

GLUCOSE METABOLISM IN GROWING LAMBS

T J Kempton and R A Leng

Department of Biochemistry and Nutrition, University of New England,
Armidale NSW 2351, Australia

Glucose entry rates were measured in lambs on two diets to which various supplements were added in order to produce a range of feed intakes and growth rates. In Experiment 1 the lambs were given a low protein diet of oaten chaff and supplemented with either urea, urea and casein or urea and formaldehyde-treated-(HCHO) casein. In Experiment 2 the lambs were given a low protein diet of bagasse, sugar and lucerne chaff supplemented with urea and either fish meal, or rice bran or both.

Glucose entry rates were estimated from data obtained following a single injection of (2-³H) glucose. Examination of the glucose entry rates measured at intervals of 6 h throughout 24 h period in lambs fed at frequent intervals indicated that there was no difference in glucose entry rate measured during any of these periods. Therefore the entry rate of glucose estimated over a single 3 h period was taken to indicate the entry rate of glucose (g/d) over the whole 24 h period.

Glucose entry rates were linearly related to DE intake. From the slope of this relationship it appeared that 14.7% of the DE passed through the glucose pool.

Glucose entry rates were linearly related to the rate of liveweight gain. Where lambs were growing at 250 g per day the glucose entry rate was 13.5 g/kg^{0.75}/d.

Key words: Glucose entry rates, lambs, bypass protein

In ruminants glucose is provided by glucogenic precursors including propionate and amino acids, and also on some diets by its absorption from the small intestines. In mature sheep, glucose entry rates have been shown to increase linearly with an increase in digestible energy (DE) intake (Judson and Leng 1968; Lindsay 1970). Similarly in cattle under a wide variety of conditions DE intake appears to 'control' glucose entry rate (Herbein et al 1978; Smith et al 1979; Raja et al 1981).

In the studies presented here glucose entry rates were measured using (2-³H) glucose in lambs on ad libitum intakes of a number of diets and growing at different rates. There were linear relationships between glucose entry rate and both DE intake and growth rate.

Materials and Methods

Experimental animals: Border Leicester x Merino wether lambs (average weight 21 kg) were held in individual pens on slatted floors in an animal house.

Experiment 1:

Design and treatments: Four lambs were allocated at random to each of the five treatments described below. A basal diet of oaten chaff which contained (g/kg chaff) 5 NaCl, 5 Na₂SO₄ and 5 mineral mix (Kempton and Leng

quenching using the channels ratio method of Bruno and Christian (1961). Radioactivity in the glucose of the injected solution was also assayed as the pentaacetate derivatives.

Faeces were digested by the method of Stevenson and De Langen (1960) and chromium content determined on an atomic absorption spectrophotometer (Perkin-Elmer Australian Pty Ltd, Melbourne, Australia) using an acetylene-nitrous oxide flame.

Calculations: The specific radioactivity-time curve of plasma glucose following a single injection of tracer was plotted on semilogarithmic coordinates and a straight line fitted by least squares to the initial rectilinear portion of the curve, which was apparent from about 20 min to 3 h post injection of the isotope. 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 kinetic process was described by Uden and Leng (1972).

In Experiment 1, the digestible energy (DE) intake of lambs was calculated assuming the DE content of oat chaff and casein was 6.8 and 18 kg/DM respectively.

Statistical methods: Comparison between treatment effects was made by analysis of variance. Differences between mean digestibility coefficients of animals given the individual diets in Experiment 2 were tested using analysis of covariance with organic matter intake as the covariate (Snedecor & Cochran 1968).

Results

Dry matter intake and liveweight gain.

