glucose entry rate a single injection of approximately 0.3 mCi 2-^{3}H glucose was given to each animal through one catheter and blood samples were taken at interval from the other catheter. In the morning before the labelled glucose was injected, samples of blood were withdrawn from the catheter for determination of plasma urea nitrogen (PUN) concentrations.

Analytical methods. Chemical composition of feed was determined using a standard method as described by AOAC (1970). Ammonia concentration in rumen fluid was determined by steam distillation with a Kjeltec Auto 1030 Analyser (Tecator), while the concentration of VFA's in rumen fluid was analysed by gas liquid chromatography (Hewlet Packard, Model 5830 A) using iso-caproic as an internal standard.

PUN concentrations were determined utilising Barthelot's reaction using Urea Test Kit (Boehringer Mannheim catalog no. 124788) and reading of absorbance with a spectrophotometer (Beckman DU-5) at wave length 550 nm.

Plasma glucose concentrations were determined by the glucose oxidase, peroxide procedure using Test combination kit (Boehringer Mannheim, catalog no.124036). Plasma was deproteinized by a modification of Somogyi (1945) using $ZnSO_4$ and NaOH. Plasma samples containing 2-^{3}H were prepared for 2-^{3}H assay by ion exchange chromatography (Mills et al., 1981) and mixed with scintillant (Emulsifier-safe, Packard Australia) at ratio 1 ml : 9 ml, respectively before radioactivity was counted using a Beta counter (Packard Instrument, Tricarb 1900).

The specific radioactivity-time curve for plasma glucose following a single injection of tracer was plotted on semi logarithmic coordinates and a straight line was fitted bt least squares to the initial rectilinear portion of the curve. The log specific radioactivity of glucose with time was a single exponential equation and therefore pool size (g), half time (t 1/2: min) and glucose entry rate (mg/min) were calculated assuming that a first order dilution process applied as described by Judson and Leng (1972).

Statistical analysis. Treatment effects were assessed by regression analysis using a computer program of MICROSTA.

Results and Discussion

Chemical composition of dietary ingredients. Table 1 describes the results of proximate analysis of dietary ingredients.

Table 1. Chemical composition of feed ingredients (% of DM)

	DM	OM	N
Barley straw	89.19	89.98	0.213
Mineral mix	97.05	42.51	0.636
Molasses	74.94	83.73	1.02
Urea solution	-	-	35.78 *
Anhydrous glucose	90.75	100	-

* expressed as mgN/ml solution

Feed intake, digestibility and N economy. Table 2 shows effects of glucose infusion on the mean intake and digestibility of feed. The actual amount of glucose infused into the abomasum was different to the intended infusion levels. Regression analysis upon levels of glucose infusion vs. each parameter indicated that straw dry matter intake (DMI) and total nitrogen intake (TNI) remained unchanged, but total DMI (TDMI) and total OM intake (TOMI) were significantly improved by infusion ($P<0.01$). There were positive linear increases ($P<0.05$) in apparent digestibilities of DM and OM which can be attributed to glucose infusion, but N digestibility remained similar among infusion levels. Faecal N excretion was similar among treatments but urinary N excretion decreased significantly ($P<0.01$) as the level of glucose was progressively increased.

When expressed as g/d or as % of TNI, NB was enhanced ($P<0.01$) by glucose infusion ,but the association became insignificant when NB was expressed as g/kgLW/d) or g/kgDOMI. Multiple regression analysis between NB (g/kgLW/d) as a dependent variable and selected independent variables, viz. glucose infusion (gDM/d) and TNI (g/kgLW/d) showed better association between parameters. The relationship was best fitted by the following equation : $Y = -0.1356 + 0.000151\ x_1 + 0.8532\ x_2$ (Multiple R = 0.92; RSD = 0.011; $P<0.05$), where Y = NB (g/kgLW/d) ; x_1 and x_2 are glucose infusion (gDM/d) and TNI (g/kgLW/d), respectively.

