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Whole-body fuel selection in ruminants: nutrient supply and utilization by major tissues

BY ISABELLE ORTIGUES AND ANNE-LAURE VISSEICHE
Laboratoire Croissance et Métabolismes des Herbivores, INRA, Theix, 63122 Saint Genès Champanelle, France

Sélection de substrats énergétiques par le corps entier chez les ruminants: apport et utilisation de nutriments par les principaux tissus

RÉSUMÉ

L'utilisation de l'énergie par l'animal dépend de l'utilisation de l'énergie par les différents tissus corporels. Chez les ruminants, les viscères drainés par le sang portal et le foie représentent respectivement jusqu'à 12 et 2% du poids vif, mais contribuent pour 16–29% et 17–31% aux dépenses énergétiques totales. A l'opposé, la contribution des masses musculaires (35–50% du poids corporel) aux déponses n'est que de 8–16%. L'augmentation de la production de chaleur par l'animal entier, avec le niveau d'alimentation, provient pour 17–56% des viscères drainés par la veine porte, pour 16–44% du foie, et pour 5–7% de la carcasse. Ces incréments varient avec la nature du régime alimentaire, et donc, avec le type des nutriments disponibles pour les tissus. Les objectifs de cette revue sont de décrire quantitativement l'influence du niveau d'alimentation et de la composition du régime alimentaire (d'après les teneurs en cellulose brute et en matières azotées totales) sur l'apporten nutriments aux principaux tissus corporels (viscères drainés par le sang portal, foie, et train arrière), et leurs flux nets dans ces tissus. Pour ce travail, nous avons compilé les résultats de la littérature obtenus chez les bovins et ovins en croissance, et chez les brebis adultes, non lactantes et non gestantes, avec des techniques de différences artério–veineuses *in vivo*. Nous avons établi des équations de régression dans la mesure du possible, entre l'énergie métabolisable ingérée, la composition du régime alimentaire et les apports et flux de nutriments. Les nutriments étudiés étaient les principaux acides gras volatils (acétate, propionate, butyrate), le glucose, le lactate, les corps cétoniques, les acides gras libres, l'ammoniaque, l'urée et l'azote-α-aminé. Les résultats obtenus au niveau des tissus sont intégrés, et les conséquences sur l'utilisation de l'énergie par l'animal entier sont discutées.

Whole-body energy utilization by ruminants varies with plane of feeding and diet composition which modulate the amounts of and the balance between digestion endproducts. For example, efficiency of energy utilization is generally low (about 0·4) with forage diets for which the percentage of energy absorbed as volatile fatty acids averages 66 (33 acetate, 14 propionate and 19 *n*-butyrate) and where amino acids, long-chain fatty acids and glucose account for 22, 8 and 4 respectively. By contrast, efficiencies are higher with maize-based concentrate diets (about 0·5) for which the

corresponding percentages change to 50 (19, 18 and 13), 24, 10 and 16 (Institut National de la Recherche Agronomique, 1978). These nutrients are absorbed and used by body tissues which have specific requirements for energy (Ortigues & Doreau, 1995) and nutrients (Forbes & France, 1993). In ruminants, the portal-drained viscera (PDV), the liver and muscles represent 5–11, 1–2·5 and 35–50% body weight respectively but account for 16–29, 17–31 and about 16% of whole-body energy expenditure respectively (Ortigues, 1991).

The main objective of the present review is to establish, using published work based on *in vivo* arterio–venous techniques, predictive quantitative relationships that describe the influence of changes in the level of intake and diet composition, evaluated by the crude fibre (CF) and crude protein (N × 6·25; CP) contents, on energy requirements of the major body tissue compartments and on partition of net nutrient use by these tissues. The secondary objective is to relate these changes to those of whole-animal energy metabolism. A better understanding of nutrient use by tissues should help to identify means of improving the efficiency of energy utilization for a given animal production system.

DESCRIPTION OF DATA

The present work was based on data from growing cattle and sheep; these data did not show any clear quantitative differences when expressed on a metabolic body weight ($kg^{0·75}$) basis and they had similar variability. Data were collected from a total of eighty-six publications (52% cattle), describing 164 different nutritional situations (57% cattle) in growing cattle (weight ranging from 107 to 467·5 kg) as well as in growing or adult sheep (25·1–73·8 kg; 23·6% growing lambs). Cattle were fed between 314 and 1210 kJ metabolizable energy (ME)/d per $kg^{0·75}$, with 90% of the data evenly spread across the above maintenance feeding levels. Cattle data were evenly spread across all CF levels. Sheep were fed between 184 and 996 kJ ME/d per $kg^{0·75}$ but most (78%) of the adult wethers and ewes were fed below 481 kJ ME/d per $kg^{0·75}$. The inclusion of data from mature sheep was justified by the fact that they were representative of near or below maintenance conditions. The majority of sheep received forage diets (62% of the ovine diets contained at least 300 g CF/kg). The CP content for 74% of the cattle and sheep was evenly spaced between 100 and 200 g/kg. When forage diets were used, they were mostly based on lucerne (*Medicago sativa*) hay (59%), and to a lower extent on grass hays (32%) or silages (9%). With concentrate diets, the main ingredient (96% of those diets) was maize. Generally, high levels of feeding (>837 kJ ME/d per $kg^{0·75}$) were achieved with high-concentrate diets, such that the metabolizable energy intake (MEI) and CF were significantly and negatively correlated (r −0·47). A slight positive correlation (r 0·33) was also noted between CF and CP since high-forage diets were generally based on protein-rich legume hays. No correlation existed between MEI and CP levels. It should be noted that data obtained on fasting animals were not included in the data-set.