Experiment 1: The diets (basal, U, U + C, U + F/C and U + C + F/C) contained on average 90% DM and 9.0, 18.9, 30.7 and 30.7 g N/kg DM respectively. Mean values for the intake (g/d) liveweight gain (g/d) and calculated conversion ratio for each diet are given in Table 1. Dietary supplement

Table 1:

Dry matter intake, liveweight gain and feed conversion of lambs given a basal diet of oat chaff and supplements of urea (U), casein (C) or formaldehyde-treated casein (F-C) (Experiment 1)

	Basal	U	U+C	U+F/C	U+C+F/C	SEX	S
DM intake, kg/d	493	536	519	620	570	±43	
Initial LW, kg/d	22.9	23.0	22.3	22.7	22.7	± .86	
LW change, g/d	9 ^a	33 ^b	23 ^{ab}	50 ^c	60 ^c	± .33	P
Feed conversion ¹	55	16	23	12	10	-	

^{abc} Values within same row with the same superscripts are not significantly different.

¹ DM intake/LW change, kg/kg.

of HCHO-casein and soluble casein plus HCHO casein significantly ($P < .001$) increased liveweight gain. Live weight gain (Y , g/d) was related to DE intake (X , MJ/d) on all diets and was described by the equation:

$$Y = 27.3 (+ 5.18)X - 74.4 \quad R^2 = 0.60 \quad RSD = 21.0$$

Experiment 2: The diets contained on average 94% DM and 18 MJ gross energy/kg DM. Supplements of 12.5% fish meal, and 25% fish meal and 25% rice bran in the basal diet significantly ($P < 0.001$) increased DM intake and liveweight gain of lambs in comparison with that in lambs given the basal diet (Table 2). The greatest response in both DM intake and liveweight gain was to supplementation with fish meal at both levels or 12.5% fish meal and 12.5% rice bran. Liveweight gain (Y , g/d) was related to DE intake (X , MJ/d) on all diets and was described by the equation:

$$Y = 23.6 (+ 4.90)X - 55.7 \quad R^2 = 0.49 \quad RSD = 50.5$$

Organic matter digestibility was significantly ($P < 0.05$) greater on the 25% rice bran supplemented diets in comparison with all the other diets, which were not significantly different (Table 2).

Table 2:

Mean values ($n=5$) for dry matter (DM) intake, average daily gain and calculated feed conversion ratio of lambs in Experiment 2 given a basal diet of bagasse, sugar and lucerne chaff for a 5 week period. Supplements were 12.5 or 25% fish meal (F), 12.5 or 25% rice bran (RB) and 12.5% F plus 12.5% RB. Mean values for organic matter (OM) digestibility adjusted to a common OM intake by covariance analysis are also given

	Basal diet	Basal diet plus:					SE \bar{x}	Signif.
		12.5F	25F	12.5RB	25RB	12.5F+12.5RB		
N in diet, g/kg DM	20	29	37	21	21	27		
DM intake, g/d	451 ^a	665 ^{bc}	734 ^c	497 ^a	622 ^b	728 ^c	31	$P < .001$
Initial LW, kg	20.6	20.9	21.1	20.8	21.1	21.0	1.16	NS
LW change, g/d	40 ^a	171 ^c	191 ^c	63 ^a	129 ^b	197 ^c	13	$P < .001$
Feed conversion ¹	11	4	4	8	5	4		
OM digestibility, %	63.7 ^{ab}	62.9 ^{ab}	62.6 ^{ab}	68.6 ^{bc}	72.7 ^c	57.5 ^a	3.26 ²	$P < .05^3$

^{abc}Values within the same row with the same superscripts are not significantly different.

¹DM intake/LW change, kg/kg.