The most limiting nutrient in ruminants consuming low-quality forages has been the subject of controversial debate (Ørskov, 1980; Preston and Leng, 1980). A high portion of carbohydrates which is bound with lignin cannot be utilised by the animal. It is not surprising then that intake of low-quality forages seldom meets metabolisable energy requirement even for maintenance unless pre-treatments are applied to such forages (Doyle et al., 1986). Under conditions of sub maintenance level of feeding animals have to provide energy from body reserves of fat and protein. At levels of maintenance and above utilisation of acetate for fat deposition may be limited by glucose precursors for NADPH production (MacRae and Lobley, 1982). Use of protein for glucose may limit N balance. Unfortunately, this contention has been tested with equivocal conclusions as to whether energy in the form of glucose or protein is the most limiting nutrient (Ørskov, 1980; Preston and Leng, 1987; Ørskov and Reyle, 1990). This largely stems from inconsistent responses in N balance in ruminants that were infused with glucose (Eskeland et al., 1974; Clark et al., 1977; Ranawana and Kellaway, 1977; Asplund et al., 1985 and Mahyuddin and Teleni, 1988).

Glucose infusion into the abomasum of steers did not significantly reduce the intake of barley straw, yet TDMI and TOMI were all significantly enhanced (Table 2). These findings are in agreement with previous studies reported by a number of authors (e.g.Ørskov et al.,1977;). More recently, Hynd (1989) also found that neither infusion of abomasal glucose nor fish meal supplementation impaired the voluntary intake of herbage in grazing cattle, yet TOMI was enhanced. Barley straw used in the present study had a similar composition to that used in the sheep experiments (Soetanto et al., 1990) and was considered to be of low nutritive value. Apparent digestibility of feed DM and OM in a control animal showed a higher digestibility value than that in sheep (60 vs 40). Recognizing that these were two different experiments it still suggests that steers have a better capacity to utilise a low quality feed than sheep. This may be associated with a longer retention time of feed particles in the rumen of steers than sheep (Poppi et al., 1981a,b). It was also found that even in the control treatment that the animal showed a positive nitrogen balance (NB). This may be attributed to the digestibility value of the basal diet which may enable the animals to meet the requirement for maintenance. Jackson (1981) stated that voluntary feed intake of low-quality diets can be doubled if digestibility and N content can be increased by 5 and 3%, respectively.

Improved NB in the present studies was attributable to a significant decrease in urinary N excretion rather than a decrease in faecal N

excretion. Thus increased supply of exogenous glucose has led to a greater N sparing effect and apparently reduced deamination of amino acids for glucose. A similar effect of glucose infusion leading to a reduction in urinary N excretion was also reported by Eskeland et al. (1973;1974) in lambs and more recently in steers by Ku-Vera et al. (1988) and in growing wether lambs by Matras and Preston (1989).

Rumen metabolites and plasma urea nitrogen (PUN). As was expected, mean levels of rumen ammonia were above the suggested minimum requirement (i.e. 50 mgN/L) for normal microbial growth, except that animal number 1 which was on a control diet, was only 39.4 mg/L. This surprisingly lower value of rumen ammonia may be due to improper mixing of rumen fluid samples as the sampling device used was positioned in dorsal sac of the rumen. Regression analysis between levels of glucose infusion and rumen metabolites showed that rumen ammonia, total VFA (TVFA) and individual VFA concentrations had no significant relationships ($P>0.1$) with levels of glucose infused. The most abundant VFA in all animals was acetate (about 70-75 %) followed by propionate (@ 15 - 18 %) and butyrate (@ 6 - 8 %). Other longer and branched VFA's such as valerate and iso-valerate were only detected at negligible amounts (less than 1 %). Mean value for each parameter is presented in Table 3. The data presented in Table 3 suggest that no treatment significantly affected rumen metabolite concentrations. This is not surprising as this study was designed to supply each animal with approximately equal amounts of forage, N and mineral mix. Some variation was found in rumen ammonia levels in the control animals. This is more likely associated with improper mixing of the samples as the sampling device used for aspirating rumen fluid (i.e. a probe connected with a disposable syringe) was positioned in the dorsal sac.