Substrates considered were acetate, propionate, *n*-butyrate, glucose, L-lactate, non-esterified fatty acids (NEFA), β-hydroxybutyrate as well as α-NH_2-N, urea-N and NH_3-N. The last two metabolites were included as they incur specific energy requirements at the hepatic level. Other substrates, especially lipids, were not considered because of insufficient data. O_2 was also included. Data related to PDV and liver were

analysed by multiple linear regressions with MEI, CF and CP levels as the independent variables. No multiple-regression analysis could be established for the hindquarters except for blood flows because of insufficient data. Interpretation of results was based on correlation coefficients and slopes for each independent variable which were tested using the Student's *t* test. Conclusions were modulated by the confounding effect that existed between high MEI and maize-based concentrate diets, as well as between high CF levels and lucerne diets. Since the range of MEI data was wider than that of CF, it is likely that some of the CF effects were attributed to feeding level.

Detailed description of the calculated regression equations is available from the author. The present paper discusses only the effects which have been found to be significant as well as some of the major points raised by the data. For the purpose of illustrating some of the effects predicted by the regressions, two levels of MEI (481 and 962 kJ/d per $kg^{0.75}$), two levels of dietary CF (100 and 350 g/kg) and of dietary CP (100 and 150 g/kg) are considered.

EFFECT OF FEEDING LEVEL

Nutrient supply to the portal-drained viscera

Because of the anatomical position of PDV, metabolism of these tissues is sustained by the supply of both endproducts of digestion and arterial-blood metabolites, as shown for acetate (Bergman & Wolff, 1971; Seal & Reynolds, 1993), glucose (Piccioli Cappelli *et al.* 1993) and amino acids (MacRae *et al.* 1993). Of the total endogenous plus dietary (endproducts of digestion, assimilated to MEI) energy supply to PDV, 83–87% is of endogenous origin.

Feeding level generally alters the amount but not the proportions of the endproducts of digestion, except in the case of maize-based diets where, at high intakes, larger proportions of maize starch escape rumen fermentation and are absorbed as glucose by the small intestine (Ortigues & Doreau, 1995). On the other hand, supply of arterial-blood metabolites increases with intake, mainly as a result of a rise in portal blood flow (Table 1, equation 1), as already widely documented (Ortigues, 1991). The predicted arterial propionate and glucose levels were higher and NEFA concentrations were lower at the higher intake (Fig. 1(a)). The first two predictions are probably more indicative of increased dietary proportions of maize-based concentrates than of a direct effect of intake (Reynolds & Huntington, 1988*a*,*b*). Consequently, the higher total energy supply to PDV tissues at the higher intake was associated here with proportionally higher propionate and glucose supply and lower arterial NEFA supply.

Net nutrient fluxes through portal-drained viscera

Generally, net absorption across PDV was higher at the higher intake ($P<0{\cdot}05$) for all nutrients, except glucose, NEFA and urea (Fig. 2(a)), in agreement with Reynolds *et al.* (1991, 1992*b*, 1993*a*,*b*) and Burrin *et al.* (1991). These effects were mainly associated with changes in blood flows.

The net absorption of glucose predicted at low MEI–low CF content was changed to a net uptake by the PDV at the higher intake (Fig. 2(a)); similarly there was net glucose uptake by the PDV at the high-CF-diet intake, probably associated with higher glucose requirements of an increase in gut mass (Reynolds *et al.* 1991, 1992*a*). Limited

Table 1. *Coefficients of the multiple linear regressions established to predict changes in portal-drained viscera (PDV), liver and hindquarters blood flows, oxygen consumption and oxygen extraction rates with metabolizable energy intake (MEI; MJ/d per $kg^{0.75}$), dietary crude fibre (CF; g/kg) and dietary crude protein (CP; g/kg) levels, and correlation coefficients and number of observations used to calculate the prediction equations*

(Values are means with their standard errors; regression equation: variable = a MEI + b CF + c CP + d)

Variable	Equation no.	MEI		CF		CP		Intercept		r	n
		a	SE	b	SE	c	SE	d	SE		
Blood flows (litres/h per $kg^{0.75}$)											
Portal vein	1	7·37**	0·57	0·007	0·013	–0·043	0·043	3·33	1·37	0·81**	111
Hepatic vein	2	6·43**	0·86	0·019	0·018	–0·078	0·066	5·45	1·50	0·73**	63
Hepatic artery	3	0·15	0·38	0·001	0·008	–0·016	0·032	1·51	0·66	0·10	62
Hindquarters	4	0·83	1·47	–0·048	0·041	0·152*	0·072	0·93	1·29	0·67**	23
O_2 consumption (mmol O_2/h per $kg^{0.75}$)											
PDV	5	12·43**	1·26	0·080	0·027	0·049	0·081	0·66	1·87	0·85**	47
Liver	6	11·09**	1·93	–0·023	0·054	–0·039	0·162	4·58	2·44	0·78**	32
Hindquarters	7	2·58	2·25	–0·024	0·078	0·324*	0·151	–0·50	1·95	0·70*	19
O_2 extraction rate (%)											
PDV	8	4·65*	1·92	0·079	0·041	0·112	0·166	18·70	2·33	0·50*	31
Liver	9	9·61**	3·30	–0·154	0·095	0·021	0·401	21·98	3·76	0·67**	25

*P<0·05; **P<0·01.

