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Original article

The influence of processing corn grain on glucose metabolism in ewes

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Summary — Glucose metabolism was studied in ewes fed 800 g chopped alfalfa hay (H) or 400 g alfalfa hay and 400 g corn grain given in whole (HWC), ground (HGC) or extruded (HEC) form. Daily intake of metabolisable energy and crude protein were: 5.8 MJ, 109 g; 9.0 MJ, 84 g; 9.5 MJ, 84 g and 8.5 MJ, 88 g in H, HWC, HGC and HEC, respectively. *In situ* ruminal degradability ranked whole, ground, and extruded corn in ascending order. Ruminal pH and concentration of acetic acid were lower and of propionic acid higher ($P < 0.05$) in HEC than in HGC and HWC groups. Plasma level of glucose ($P < 0.10$), insulin ($P < 0.05$), and the ratio of insulin to non-esterified fatty acids (NEFA) ($P < 0.01$) were higher in HEC than in other groups. Glucose irreversible loss (GILR) and entry rate (GER), recycling (GRec) and reentry (GRee) were determined by double isotope dilution procedure. GER, but not GILR, was higher in HWC than in H and HGC (6.98 mg/min/kg $BW^{0.75}$ *vs* 3.97 and 4.24 mg/min/kg $BW^{0.75}$, respectively; $P < 0.05$) and than in HEC (4.84 mg/min/kg $BW^{0.75}$; $P < 0.10$). GRec and GRee were higher in HWC than in the other treatments. Grinding or extruding the grain increased ruminal degradability and decreased glucose entry rate.

glucose metabolism / sheep / starch utilisation / corn grain

Résumé — Influence du traitement du grain de maïs sur le métabolisme du glucose chez la brebis. *Le métabolisme du glucose a été étudié chez des brebis recevant 800 g de foin de luzerne haché (H) ou 400 g du même foin et 400 g de grain de maïs distribué entier (HWC), broyé (HBC) ou extrudé (HEC). L'ingestion journalière d'EM et de MAT a été : 5,8 MJ, 109 g; 9,0 MJ, 84 g; 9,5 MJ, 84 g; 8,5 MJ, 88 g pour les rations H, HWC, HGC et HEC, respectivement. Le degré de dégradation ruminale* in situ *du maïs a été : entier < broyé < extrudé. Le pH du contenu ruminal et la teneur en acide acétique étaient inférieurs et la teneur en acide propionique supérieure, chez les brebis HEC, par rapport aux brebis HWC et HGC. La concentration de glucose (P < 0,10), d'insuline (P < 0,05), et le rapport insuline/acides gras non esterifiés (P < 0,01) étaient les plus élevés dans le plasma des brebis HEC. Les taux d'entrée (GER), d'utilisation (GILR), de recyclage (GRec) et de ré-entrée (GRee) du glucose ont été mesurés après injection de 2 isotopes. le GER, mais non le GILR du*

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groupe HWC, a été supérieur à celui des groupes H et HGC (6,98, 3,97 et 4,24 mg.min^{-1}.kg^{-1}.PV$^{-0,75}$, P < 0,05) et HEC (4,84 mg.min^{-1}.kg^{-1}.PV$^{-0,75}$, P < 0,10). Les brebis HWC ont recyclé plus de glucose que celles des autres groupes. Le broyage et l'extrusion des grains augmentent la dégradation ruminale mais diminuent le taux d'entrée du glucose.

métabolisme du glucose / mouton / utilisation de l'amidon / grain de maïs

INTRODUCTION

The importance of glucose in physiological processes associated with increasing small ruminant productivity has been gaining recognition in recent years. In addition to its being a precursor of 85% of the lactose exported in milk (Annison and Linzell, 1964), glucose has been shown to be involved in determining ovulation rate (Teleni *et al,* 1989). Glucose is the main substrate for provision of energy to the uterus and fetuses (Wolff and Meschia, 1982). Impairment of glucose supply during late pregnancy may restrict growth of fetuses – mainly from multiple litters – and markedly decrease colostrum production (Barry and Manley, 1985). Birth weight (Goot *et al,* 1984; Hich *et al,* 1985) and colostrum supply to the newborn (Campbell *et al,* 1977) are key factors in lamb survival and in profitability of sheep farming.