With respect to rumen ammonia levels, there seems no agreement among researchers concerning the minimum level below which the activity of microbes will be impaired. At present a concentration of 50 mgN/L is the most widely accepted figure required to ensure normal activity of rumen microbes (Satter and Slyter, 1974). However, Hoover (1986) summarised results from a number of studies in which he concluded that maximum microbial growth and organic matter digestion in the rumen could be obtained over a wide range of rumen ammonia levels varying from 10 to 60 mgN/L. Thus, it is doubtful if the lower concentration of rumen ammonia in the control animal from the present study would lead to impairment of microbial activity and be responsible for lower apparent digestibilities of DM and OM. In addition, the relatively unchanged concentrations of total VFA and the proportion of individual VFA indicated that there was no such alteration in the rumen fermentation attributable to treatment effects.

There was a negative but not statistically significant relationship between concentrations of PUN and levels of glucose infusion. The steer that received 124.4 g glucose/d exhibited the lowest concentration of PUN ,i.e. 4.62 mg/dl and the highest concentration, i.e. 18.84 mg/dl ever recorded was found in the steer receiving 50 g glucose/d (Table 3). This was also reported in sheep receiving intravenous glucose infusion by Asplund et al. (1985) and Mahyuddin and Teleni (1988). A low concentration of PUN is usually associated with less circulating N in the blood or is a result of less catabolism of tissue protein for recycling of N into the rumen (Preston and Leng, 1987).

As the concentration of rumen ammonia in all animals was considered above the minimum requirement for rumen microbes, it therefore is likely that in glucose infused animals, the tendency of lower concentrations of PUN was associated with less deamination of tissue protein due to increased N sparing effect. Dror et al. (1969) observed a decrease in blood urea nitrogen in sheep in response to starch supplementation. This was accompanied with a significant increase in N retention suggesting that protein utilisation was improved. However, it should be noted that inconsistent findings are also found in the literature (e.g. Eskeland et al., 1974).

Glucose kinetics. Mean glucose concentrations were between 473 and 568 mg/L but the values fluctuated during the sampling time and were not significantly affected by infusion. In all instances specific radioactivity (SRA) in plasma samples declined exponentially and was best fitted with a single exponential equation (R^2 = 0.96 - 0.99). Thus, SRA at any given time (SRA_t) can be estimated from the following equation:

$$SRA_t = SRA_0 * e^{-kt}$$

Table 2. Effect of glucose infusion on feed digestion and nitrogen utilisation

Parameter	Glucose infusion (gDM/d)							LRA				
	0	50 (50)	85.6 (100)	124.4 (150)	174.2 (200)	180.0 (250)	236.5 (300)	a	b	r	RSD	Sig.
Feed intake (g/kgLW/d)												
Straw DM	17.6	19.0	16.95	18.72	23.37	16.84	21.74	17.31	0.0156	0.57	2.15	NS
Total DM	20.7	21.8	20.3	22.6	27.5	20.4	25.3	20.38	0.0191	0.63	2.23	+
Total OM	18.2	19.3	17.9	19.4	24.4	18.1	22.5	17.91	0.0175	0.63	2.02	+
Total N	0.219	0.193	0.199	0.232	0.242	0.199	0.201	0.213	0.000001	0.0006	0.021	NS
N-Excretion (mg/kgLW/d)												
Faeces	82.4	84.8	86.3	81.2	104.4	70.3	72.9	0.085	-0.00002	-0.14	0.011	NS
Urine	92.95	73.30	68.40	68.60	40.00	50.50	69.50	0.087	-0.00016	-0.77	0.013	**
App.Digestibility (%)												
Dry matter	59.45	58.4	56.0	61.0	61.2	64.5	67.3	57.59	0.0312	0.76	2.488	**
Organic matter	61.65	60.8	58.1	62.1	63.4	65.8	69.0	60.08	0.0266	0.71	2.518	**
Nitrogen	62.15	56.1	55.1	64.9	56.6	64.6	63.5	59.61	0.0096	0.21	4.271	NS
N-balance :												
g/d	11.18	9.60	10.58	17.61	21.01	19.44	15.57	10.42	0.0386	0.76	3.146	**
mg/kgLW/d	49.50	35.50	44.50	82.30	97.70	78.90	59.10	.046	0.0002	0.61	0.019	NS
g/kgDOMI	4.25	2.95	4.29	6.65	6.49	6.61	3.80	4.15	0.0072	0.41	1.507	NS
% TNI	22.42	18.17	21.31	35.00	40.20	39.44	28.96	20.94	0.071	0.71	6.612	**