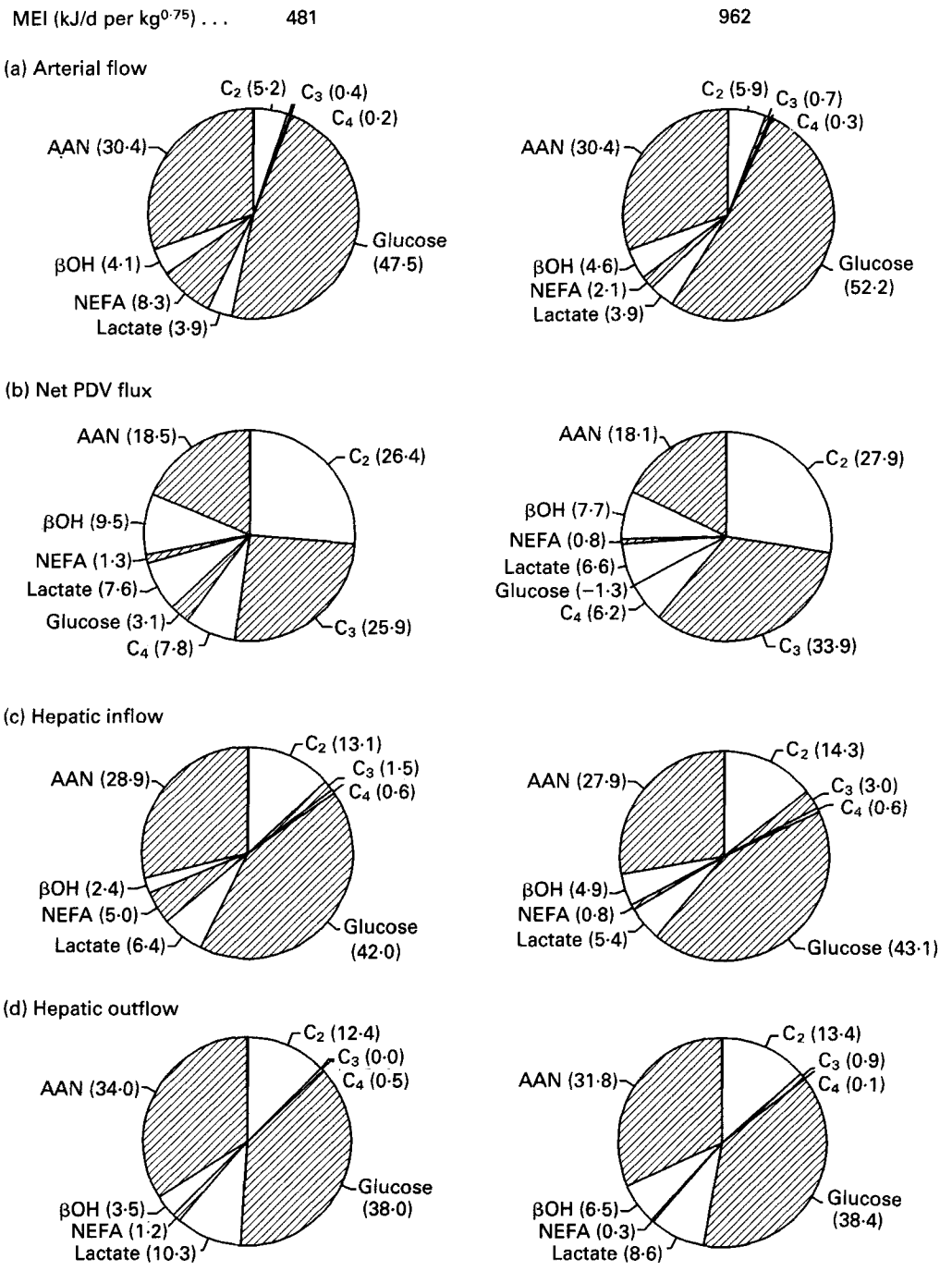

Fig. 1. Effects of metabolizable energy intake (MEI at 481 and 962 kJ/d per kg$^{0.75}$) at constant dietary crude fibre (100 g/kg) and crude protein (nitrogen × 6·25; 100 g/kg) contents on the predicted energetic contributions (%; values shown in parentheses) of acetate (C_2), propionate (C_3), *n*-butyrate (C_4), glucose, lactate, non-esterified fatty acids (NEFA), β-hydroxybutyrate (βOH), urea-N, NH_3-N and α-amino-N (AAN) to (a) arterial flow, (b) net portal-drained viscera (PDV) flux, (c) hepatic inflow and (d) outflow.