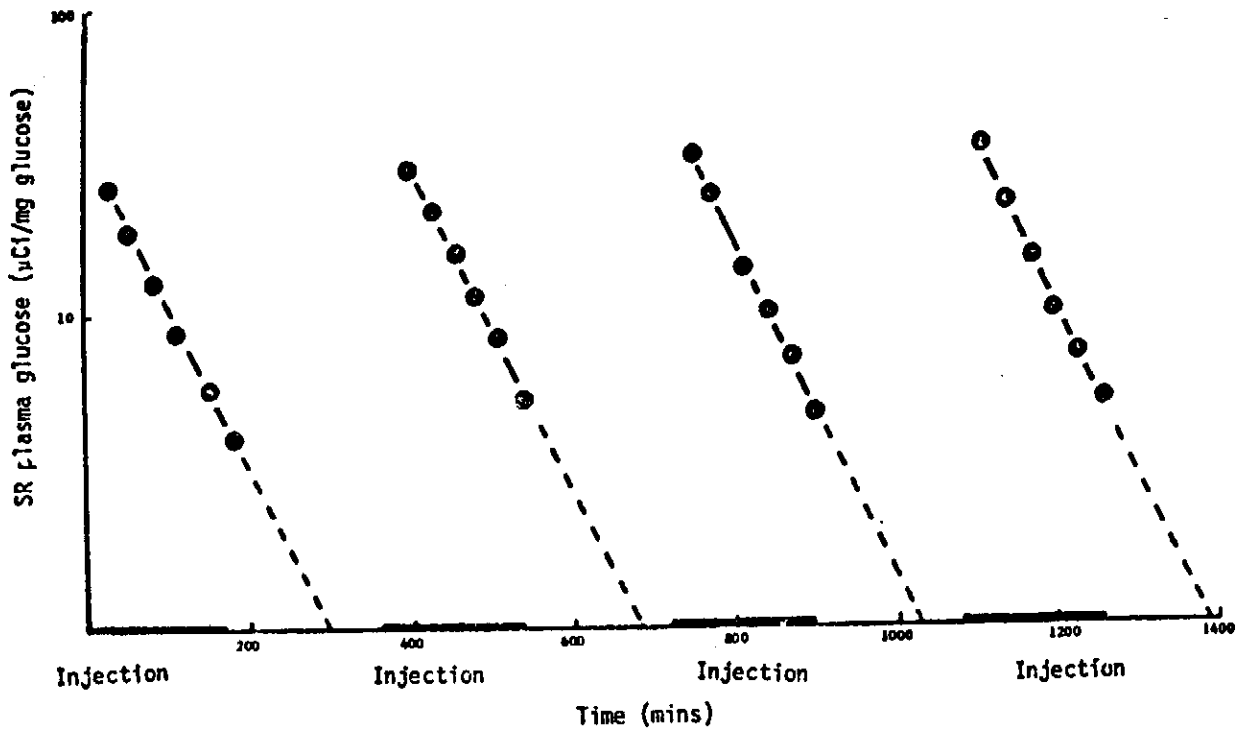
²SE of adjusted means.

³Between adjusted means.

Glucose metabolism: The relationship between the specific radio-activity of glucose in plasma with time in the four experimental periods over one day for one animal is given in Figure 1. There were no significant differences between the means of the four estimates of glucose entry rate (mg/min), pool size (mg), $t_{1/2}$ (min) or plasma glucose concentration (mg/100 ml) over

Figure 1:

Relation between the log specific radioactivity of plasma glucose with time after four consecutive single injections of (2-³H) glucose. Results for one animal are given



the 24 hr period (Table 3). Glucose space (%) was, however, significantly ($P < 0.01$) lower in all 4 lambs as estimated from the results of the last two injections in comparison with the first two injections.

Table 3:

Parameters of glucose metabolism estimated in lambs at 6 h intervals over 24 h. A single injection of (2-³H) glucose was used on each occasion. All values are the mean of 4 animals

	Estimation				SEX
	1	2	3	4	
$T_{1/2}$, min.	54	55	55	53	1.7
Pool, g	3.0	3.3	2.6	2.4	0.25
Space, litres	4.8 ^b	5.3 ^b	4.0 ^a	3.6 ^a	0.29
Glucose entry rate, mg/min.	39	41			2.8
Plasma glucose concentration, mg/100 ml	63	62	68	65	1.7