Most studies carried out with steers (Herbein *et al,* 1978), dairy cows (Wieghart *et al,* 1986) and sheep (Judson *et al,* 1968; Ulyatt *et al,* 1970) have shown that the rate of glucose production in ruminants is highly dependent on energy intake but less dependent on the nature of the diet, *eg,* source of grain or roughage-to-concentrate ratio. However, the above-mentioned results were obtained under conditions in which very little or no glucose escaped fermentation in the rumen, and the main source of glucose was gluconeogenesis.

Nevertheless, Evans and Buchanan-Smith (1975) reported that glucose production was similar in rams fed a low roughage – high corn grain ration at maintenance level or high roughage – low corn grain ration at 2-maintenance level. In addition, when glucose was infused abomasally to ewes, glucose production was higher than theoretically predicted from energy intake (Barry and Manley, 1985).

A practical way to supply glucose post-ruminally to sheep may be to feed the animals whole corn grain, which is only partially degraded in the rumen (Ørskov, 1986). Glucose produced from digestion of starch in the intestine and entering the bloodstream directly accounts for as much as 61% of the glucose utilised by sheep fed a diet containing 78% ground maize. However, endogenous glucose production is reduced when exogenous glucose absorption is increased (Janes *et al,* 1985). Therefore, there is no clear evidence whether decreasing ruminal degradability of corn grain starch may increase glucose production. Moreover, the effect of grinding or heat processing of corn grain on glucose metabolism in sheep fed mixed diets has not been documented to the best of our knowledge.

The purpose of the present study was to: i), evaluate glucose metabolism in sheep fed diets containing corn grain differing in ruminal degradability of starch; and ii), clarify the metabolic conditions necessary to increase glucose production by sheep.

MATERIALS AND METHODS

Animals and diets

The experiment was conducted with Finn x Awassi and Finn x German Mutton Merino ewes. The sheep were kept in individual metabolic cages which allowed separation of feces and urine. The sheep were given diets containing alfalfa hay (151 g/kg crude protein) chopped to a mean length of 18 mm (H) or 1:1 mixtures of hay and corn grain fed as whole (HWC), ground (HGC), or extruded (200 °C, 22 s, 70 bars; HEC) feed. The ewes were fed 2 meals of 400 g each, at 06.00 and 18.00 h. Vitaminized licking blocks (Koffolk, Tel Aviv, Israel) and water were available to the animals at all times.

Ruminal degradability of feedstuffs was established by the Dacron bags procedure, using 2 rumen-fistulated rams as described by Arieli *et al* (1989). Whole corn was hammer-cracked and brought to the same particle size (2–3 mm) as found in the rumen of intact slaughtered animals fed whole corn grain prior to slaughter (S Gur-Arie, personal communication). The particle size of ground and extruded corn was less than 1.5 mm. Incubation period in the rumen was 3, 6, 12, 24, 36 and 48 h. All bags were rinsed with tap water after removal from the rumen and dried at 55 °C for 48 h. Zero-time degradability was assessed after rinsing samples with tap water. Starch analysis of the feeds and ruminal contents was as described by Nitsan *et al* (1990).

Data were best-fitted to an equation: $p = a + b\ (1 - e^{-ct})$, where a = soluble fraction, b = rumen-degradable fraction and c is the rate parameter, using an interative linearization procedure to minimize residuals (Plotit package). Effective degradability (d) was calculated as a function of the rate of rumen outflow (k) as follows:

$$d = a + \frac{b \times c}{(c + k)}$$

Gross energy content of the feedstuffs was determined by Ballistic Bomb Calorimetry (Gallenkamp, Germany). Digestibility of the diets was established by *in vivo* trials lasting 7 days ($n = 5$ for each diet), following a 10-day adaptation period. Rumen liquor was withdrawn by tube, 3 h after the morning meal; pH was immediately recorded, aliquots were centrifuged, and supernatants were frozen at –20 °C for further analysis of VFA using gas liquid chromatography (Erwin *et al*, 1961).

Glucose kinetics studies

Indwelling cannulas (BARD-I-CATH, 14 G, 280 mm) were inserted in the 2 jugular veins and kept patent by flushing every fortnight with heparinized saline (300 IU/ml). Glucose kinetic experiments were started at least 7 days after insertion of the cannulas. Blood sampling caused only minimal disturbance to the sheep and allowed normal eating behaviour.