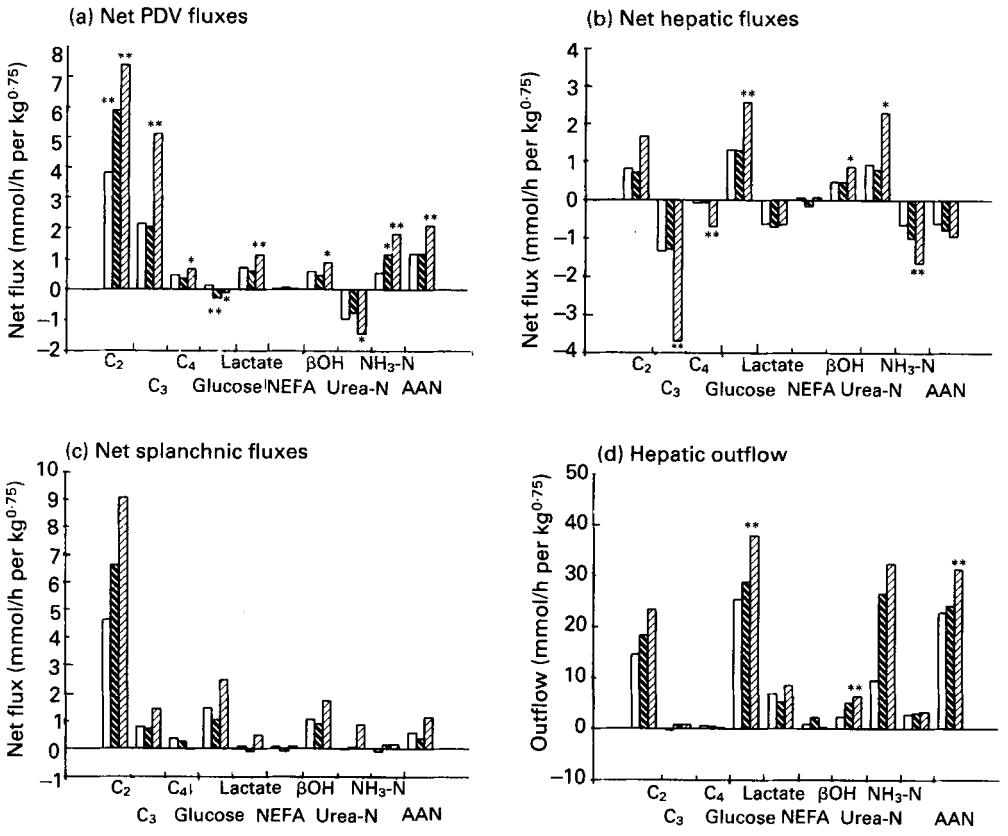

Fig. 2. Predicted effects of metabolizable energy intake (MEI; 481 and 962 kJ/d per $kg^{0.75}$) and dietary crude fibre contents (CF; 100 *v.* 350 g/kg) at constant dietary crude protein level (nitrogen × 6·25; CP; 100 g/kg) on (a) net portal-drained viscera (PDV), (b) hepatic, and (c) splanchnic nutrient fluxes, and (d) flows of nutrients leaving the liver. Values were calculated directly from prediction equations except for net splanchnic fluxes which are the sum of the net portal and hepatic fluxes. Nutrients considered are acetate (C_2), propionate (C_3), *n*-butyrate (C_4), glucose, lactate, non-esterified fatty acids (NEFA), β-hydroxybutyrate (βOH), urea-N, NH_3-N and α-amino-N (AAN). The effects of changes in MEI and CF were significant: $^*P<0.05$, $^{**}P<0.01$. (□), MEI 481 kJ/d per $kg^{0.75}$, CF 100 g/kg, CP 100 g/kg; (▨), MEI 481 kJ/d per $kg^{0.75}$, CF 350 g/kg, CP 100 g/kg; (▨), MEI 962 kJ/d per $kg^{0.75}$, CF 100 g/kg, CP 100 g/kg. For details of equations, see Table 1.

interactions may exist with the use of maize-based diets at high MEI since gut glucose uptake responds positively to increased arterial glucose (Balcells *et al.* 1992), but this may be limited in its extent (Janes *et al.* 1985). The effect of increased glucose supply to the gut would predominate here over that of increased propionate supply since intra-ruminal propionate infusions lower gut glucose uptake (Seal & Parker, 1992).

Of interest is the quantitative importance of net NH_3-N absorption across the PDV (Fig. 2(a)) which represented on average 53 (range 31–65)% of net NH_3 plus α-NH_2-N absorption; this proportion was not altered by intake. An even wider range had been noted by Huntington (1986). The improved net PDV α-NH_2-N absorption at the higher MEI intake might be associated with higher total dietary and microbial protein flow to the duodenum and with the increased net PDV propionate absorption. Indeed, the availability of rumen propionate, at constant dietary and microbial N absorption from

the digestive tract (Seal *et al.* 1993*a*), enhances the net PDV release of free amino acids (Seal & Parker, 1991) probably by sparing gut-tissue amino acids from breakdown.

Of the major contributors to energy released in portal vein (Fig. 1(b)) only the proportion of energy absorbed as propionate was notably higher at the high intake (34 *v.* 26%). The molar proportion of acetate absorbed across the PDV was lower at the high intake (55 *v.* 65%) whereas that of propionate was higher (39 *v.* 28%); butyrate did not change. This was also noted as an effect of the level of intake by Reynolds *et al.* (1993*a*,*b*) using both forage and concentrate diets, suggesting that gut requirements for acetate increase with intake. We may have overestimated this effect since increasing plane of feeding generally corresponds to a switch from a low-concentrate diet to a high-concentrate diet (Gross *et al.* 1990).

Assuming that all substrates oxidized are of dietary origin, we predict that 79–84% of MEI would be directed to the liver with no clear effect of intake on this proportion.

Nutrient supply to the liver

Of the total energy supply to the liver, net portal absorption accounted for only 7–11%, with the higher contribution noted at high intake. Consequently changes in the availability of absorbed endproducts of digestion were highly buffered by the arterial blood metabolite supply. It should first be mentioned that hepatic venous blood flows increased significantly with intake (Table 1, equation 2), whereas hepatic arterial blood flows did not seem to be affected (Table 1, equation 3), probably because the methodology used (*p*-aminohippuric acid) leads to a wide scatter of data. Over all, results suggested that increased intake resulted in a significantly higher supply of most metabolites to the liver ($P<0{\cdot}05$), except for lactate, NEFA and urea-N.