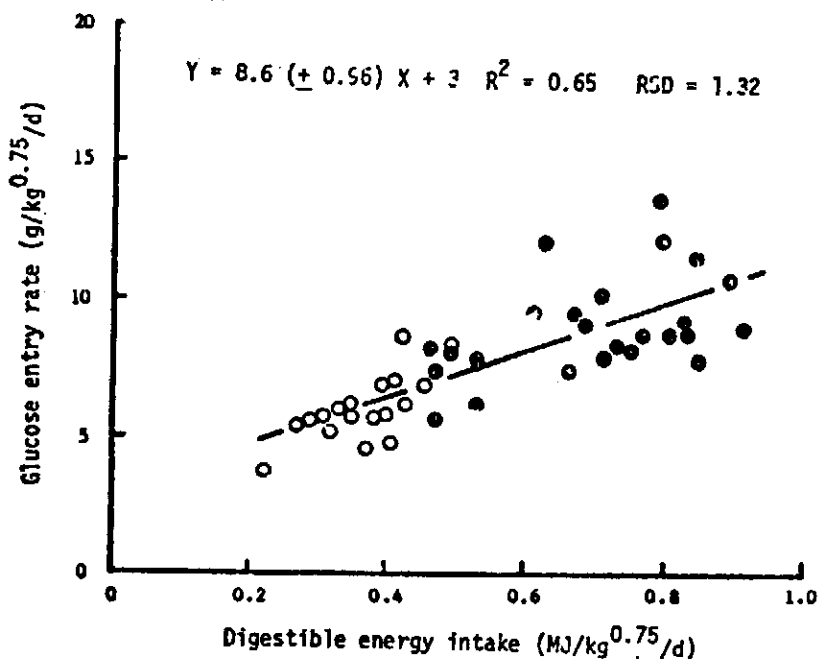
^{ab}Values within the same row with the same superscripts are not significantly different

Glucose entry rate in relation to feed intake and growth rate: Glucose entry rate (g/d) increased directly in response to an increase in DE intake (MJ/d) and therefore liveweight gain and glucose entry rate were linearly related. Since there were no significant differences between the slopes and intercepts of the relationships for lambs in the two experiments, the results were combined. The relationship between glucose entry rate (g/d) and DE intake (MJ/d) is given in Figure 2. The relationship between glucose entry rate corrected to metabolic body weight ($Y: \text{g/kg } W^{0.75}/\text{d}$) and DE intake corrected to metabolic body weight ($X: \text{MJ/kg}^{0.75}/\text{d}$) was given by the equation:

$$Y = 8.6 (\pm 0.96)X + 3 \quad R^2 = 0.65 \quad \text{RSD} = 1.32$$

Figure 2:

Glucose entry rate ($Y: \text{g/kg}^{3/4}/\text{d}$) in relation to digestible energy intake ($X: \text{MJ/kg}^{3/4}/\text{d}$) in lambs given a basal diet of either oaten chaff (O) or bagasse, sugar and lucerne chaff (●). The regression equation (with the SE of the regression coefficient) of glucose rate on digestible energy intake is



The relationship between liveweight gain ($Y: \text{g/d}$) and glucose entry rate ($X: \text{g/kg } W^{0.75}/\text{d}$) was given by the equation (Figure 3):