Blood was sampled from each sheep (n = 20) just before the morning meal *via* one of the permanent cannulas for insulin, non-esterified fatty acids (NEFA), and 3-β-hydroxybutyrate determination. Three h after the morning meal, doses of 150–200 μCi of D-[U-^{14}C]-glucose and D-[2-^{3}H]-glucose (American Radiolabeled Chemicals, St Louis, MO, USA) in 10 cm^3 saline were heated to body temperature and injected into the animals *via* one of the cannulas. Twenty-eight blood samples were collected from the second cannula at different intervals until 470 min post-dosing, according to the following sequence: 7 samples were taken every 3 min, then 4 samples every 10 min, followed by 8 samples every 15 min and finally 9 samples every 30 min. The samples were kept on ice until they were centrifuged (3 000 rpm, 10 min), within a few minutes. Non-esterified fatty acids (NEFA) in plasma were analysed according to a modification of the Dole method by Barash and Akov (1987) and 3-β-hydroxybutyrate (3-β-OHB) according to McMurray (1984). Insulin was determined by radioimmunoassay using a kit for human insulin (International CIS, Gif-sur-Yvette, France).

After deproteinization of plasma samples (Somogyi, 1954), separation of glucose from non-glucose radioactive compounds was performed by elution through a Dowex-8 (Sigma) resin ion-exchanger filled with glycine 0.1 M buffer at pH 10.2, as described by Hertz *et al* (1989). Since label from ^{3}H-glucose is lost only to body water (Wolfe, 1984), water was evaporated from eluates by heating the plasma samples in an air-

forced oven at 70 °C. After rehydration, the samples were dissolved in Triton–toluene scintillation liquid as described by Hertz *et al* (1989) and radioactivity was counted in a β-counter (Beckman 7800), using a computerised program to subtract the mutual interferences of the 2 radioisotopes in both of the counting channels. The recovery of glucose from the columns was calculated to be 100%, while negligible elution of ^{14}C- and ^{3}H-labelled pyruvate (0.039 and 0.0012%, respectively) was observed. Plasma glucose concentration was determined using a Beckman Glucose Analyzer 2 (Fullerton, CA, USA).

Calculations and statistical analysis

Specific activity (SA_t, the ratio of radioactive to non-radioactive glucose at time t post-injection, dpm/mg) was calculated for each sample of plasma. The ratio SA_t/dose *vs* t (min) served as the basis for the kinetic studies. Plots of Ln (SA/dose) were drawn and were fitted to bi-exponential curves using the "peeling off" procedure. Linear regressions were calculated and processed for each compartment, while minimizing the standard deviation of A_i and M_i estimates, as described by Shipley and Clark (1972).

$$SA_t = \sum_{i=1}^{n} A_i e^{-M_i t}$$

Where A_i = mass of compartment i (mg); M_i = slope of exponential for compartment i (mg/min); n = number of compartments of glucose pool.

Then the mass of glucose pool (Q, mg) was calculated as the ratio between the dose injected P (dpm) and the sum of glucose masses. The relative size of each compartment (A'_i, mg) was calculated. Finally, glucose-irreversible loss rate ($GILR$, mg/min), glucose entry rate (GER, mg/min), glucose reformation from compounds originating from labelled glucose, *ie*, glucose recycling ($GRec$, mg/mg, according to Katz *et al*, 1974), glucose reentry ($GRee$, mg/mg, according to Kronfeld, 1975) are quantitated as follows:

$$Q = \frac{P}{\sum_{i}^{n} (A_i)}; \quad GILR = \frac{Q}{\sum_{i=1}^{n} \frac{A'_i}{M_i}}; \quad GER = \frac{Q}{\sum_{i=1}^{n} A'_i \cdot M_i}$$

$$GRee = \frac{GER\,(^{3}H) - GIL(^{14}C)}{GER(^{3}H)};$$

$$GRec = \frac{GIL(^{3}H) - GIL(^{14}C)}{GIL(^{3}H)}$$

Statistical analysis

The differences between treatment means were evaluated by one-way analysis of variance (SAS, 1988).

RESULTS

Ruminal degradability of feedstuffs

Grinding or extruding corn grain increased the percentage of dry matter which disappeared at zero time, *ie*, before microbial degradation, from 2% for cracked corn to 6% for ground corn and 10% for extruded corn (fig 1). During incubation in Dacron bags in the rumen, the starch content of extruded corn decreased linearly and quickly up to 24 h and slowly later on. Starch content in ground corn incubates decreased linearly but more slowly than in extruded corn up to 36 h and very quickly between 36 and 48 h, whereas starch content in cracked grain decreased at a very slow and steady rate throughout the whole incubation period. Values of dry matter and starch effective degradability (%) at a ruminal outflow rate of 2%/h were calculated to be 49.3, 61.5; 68.8, 78.3; and 78.9, 91.3 for cracked, ground and extruded corn, respectively. At an outflow rate of 5%/h, the respective figures were 36.8, 49.5; 51.9, 62.5 and 69.8, 82.7.