Because of the large contribution of arterial blood, glucose was the predominant contributor to the energy supply to the liver (42%), followed by α-NH_2-N (29%; Fig. 1(c)). Generally, the contributions of propionate, glucose and β-hydroxybutyrate slightly increased with high intake while that of NEFA decreased.

Net nutrient fluxes through the liver

Changes in hepatic metabolism depended on the metabolite considered (Fig. 2(b)). Net hepatic production of acetate would always be predicted, masking simultaneous uptake and release (Seal & Reynolds, 1993); it was not significantly increased with intake. On the other hand, butyrate uptake and net β-hydroxybutyrate production, to which butyrate contributes for 26–48% (Seal & Reynolds, 1993), significantly increased with intake ($P<0{\cdot}05$).

Net hepatic glucose production was enhanced ($P<0{\cdot}01$) at elevated planes of feeding probably as a consequence of higher availability and uptake of precursors such as propionate ($P<0{\cdot}01$) and α-NH_2-N (NS). This is consistent with the high hepatic extraction rate of propionate (85–100% of net PDV absorption; Seal & Reynolds, 1993) and with the fact that propionate availability regulates gluconeogenesis from other precursors (Brockman, 1993). Here again a bias may exist due to the usual association of higher intakes with high-concentrate diets since the contribution of propionate to hepatic gluconeogenesis was found to decrease with intake of forage diets but to increase with concentrate diets (Reynolds *et al.* 1991, 1992*b*).

Urea-N production was higher at the higher intakes ($P<0{\cdot}01$), in parallel with increased NH_3-N ($P<0{\cdot}01$) and α-NH_2-N (NS) uptake. Liver NH_3-N removal generally balanced net PDV NH_3-N absorption (van der Walt, 1993), accounting, on average, for 76% of calculated liver urea release whereas α-NH_2-N accounted for a further 46%. Slightly lower or similar estimates were obtained by Reynolds *et al.* (1991). Rates of protein turnover in liver are extremely high. Protein degradation rates seem to be lower at high intakes (Lobley *et al.* 1994), but there is no clear effect on the contribution of α-NH_2-N to urea-N release. Generally a high proportion of the α-NH_2-N released by PDV is taken up by liver, but, the proportion seems to be lower at the high intakes (56 *v.* 71%), improving the availability of amino acids to peripheral tissues. However, experimental evidence does not clearly support this trend (Burrin *et al.* 1991; Reynolds *et al.* 1991, 1992*b*).

Oxidative metabolism of the liver represented 16–21% of MEI such that only 57–67% of MEI would then be available to peripheral tissues.

Release of nutrients to peripheral tissues

The flows of metabolites leaving the liver (Fig. 2(d)) combine the arterial splanchnic nutrient supply and the net nutrient fluxes through splanchnic tissues (Fig. 2(c)); they were altered by feeding level. Net hepatic release of acetate would be higher at the high intake but its percentage contribution (12–14) to the hepatic energy outflow is relatively unchanged. Except for propionate and butyrate, most other metabolite hepatic outflows were higher at higher intakes, with significant effects being noted for glucose ($P<0{\cdot}01$), β-hydroxybutyrate ($P<0{\cdot}01$) and α-NH_2-N ($P<0{\cdot}01$). Only NEFA flow tended to decrease, but not significantly. Consequently, the balance of the energy metabolites was not greatly modified with intake, apart from an increase in the contribution of β-hydroxybutyrate from 3·5 to 6·5%. The data-set used to predict changes in metabolites leaving the liver was smaller than that available on arterial concentrations and did not show the increases in propionate and glucose arterial concentrations with increasing intake.

Net nutrient fluxes through hindquarters

To examine the effects of nutritional changes on peripheral tissue metabolism, hindquarters data were collected. There were, however, too few data to establish regression equations. Only metabolite supply to hindquarters can be discussed because it involves blood flows and arterial metabolite concentrations. Blood flow to hindquarters appeared to be statistically unaffected by intake (Table 1, equation 4), even though increasing evidence suggests a rise with intake (for review, see Ortigues & Durand, 1995). Consequently, changes in nutrient supply here would arise mostly from metabolite arterial concentrations. Increases in glucose supply and, to a much smaller extent, propionate supply were predicted at the high intake as well as a decrease in NEFA supply (Fig. 1(a)). These predictions suggest that the possibility of increasing nutrient supply to hindquarters by altering the plane of feeding is limited. This point would need to be widely tested experimentally using precise methodologies.

Tissue and whole-animal energy expenditure

PDV O_2 consumption increased with intake (Table 1, equation 5). The heat increment of PDV, calculated using the McLean (1986) coefficient, amounted to 137 (SE 13·9) J/d per $kg^{0·75}$ for each increment of 1 kJ MEI/d per $kg^{0·75}$, which was slightly higher than that calculated by Seal & Reynolds (1993). It was related to increases in both blood flows and O_2 extraction ratio (Table 1, equation 8). It is worth noting, however, that this energy expended for oxidative purposes represents only 2–3% of the total energy supplied to PDV.

The rise in energy expenditure of PDV with intake was associated here with a general increase in the net absorption of energy-yielding nutrients. The latter appeared to be generally proportional to the increase in MEI, except for an increase in the proportion of energy absorbed as propionate and a decrease in that of glucose. The higher oxidative requirements appeared to be met from glucose, presumably of systemic origin, and probably acetate. They are known to be associated with changes in gut mass (Ortigues & Doreau, 1995), and stress the need to study the effect of MEI on gut protein metabolism (Lobley *et al.* 1994).