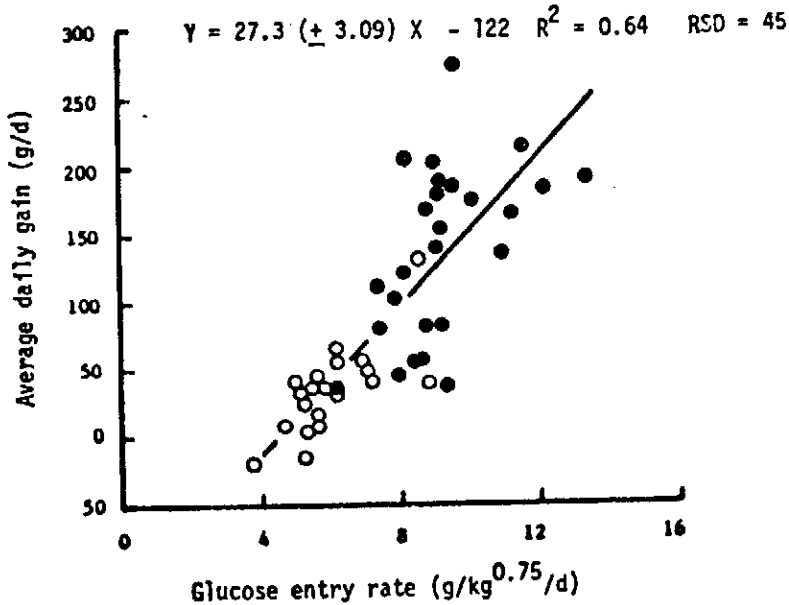
$$Y = 27.3 (\pm 3.09)X - 122 \quad R^2 = 0.64 \quad \text{RSD} = 45$$

Discussion

Growth: In the studies presented here, feed intake and lamb growth were increased by adding fish meal or HCHO-casein to the basal low protein

Figure 3:

Average daily gain (Y: g/d) in relation to glucose entry rate (X: g/kg^{0.75}/d) in lambs given a basal diet of either oat chaff (O) or bagasse, sugar and lucerne chaff (●). The regression equation (with the SE of the regression coefficient) of average daily gain on glucose entry rate is



diets. Rice bran was only effective at a high level (25% of diet DM) presumably because of its lower protein content. These findings support the concept that a deficiency of bypass protein limits feed intake (see for review Kempton et al 1977).

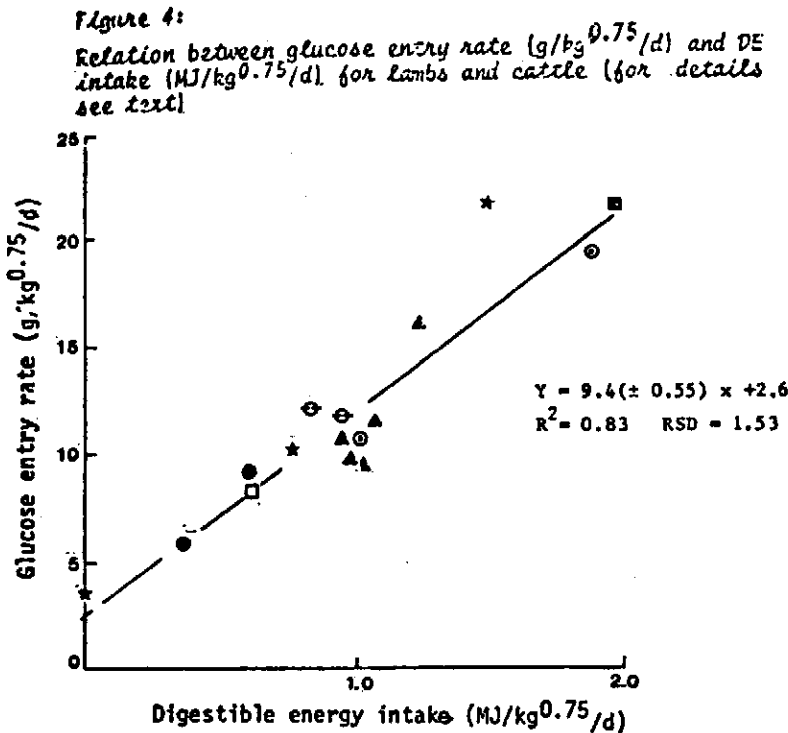
Glucose kinetics: The single injection method of isotope dilution was preferred in these studies because of the ease of carrying out such experiments in a large number of lambs. Preliminary studies indicated that in lambs fed at regular intervals, glucose entry rate over a day could be meaningfully predicted from that measured over a 3 h period (Table 3). However, glucose space and pool size were apparently decreased by 25% and 20% respectively in the experiments carried out overnight (Table 3).