Energy content of the diets and patterns of ruminal fermentation

The digestibility of organic matter (OMD) was higher in sheep fed hay and corn than

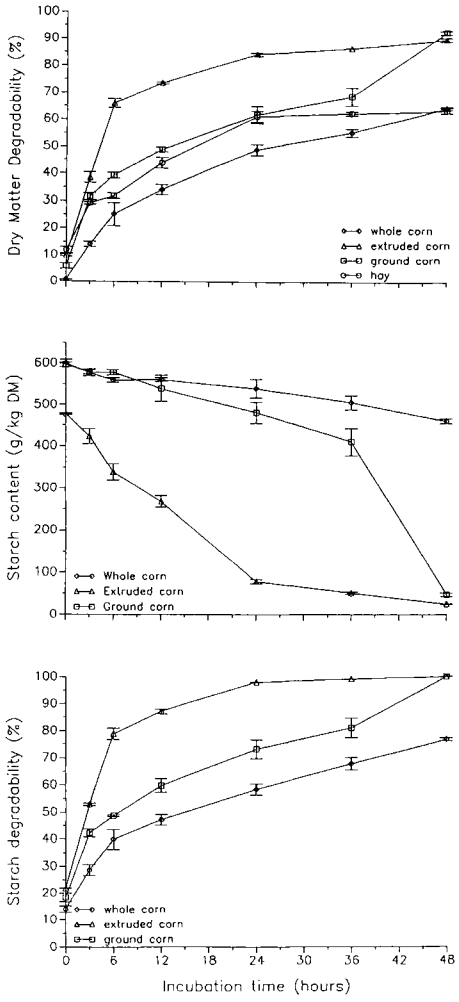

Fig 1. Dry matter degradability (%), starch content (g/kg DM) and degradability (%) of experimental feeds incubated in sheep rumen using Dacron bags *vs* time of incubation (vertical bars indicate standard errors).

hay only. OMD was higher in HGC- than in HEC-fed and intermediate in the HWC-fed sheep (table I). The calculated daily intake of metabolizable energy (MEI) was 5.8, 9.0, 9.5 and 8.5 MJ and that of crude protein 109, 84, 84, 88 g in treatments H, HWC, HGC, HEC, respectively. Ruminal pH was lowest in HEC ($P < 0.05$) and higher in H than in HGC ($P < 0.05$) and HWC (NS). The concentration of total volatile fatty acids (VFA) in rumen liquor and the percentage of butyric acid in VFA were higher in sheep fed hay and grain than in their counterparts fed hay only. The HEC diet reduced the proportion of acetic acid (C2) in rumen VFA, as compared with all other treatments ($P < 0.05$) and increased the proportion of propionic acid (C3), as compared with HGC ($P < 0.05$). Consequently, the ewes fed HEC exhibited a higher glucogenic ratio (C3/C2+C4)) in their rumen liquor than did the other groups.

Biochemical parameters in plasma

The level of NEFA was higher in sheep fed hay only than in sheep fed HEC and HGC diets ($P < 0.05$), while sheep fed HWC were intermediate (table II). Insulin levels were higher in HEC than in H or HGC groups ($P < 0.05$), and intermediate in sheep fed whole grain. Levels of β-OHB did not differ between experimental groups.

Glucose metabolism

Glucose concentration in plasma was found to be very steady over 11 h after meals, and varied by less than 10% in all treatments. Sheep fed HEC had higher plasma glucose concentration than HWC and HGC (table III). Glucose irreversible loss, calculated from ^{14}C curves, did not differ between treatments. Glucose entry rate, calculated from 2-^{3}H curves, was highest in ewes fed HWC, significantly different from H and HGC groups ($P < 0.02$). It tended to be lower in HEC- than in HWC-fed animals ($P < 0.10$). Glucose recycling and reentry were also higher in HWC-fed sheep than in all the other groups ($P < 0.07$ and $P < 0.10$, respectively).

Table I. Organic matter digestibility (OMD, %), ruminal pH, total VFA concentration (VFA, mM/l), VFA composition (% of VFA) and the glucogenic ratio (GR; C3/C2+C4) in ruminal juice of sheep fed the experimental diets (average of 5 sheep, with SE in parentheses).