Energy expenditure by liver increased with intake to an extent similar to that of PDV, i.e. by 122 (SE 18·2) J/d per $kg^{0·75}$ for each increment of 1 kJ MEI/d per $kg^{0·75}$ (from equation 6, Table 1), and was partly related to enhanced hepatic O_2 extraction ratios (equation 9, Table 1). It should not be extrapolated to lower intakes than those used here (<184 kJ/d per $kg^{0·75}$) since experimental results suggest that a 3 d fast activates hepatic metabolism leading to higher 'basal' energy expenditure (110 kJ; Eisemann & Nienaber, 1990; Huntington *et al.* 1990) than that predicted from the intercept of equation 6 (50 kJ; Table 1).

Hepatic O_2 consumption was highly correlated with net hepatic glucose (r 0·81) and net urea-N (r 0·62) production and to a lower extent with α-NH_2-N uptake (r 0·56). Consequently, level of feeding seemed primarily to enhance the hepatic metabolic pathways involved in glucose and N metabolism. It is associated also with changes in liver mass (Johnson *et al.* 1990; Ortigues & Doreau, 1995).

In the hindquarters, energy expenditure appeared to remain unaltered with feeding level (Table 1, equation 7). Available experimental evidence reviewed by Ortigues & Durand (1995) generally showed no influence of feeding level on O_2 consumption in the hindquarters; however, changes in the posture or physical activity may introduce a bias in the results.

Consequently, at the whole-animal level it can be calculated for high-concentrate diets having an efficiency of energy utilization for growth and fattening of 0·5 (Institut National de la Recherche Agronomique, 1978) that half the increase in energy expenditure above maintenance would originate from both PDV and liver, with similar contributions from each. The remainder of the heat increment could not be attributed to carcass metabolism (Ortigues & Doreau, 1995) and its origin remains to be elucidated.

EFFECT OF DIETARY CRUDE FIBRE CONTENT

The effects of CF were mostly limited to PDV. Small significant effects were noted in the liver for β-hydroxybutyrate and NEFA. However, the latter did not appear consistently at all levels and, therefore, will not be discussed.

Nutrient supply and net fluxes through portal-drained viscera

First it is noteworthy that CF had no effect on portal blood flow (Table 1, equation 1). Contradictory results were found in the literature (Reynolds & Huntington, 1988*a*; Huntington, 1989; Reynolds *et al.* 1991; Reynolds & Tyrrell, 1991; Seal *et al.* 1992). With forage diets, peristalsis and, hence, smooth muscle contraction work is enhanced by bulk, which could have increased blood flows through the muscular tissues of the gut. However, there were no detectable overall changes probably because mass-specific blood flow of the muscular layers is only 1·7–6·9% that of the highly vascularized epithelium (Ortigues & Doreau, 1995). On the other hand the balance of nutrients available for absorption (acetate, propionate, butyrate and glucose) had no effect on portal blood flows (Huntington *et al.* 1983; Harmon & Avery, 1987; Gross *et al.* 1990; Krehbiel *et al.* 1992).

No significant changes in arterial-blood-metabolite concentrations were predicted with change in CF. There were only tendencies (NS) for acetate and NEFA concentrations to increase. Consequently, most changes noted at the PDV level with change in CF were due to the balance of endproducts of digestion, with predominantly an increase in acetate production (Institut National de la Recherche Agronomique, 1978).

Higher CF content increased the net PDV release of acetate (Fig. 2(a)) which then represented a much larger percentage of the energy absorbed (40 *v.* 26%), at the expense of most nutrients except α-NH_2-N. Net glucose utilization by PDV tissues increased with increased CF as shown *in vitro* in rumen tissues (Harmon, 1986). This is also consistent with a lower glucose availability in forage *v.* maize-based-concentrate diets. Indeed, the net glucose PDV extraction noted with forage diets switched to a net glucose absorption when duodenal starch flow was increased (Janes *et al.* 1985; Seal *et al.* 1993*b*). Thus, it is unlikely that the increased acetate availability would have been sufficient to substantially spare glucose from oxidation (Huntington *et al.* 1983).

High CF significantly increased net appearance of NH_3-N in portal blood, while α-NH_2-N net flux was unaffected as shown experimentally by Reynolds *et al.* (1991). The increase in dietary CF content is associated here with the frequent use of lucerne, with a high CP content. Consequently, at equal MEI, N intake was higher in forage than in concentrate diets. In most diets used, rumen capture of NH_3 by rumen micro-organisms would be primarily limited by ME availability, thus explaining the higher NH_3-N absorption predicted. A significant correlation (r 0·48) between net NH_3-N absorption across PDV and the N:ME intake ratio confirms this point. A direct effect of acetate is unlikely since intraruminally-infused acetate did not modify the net portal appearance of NH_3-N (Huntington *et al.* 1983). The contribution of α-NH_2-N to the net energy absorbed remained unaltered at 18%.

Net nutrient fluxes through the liver

None of the hepatic metabolite uptakes or releases appeared to be influenced by CF (Fig. 2(b)). Flows of nutrients leaving the liver towards peripheral tissues (Fig. 2(d)) were not statistically altered by CF. The increased net PDV absorption of acetate was not sufficient to alter the contribution of acetate to the energy flow leaving the liver. In an experiment designed to predict the effect of dietary hay:concentrate ratio on urea flux in steers, liver output of urea-N was found to be minimal when concentrate was less than

200 g/kg and to increase to a maximum when concentrate was 500 g/kg (Huntington *et al.* 1993). Such an effect was not detected here as there was a large variability associated with urea results.