LRA = linear regression analysis for independent variable of glucose infusion levels. + significant at P<0.1; ** at P<0.01; NS = not significant (P>0.1); RSD = residual standard deviation. Value in parentheses is intended level of glucose infusion.

Table 4 summaries the parameters obtained from glucose kinetic measurements. It was found that glucose pool size (g) was not affected by treatments imposed, but glucose entry rate (GER) and T½ increased linearly (r values = 0.72 and -0.84, respectively) with levels of glucose infusion. The endogenous glucose entry (i.e. calculated as GER -exogenous glucose supply) tended to increase in response to glucose infusion but the relationship was not statistically significant. There was a positive linear relationship between N-balance and GER and best fitted by the following equation :

$Y = -0.0396 + 0.713 \times$ ($r = 0.82$; RSD = 0.013; significant at $P < 0.05$),

where

Y = NB (g/kgLW/h) and x = GER (g/kgLW/d).

The effect of increased supply of glucose in ruminants has been reported with varying degrees of success in terms of elevation of plasma glucose concentrations. Ulyatt et al. (1969), for instance, could detect no significant difference in plasma glucose concentrations attributable to large differences in the amounts of α - linked glucose polymer altered by dietary treatments. Infusion of glucose or sodium caseinate into the abomasum of dairy cows has given similar results (Clark et al., 1977). In contrast, Judson and Leng (1972), Asplund et al. (1985) and Abdalla et al. (1986) observed a significant elevation of plasma glucose concentration in sheep in response to intravenous infusion of glucose. This is recently supported by evidence from a similar study utilising beef cows (McCaughey et al., 1988). The indication from the present study was that plasma concentrations of glucose remained similar regardless of the levels of glucose infusion (Table 4). Published observations in this field showed that intravenous infusion of glucose almost always is associated with the elevation of plasma glucose concentration (Judson and Leng, 1972, Asplund et al., 1985; Abdalla et al., 1986). In contrast, abomasal infusion of glucose or glucogenic compounds produced inconsistent results in terms of elevation of plasma glucose infusion (Ulyatt et al, 1969, Clark et al., 1977; Hynd, 1989; Kreikemeier et al., 1990). It is likely that the inconsistent results between studies referred above are associated with the role of the liver in

gluconeogenesis and the route of entry of glucose (Young, 1977).

Infusion of glucose is associated with a linear increase in GER (Table 4). This indicated that a greater availability of glucose (up 50%) occurred in the infused animals as compared with their control counterparts. On average the increment in GER was greater than the approximate amount of glucose (g/d) infused into the abomasum suggesting that not only was most of the exogenous glucose absorbed but endogenous glucose entry (EGE) was also increased although this was not significant (Table 4). However, contrary results were observed in sheep following infusion of glucose where EGE either decreased (Mahyuddin and Teleni, 1987) or increased (Mahyuddin and Teleni,1988). It has been argued by Mahyuddin and Teleni (1987) that loading exogenous glucose may only have a transient effect on depression of endogenous glucose entry and that with a longer period such an effect is reduced. The animals in the present study had been subjected to sufficient time to accustom them to the experimental treatments (approximately 4 weeks). Therefore, the absence of EGE depression in glucose-infused animals may be related to the relatively longer duration of glucose infusion before glucose kinetic measurements were carried out. By comparison similar studies in the literature were usually performed after a relatively short duration of glucose infusion (ranged from 4 to 7 days) before glucose kinetics were studied. To clarify this contention prolonged infusion of glucose combined with concomitant repeated measurements of glucose kinetics deserves further study.