Treatment	*OMD*	*pH*	*VFA*	*VFA composition*				*GR*
				C2	*C3*	*C4*	*C_i5*	
H	53.5^{c}	7.0^{a}	43.8^{b}	71.4^{a}	20.7^{ab}	6.7^{b}	1.5^{a}	0.265^{b}
	(1.6)	(0.04)	(3.8)	(1.3)	(1.8)	(0.8)	(0.1)	(0.013)
HWC	75.3^{ab}	6.7^{ab}	66.1^{a}	67.1^{a}	19.4^{ab}	12.5^{a}	1.0^{c}	0.249^{b}
	(1.1)	(0.04)	(0.9)	(1.1)	(2.1)	(1.0)	(0.04)	(0.034)
HGC	78.3^{a}	6.4^{b}	60.2^{a}	66.0^{a}	17.3^{b}	15.7^{a}	1.1b^{c}	0.209^{b}
	(0.04)	(0.08)	(3.2)	(0.4)	(0.8)	(1.2)	(0.04)	(0.012)
HEC	71.3^{b}	5.7^{c}	61.2^{a}	57.2^{b}	26.1^{a}	15.2^{a}	1.5^{a}	0.360^{a}
	(0.8)	(0.09)	(2.1)	(1.6)	(1.7)	(0.4)	(0.04)	(0.034)

Within columns, means with a common superscript do not differ significantly ($P < 0.05$).

Table II. Non esterified fatty acids (NEFA, μeq/l), insulin (mU/l), and 3-β-hydroxybutyrate (mg/l) in plasma of sheep fed the experimental diets (mean values with SE for 5 animals per group).

Treatment	*NEFA***		*Insulin**		*3-β-OHB*	
	Mean	*SE*	*Mean*	*SE*	*Mean*	*SE*
H	403^{a}	56	8.1^{b}	1.2	80	4.9
HWC	295^{ab}	37	11.8^{ab}	2.4	100	9.4
HGC	195^{b}	56	8.9^{b}	0.8	72	6.7
HEC	117^{b}	14	16.6^{a}	2.1	74	15.6

Within columns, means with a common superscript do not differ significantly (* $P < 0.05$, ** $P < 0.01$).

DISCUSSION

Relationship between energy intake and glucose metabolism

There is some confusion concerning which of the glucose metabolism parameters is the most relevant to characterize glucose production status in ruminants. Irreversible loss reflects glucose utilisation by tissues and is considered by some authors as the best parameter to describe glucose production (*eg* Herbein *et al,* 1978, McNiven, 1984). The importance of glucose recycling in ruminants was stressed by Kronfeld (1975) and recently by Russell and Young (1990). The latter suggested that

Table III. Plasma glucose concentration (*G*, mg/l), rates of glucose irreversible loss and entry (*GILR* and *GER*, mg/min/kg $BW^{0.75}$), glucose recycling and glucose reentry (*GRec* and *GRee*, g/g) in sheep fed the experimental diets (means with their standard errors for 5 animals per group).

Treatment	G		GIL *(^{14}C)*		GER *(^{3}H)**		GRec		GRee	
	Mean	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*
H	609^{ab}	15.3	2.38	0.57	3.97^{b}	0.92	-0.02^{b}	0.11	0.38^{bc}	0.02
HWC	597^{b}	30.3	2.67	0.48	6.98^{a}	1.02	0.33^{a}	0.11	0.59^{a}	0.03
HGC	570^{b}	15.9	2.90	0.19	4.23^{b}	0.38	0.08^{b}	0.04	0.30^{c}	0.08
HEC	664^{a}	26.5	3.28	0.41	4.84^{ab}	0.87	-0.05^{b}	0.05	0.36^{bc}	0.09
$P<$	0.10		NS		0.05		0.07		0.10	

Whithin columns, means with a common superscript do not differ significantly ($P < 0.05$). * for *GER* $P < 0.02$ between HWC and H or HGC; $P < 0.10$ between HWC and HEC.

glucose recycling is a means of conserving glucose carbon as glucose or in the form of metabolites which are easily transformed to glucose, for example, lactate. Therefore glucose entry rate, *GER*, which includes recycled glucose, has more metabolic significance than glucose irreversible loss rate, *GILR*, particularly in experiments with ewes at maintenance, since their glucose demand is low. In the present study, ewes fed a low-energy diet (H) displayed lower glucose entry rate than ewes given grain in addition to hay. This confirms that glucose metabolism in ruminants is highly dependent on energy intake (Ulyatt *et al,* 1970; Herbein *et al,* 1978; Schmidt and Keith, 1983; Wieghart *et al,* 1986). However, in ewes fed hay and grain, the entry rate of glucose did not rank in the same order as intake of energy. It seems, therefore, that ME intake alone cannot provide an accurate prediction of glucose metabolism in sheep. Diets containing similar amounts of energy may differ in available substrates or induce different hormonal conditions resulting in a wide range of glucose production rates.