Nutrient supply to hindquarters

Hindquarters blood flow appeared to be unresponsive to changes in CF with the possible exception of slight changes in arterial concentrations, e.g. the percentage of glucose in the energy supply to the hindquarters decreased from 47 to 42%, while that of NEFA tended to increase from 8 to 14%. Contributions of acetate and α-NH_2-N to this energy supply would remained stable at approximately 6 and 30% respectively.

Tissue and whole-animal energy expenditure

Higher dietary CF content increased O_2 consumption by PDV (Table 1, equation 5). The increment in energy expenditure was unrealistically high with a large variability at 880 (SE 298·1) J/d per $kg^{0.75}$ for each percentage unit increase in CF. It was associated with a higher glucose uptake and a higher value for net acetate:α-NH_2-N absorbed across the PDV. Higher energy requirements of PDV could possibly be related to enhanced muscular work to sustain a higher peristalsis. Other factors could have been assumed to alter PDV energy expenditure with changes in CF; for example, changes in gut mass through a bulk effect. However, in ruminants the influence of the dietary forage:concentrate ratio on gut mass has led to unclear results (Ortigues & Doreau, 1995). A direct stimulatory effect of rumen butyrate on *in vivo* epithelial cell proliferation (Galfi *et al.* 1991) is also unlikely considering the lack of significant changes in the net PDV butyrate and β-hydroxybutyrate fluxes. Finally, increased energy expenditure associated with cellular transport activities is little affected by the pattern of available nutrients (McBride & Kelly, 1990).

Hepatic energy expenditure was unresponsive to diet composition (from equation 6, Table 1) in agreement with the lack of significant changes in net hepatic nutrient fluxes. Direct experimental evidence for a clear effect of the forage:concentrate ratio is also lacking (Ortigues & Doreau, 1995). Similarly, energy expenditure of hindquarters was unaffected by CF content (Table 1, equation 7). Consequently, the known lower efficiency of energy utilization for forage diets at the whole-animal level would be attributed here to increased energy expenditure of PDV. Nevertheless, quantification of the latter value would have to be checked experimentally since the predicted increment appears to be much higher than the calculated increase in whole-animal energy expenditure when average k_f drops from 0·5 with concentrate diets to 0·4 with forage diets.

EFFECT OF DIETARY CRUDE PROTEIN CONTENT

The influence of the dietary CP content seemed to be limited to the following metabolites: urea-N, NH_3-N and β-hydroxybutyrate.

Nutrient supply and net fluxes through portal-drained viscera

An increased dietary CP content at fixed MEI and CF content was predicted to result in higher net portal appearance of NH_3-N ($P<0·01$), while that of α-NH_2-N would remain