In this study, glucose entry rate varied with liveweight gain and DE intake, and additional 44 g glucose/d being synthesised for a liveweight increment of 100 g/d. At zero liveweight gain, glucose entry rate was 48 g/d or 4.5 g/kgW^{0.75}/d, which is within the range of values for glucose entry rate obtained from mature sheep at maintenance (from Leng 1970). In lambs in which liveweight gain varied from 50 to 250 g/d, between 70 and 157 g glucose/d (or 6.3 to 13.6 g/kgW^{0.75}/d) passed through the glucose pool. Furthermore, extrapolating from the relationship between glucose entry and liveweight gain for lambs growing at close to the maximum rate of 400 g/d (see Orskov et al 1974) indicated that 222 g glucose/d (or 19.1 g/kgW^{0.75}/d) would be synthesised. This rate is similar to the glucose entry rate in

ruminants in other highly productive states. For instance, in lactating cows, average glucose entry rates were 19 to 22 g/kg^{0.75}/d in comparison with 10 g/kg^{0.75}/d in non-pregnant non-lactating cows (Wiltrout and Satter 1972; Herbein et al 1978).

Glucose entry rate was directly related to the DE intake of lambs. For an increase in DE intake of 1 MJ/d an addition 9.4 g glucose was synthesised. This suggests that 14.7% of an increase in DE intake above maintenance apparently passed through the glucose pool. At maintenance (2.05 MJ DE/d) 37% of the DE intake passed through the glucose pool.

Figure 4 shows the relationship between glucose entry rate (g/kg^{0.75}/d) and DE intake (MJ/kg^{0.75}/d) in lambs (this study), mature sheep (Judson and Leng 1968; Lindsay 1970), calves (Young et al 1974), steers (Yost et al 1977;



Herbein et al 1978; Smith et al 1979) and lactating cows (Wiltrout and Satter 1972; Clark et al 1977). It is evident from this relationship that estimates of glucose entry rate may possibly be used to predict DE intake in ruminants under different dietary and production conditions.

Of particular interest is that, in ruminants on certain diets, considerable amounts of dietary carbohydrates may escape rumen fermentation and pass intact to the small intestines where they are digested to glucose (see review by Armstrong and Smithard 1979). Glucose is readily absorbed from the small intestines (Ørskov et al 1971) and would contribute to the total DE available to the animal, although the absorbed glucose may reduce gluconeogenesis (Annison and White 1961; West and Passey 1967). It may be necessary, there-

fore, to re-examine the relationship between glucose entry rate and DE intake and liveweight gain in ruminants given diets in which a considerable portion of the dietary carbohydrate is digested in the intestines before attempting to use any relationship for prediction.

Acknowledgements

We would like to thank the Australian Wool Corporation and the Australian Meat Research Committee for financial support for this project. We thank Mr F Ball, Mr V Scollen and Mr J Hiscox for valuable technical assistance.