Starch degradability, ruminal VFA and glucose metabolism

The mixed diets provided energy and protein which were slightly above maintenance requirements. At this level of energy intake, the rate of outflow from the rumen is approximately 5%/h if long fibre roughage is given (Hadjipanayiotou, 1988) but may be as low as 2% if roughage is chopped (ARC, 1984). Ruminal starch degradability of whole, ground and extruded corn was calculated assuming 2% ruminal outflow per hour. The values were 61.5%, 78.3% and 91.3%, respectively. Many authors agree that total digestibility of corn starch in the gastrointestinal tract of sheep is very close to 100%. Ruminal corn starch digestibility in sheep at maintenance is 70% when grain is given whole (Oke and Loerch, 1989), 80% when given ground (Tucker *et al,* 1968; Beever *et al,* 1970; Janes *et al,* 1985), and above 95% when steam-flaked corn is used (Beever *et al,* 1970). It seems, therefore, that a positive relationship exists between the extent of processing and ruminal digestibility of corn

starch. Values for *in situ* starch degradability in the present study fit *in vivo* data in the literature. Whole, ground and extruded corn are, respectively, representatives of low, medium and high ruminal starch degradability. Thus, the experimental diets seem to provide a useful model for studying the relationship between ruminal starch degradability and glucose metabolism.

The calculated amount of starch reaching the small intestine in the present study was 98, 61 and 27 g/d, in sheep fed whole, ground and extruded corn, respectively. Starch digested in the intestine could account for 18% of glucose entry in sheep fed HEC and approximately 50% in those fed HWC and HGC, in agreement with the data of Janes *et al* (1985) obtained by direct methods.

Propionic acid is known to be utilized efficiently by hepatocytes for gluconeogenesis (Demigné *et al,* 1986; Looney *et al,* 1987). Propionate concentration in the rumen of sheep fed the HEC diet was higher than in the other groups (table I), but their glucose entry rate was lower than in sheep fed the HWC diet. A similar finding was reported earlier by Judson *et al* (1968). A high level of insulin in the plasma of HEC-fed ewes, resulting from large supply of propionate (Istasse and Ørskov, 1984), may provide an explanation for the lower glucose entry rate in this group as compared with the HWC treatment, since insulin is known to have a depressing effect on hepatic gluconeogenesis (Brockman and Laarveld, 1985). The relatively low glucose production in sheep fed HGC seems to be mainly due to the low levels of propionate in the rumen, and possibly to impairment of gluconeogenesis following absorption of large amounts of butyric acid (Aiello *et al,* 1989).

Glucose recycling

Values of 8% or 5% for glucose recycling in non-pregnant sheep have been reported by Judson and Leng (1972) and Wastney *et al* (1983), respectively. Similar values have been found in ewes from H, HGC and HEC treatments. Therefore, the value of 33% recorded for glucose recycling in the HWC group (table III) seems to be particularly high. Glucose recycling represents chemical recycling *via* the phosphogluconate pathway or Cori cycle, while reentry represents the sum of chemical and physical recycling (Russell and Young, 1990). High recycling values found in the animals in the HWC treatment may indicate a delay in distribution of glucose in the extracellular space. Since glucose demand at maintenance is low, glucose availability was in excess in HWC-fed ewes. It is suggested that a glucose conserving mechanism acted by enhanced recycling of excess glucose.

According to MEI, all the groups fed hay and corn grain were expected to have similar glucose entry rate. However, certain metabolic and hormonal conditions seem to be required in addition to MEI in order to maximize this rate. HWC-fed sheep, which had the highest glucose entry rate, had the lowest ruminal starch degradability, relatively low glucogenic level in rumen fluid, and quite low levels of plasma insulin. The 2 other groups consuming hay and corn grain, *ie*, similar MEI, had either low plasma insulin but high ruminal starch degradability (HGC), or high plasma insulin and high ruminal starch degradability (HEC). These metabolic conditions presumably prevented the achievement of a high glucose entry rate.

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