Although a significant correlation was found between glucose infusion and GER, this study could detect no significant improvement in glucose pool size and glucose space. This suggests that the improvement in glucose entry was not mediated through an increase in the body pool of glucose but through an increased rate of utilisation as indicated by a strong negative correlation between glucose infusion and T½ (Table 4). Ferreiro et al. (1979) noted in cattle that were on sugar cane based diets that supplying the animals with various amounts of rice polishing increased GER from 360 to 550 mg/minute and decreased T½ from 98 to 59 minutes, but glucose pool size remained unchanged. In addition, Young (1977) has suggested that variation in glucose metabolism studies may be due to several factors such as "(1) method of isotope administration; (2) isotope label and molecular positioning of the label glucose; (3) feeding regime; (4) sampling interval; and (5) analysis to determine specific activity of glucose ".

Table 3. Mean values for rumen ammonia, VFA and plasma urea nitrogen (PUN) concentrations in steers as affected by graded levels of glucose infusion.

	Glucose Infusion (gDM/d)							L R A				
Parameter	0	50	85.6	124.4	174.2	180	236.5	a	b	r	RSD	Sig.
Rumen NH3 (mgN/L)	39.4	207.4	88.4	105.9	138.1	140.5	73.6	85.54	0.174	0.265	59.85	NS
Total VFA (mM)	67.4	62.1	64.4	44.0	69.6	48.8	52.2	65.94	-0.061	-0.544	8.859	NS
Acetate (%)	73.7	77.8	75.1	75.3	72.2	71.4	72.5	75.58	-0.014	-0.609	1.760	NS
Propionate (%)	18.4	18.2	16.9	17.2	19.5	19.1	18.8	17.87	0.004	0.384	0.871	NS
Butyrate (%)	6.9	4.1	7.6	7.0	7.4	9.2	7.7	6.21	0.008	0.499	1.340	NS
P : A ratio	0.25	0.23	0.23	0.23	0.27	0.27	0.26	0.24	00001	0.515	0.016	NS
PUN (mgN/dl)	10.94	18.84	15.59	4.62	12.01	8.80	9.96	13.18	-0.016	-0.328	4.414	NS

LRA = linear regression analysis for independent variable of glucose infusion levels. NS = not significant (P>0.1); RSD = residual standard deviation. P : A = propionate : Acetate

Table 4. Glucose kinetics in steers given a basal diet of barley straw as affected by graded levels of abomasal glucose infusion

	Glucose infusion (gDM/d)							LRA				
Parameter	0	50	85.6	124.4	174.2	180	236.5	a	b	r	RSD	Sig.
Liveweight (kg)	227.3	270.5	237.5	214.0	215.0	246.5	263.5					
Plasma glucose conc.(mg/L)	511	523	568	510	496	473	518	523.25	-0.0894	-0.29	8.143	NS
Pool size (g)	1.02	8.38	67.71	64.54	59.76	82.79	0.92	4.83	.0271	0.24	.190	NS
Glucose entry rate:												
- g/h	6.93	3.86	0.47	2.91	38.10	46.19	37.02	7.87	0.0526	0.72	.728	*
- g/kgLW/h	0.118	0.125	0 .128	0.154	0.177	0.187	0.141	0.12	0.0002	0.65	.021	+
Glucose space (as % LW)	53.03	55.40	50.19	59.14	56.04	71.01	51.96	53.43	0.0213	0.24	.056	NS
T½ (minute)	94.31	96.26	92.41	81.54	68.62	74.53	79.67	95.95	-0.1010	-0.84	.160	**

LRA = linear regression analysis for independent variable of glucose infusion level. # LRA between Endogenous glucose entry (Y) and exogenous glucose supply (x). + significant at P<0.1; * at P<0.05;** at P<0.01; NS = not significant (P>0.1); RSD = residual standard deviation.

Conclusions

From this experiment one noteworthy conclusion can be drawn, viz. there was a close relationship between improved NB and GER in response to exogenous glucose supply into the abomasum. This finding substantiates the contention that exogenous glucose supply is likely to be limiting production in ruminants given low-quality diets. The significant reduction in urinary N excretion suggests that amino acids were diverted from catabolic to synthetic pathways when exogenous glucose supply was increased.

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