References

- Annison E F & White R G 1961 Metabolic interrelations of glucose and lactate in sheep. *Biochemistry Journal* 88:243
- Armstrong D G & Smithard R R 1979 The fate of carbohydrates in the small and large intestine of the ruminant. *Proceedings of Nutrition Society* 38:283
- Bruno G A & Christian J E 1961 Correlation for quenching associated with liquid scintillation counting. *Analytical Chemistry* 33:650
- Clark J H, Spiers H R, Derrig R G & Bennick M R 1977 Milk production, nitrogen utilisation and glucose synthesis in lactating cows infused post-ruminally with sodium caseinate and glucose. *Journal of Nutrition* 107:631-644
- Ferguson K A, Hemsley J A & Reis P J 1967 Nutrition and wool growth. The effect of protecting dietary protein from microbial degradation in the rumen. *Australian Journal of Science* 30:215
- Frings C S, Ratliff C R & Dunn R T 1970 Automated determination of glucose in serum or plasma by a direct O-toluidene procedure. *Clinical Chemistry* 16:282
- Herbein J H, van Maanen R W, McGilliard A D & Young J W 1978 Rumen propionate and blood glucose kinetics in growing cattle fed isoenergetic diets. *Journal of Nutrition* 108:994-1001
- Jones G B 1965 Determination of the specific activity of labelled blood glucose by liquid scintillation using glucose pentaacetate. *Analytical Biochemistry* 12:249
- Judson G J & Leng R A 1968 Effect of diet on glucose synthesis in sheep. *Proceedings of Australian Society for Animal Production* 7:354
- Judson G J & Leng R A 1972 Estimation of the total entry rate and resynthesis of glucose in sheep using glucose uniformly labelled with ^{14}C and variously labelled with ^3H . *Australian Journal of Biological Science* 25:1313
- Kempton T J, Nolan J V & Leng R A 1977 Principles for the use of NPN and bypass proteins in the diets of ruminants. *World Animal Review* 22:2-10
- Kempton T J, Nolan J V & Leng R A 1979 Protein nutrition of growing lambs 2 Effect on nitrogen digestion of supplementing a low-protein-cellulosic-diet with either urea, casein or formaldehyde-treated-casein. *British Journal of Nutrition* 42:303
- Kotb A R & Luckey T D 1972 Markers in nutrition. *Nutrition Abstracts and Reviews* 42:814
- Leng R A 1970 Glucose synthesis in ruminants. *Advances in Veterinary Science and Comparative Medicine* 14:209
- Lindsay D B 1970 Carbohydrate metabolism in the ruminant In: *Digestion and Metabolism in the Ruminant* p 438 (Editor: A T Phillipson) Oriel Press: Newcastle - upon - Tyne
- Ørskov E R, Fraser C, McDonald I & Smart R 1974 Digestion of concentrates in sheep 5 The effect of adding fish meal and urea together to cereal diets on protein digestion and utilisation by young sheep. *British Journal of Nutrition* 31:89
- Ørskov E R, Mayes R W & Penn A 1971 The capacity for removal of glucose from the small intestines by mature sheep. *Proceedings of Nutrition Society* 30:44A
- Raja R H, Moss R, Murray R M & Leng R A 1981 Growth and glucose metabolism in young calves grazing tropical pasture - the effects of supplementation with maize or cottonseed cake. *Tropical Animal Production* 6:105-115

- Smith G H, Kempton T J & Leng R A 1979 Glucose metabolism and growth in cattle given molasses urea based diets. *Tropical Animal Production* 4:138-144
- Snedecor G W & Cochran W G 1968 *Statistical methods* (6th edition) Iowa State Press: Ames Iowa pp 258-296
- Stevenson A E & De Langen H 1960 Measurement of feed intake by grazing cattle and sheep VII Modified wet digestion method for determination of chromic oxide in faeces. *New Zealand Journal of Agricultural Research* 3:314
- West C E & Passey R F 1967. Effect of glucose load and of insulin on the metabolism of glucose and palmitate in sheep. *Biochemistry Journal* 102:58
- Wiltout D W & Satter L D 1972 Contribution of propionate to glucose synthesis in the lactating and nonlactating cow. *Journal of Dairy Science* 55:307
- Yost W M, Young J W, Schmidt S P & McGilliard A D 1977 Gluconeogenesis in ruminants: Propionic acid production from a high-grain diet fed to cattle. *Journal of Nutrition* 107:2036-2043
- Young J W, Trott D R, Berger P J, Schmidt S P & Smith J A 1974 Gluconeogenesis in ruminants: Glucose kinetic parameters in calves under standardised conditions. *Journal of Nutrition* 104:1049-1055

Received 4 October 1983