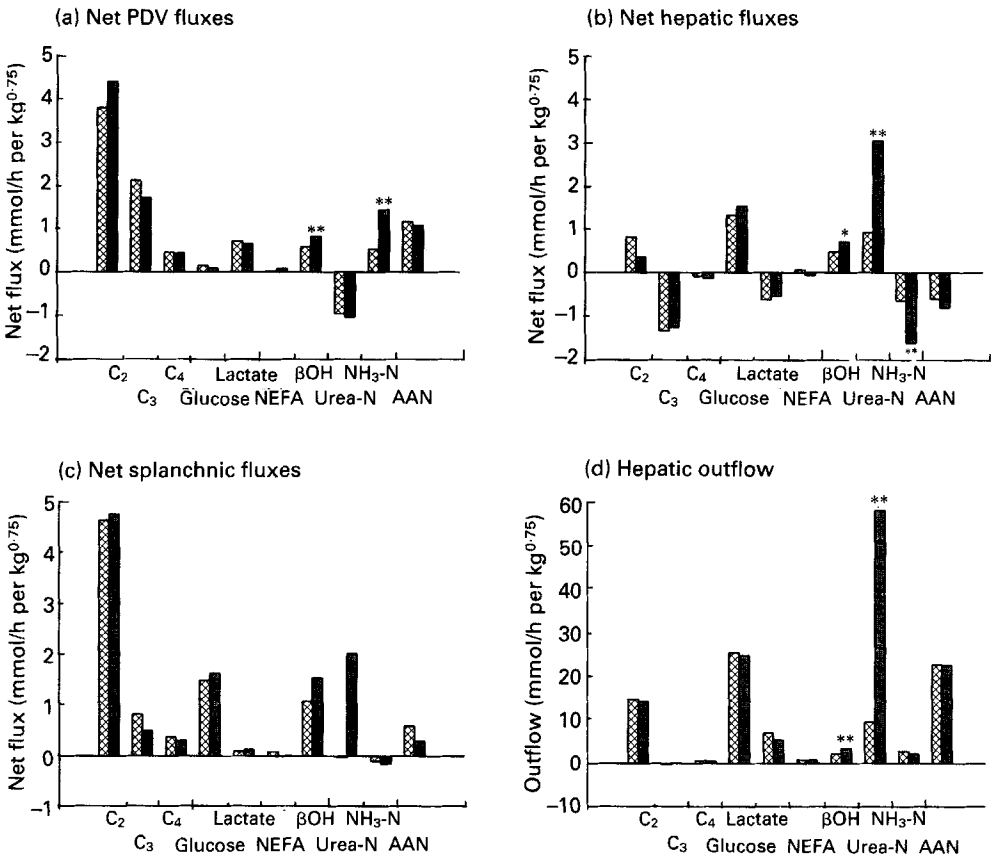

Fig. 3. Predicted effects of dietary crude protein level (nitrogen × 6·25; CP; 100 (▨) and 150 (■) g/kg) at constant metabolizable energy intake (MEI; 481 kJ/d per $kg^{0·75}$) and dietary crude fibre content (CF; 100 g/kg) on (a) net portal-drained viscera (PDV), (b) hepatic, and (c) splanchnic nutrient fluxes, and (d) flows of nutrients leaving the liver. Values were calculated directly from prediction equations except for net splanchnic fluxes which are the sum of the portal and hepatic fluxes. Nutrients considered are acetate (C_2), propionate (C_3), *n*-butyrate (C_4), glucose, lactate, non-esterified fatty acids (NEFA), β-hydroxybutyrate (βOH), urea-N, NH_3-N and α-amino-N (AAN). The effects of changes in CP were significant: $*P<0·05$, $**P<0·01$.

statistically unchanged (Fig. 3(a)). Since the diets considered were generally not deficient in rumen-degradable N, rumen NH_3 capture by micro-organisms and microbial protein synthesis would depend primarily on ME supply. Seal & Reynolds (1993) also indicated that amino acid release by PDV was not correlated with dietary N supply but with MEI. The high-CP diets considered in the present data-set generally did not include rumen-undegradable protein sources. Even so, no clear relationships seem to exist between rumen degradability of N sources and net portal amino acid absorption (Huntington, 1987). Improved net appearance of α-NH_2-N in portal blood had only been noted in cases of abomasal casein infusion (Guerino *et al.* 1991) or of dietary supplementation with protected soyabean meal (Cleale *et al.* 1987) or methionine and lysine (Maltby *et al.* 1991). Changes in protein metabolism of the gut wall may explain the limited changes of net PDV α-NH_2-N absorption since a greater metabolism of amino acids has been reported with higher CP contents (van der Walt, 1993).

High CP content also resulted unexpectedly (Maltby *et al.* 1991) in an increased net portal appearance of β-hydroxybutyrate ($P<0{\cdot}01$).

Nutrient supply and net fluxes through liver

In the liver, removal of blood NH_3-N and net production of urea were significantly enhanced ($P<0{\cdot}01$) by higher CP; net release of β-hydroxybutyrate also increased (Fig. 3(b); $P<0{\cdot}01$). This minor change (from 3·5 to 5·2%) in the energetic contribution of the nutrients to total energy flow reaching or leaving the liver was the only one affected by CP.

No changes were predicted here in terms of flow of α-NH_2-N reaching the liver or net hepatic α-NH_2-N flux. In the literature, an increase in net PDV absorption of α-NH_2-N was generally countered by greater hepatic uptake for gluconeogenesis (Judson & Leng, 1973) or possibly hepatic protein synthesis (Guerino *et al.* 1991) such that splanchnic release to peripheral tissues was not significantly modified. This point would warrant further studies coupled in particular with net peptide (Webb *et al.* 1986) fluxes through splanchnic tissues. In the present predictions, the proportions of the various energy nutrients leaving the liver were not altered (Fig. 3(c and d)).

When N intake was chosen as the independent variable in the multiple regressions instead of CP, correlations were not modified, confirming that MEI is the primary predictive variable of interest for most energy nutrients. The most notable effect of N intake or CP level is on the variable efficiency of rumen NH_3 capture.

Nutrient supply to hindquarters

One interesting effect of the dietary CP level that would require experimental validation is the stimulation of hindquarters blood flow ($P<0{\cdot}05$; Table 1, equation 4) which would increase nutrient supply to the hindquarters without any changes in the balance of energetic nutrients available. There has been one report of this effect on blood flow (Ahmed *et al.* 1983). Transient redistribution of cardiac output among body tissues in favour of peripheral tissues, associated with excess NH_3 loading (Orzechowski *et al.* 1987; Fernandez *et al.* 1990) could be under adrenergic regulation (Barej *et al.* 1980). In the present case arterial urea-N but not NH_3-N concentrations were increased ($P<0{\cdot}05$) with increased CP. It is interesting to note that the coefficients for CP in the multiple regressions established for portal and hepatic blood flows were negative, although high standard errors were associated with these estimates.

Tissue and whole-body energy expenditure

The dietary CP level appeared, generally, to have no effect on PDV O_2 consumption (Table 1, equation 5). Dietary supplementation with urea or protected amino acids (Maltby *et al.* 1991) or absomasal infusion of casein (Guerino *et al.* 1991) were also without any effect, whereas raising the soyabean meal content of a 750 g concentrate/kg diet led to higher PDV O_2 consumption (Reynolds *et al.* 1992*a*).

Energy expenditure by liver was unresponsive to diet CP level (from Table 1, equation 6). The nature of the N sources as well as N intake were thought to influence hepatic O_2 consumption via hepatic ureagenesis; however, theoretical considerations suggest that

this may depend on the oxaloacetate precursor (Reynolds, 1992). Increased N supply, as soyabean meal (Reynolds *et al.* 1992*a*), urea or protected amino acids (Maltby *et al.* 1991) or as abomasal casein infusion (Guerino *et al.* 1991) failed to show significant increases in hepatic O_2 consumption, lending support to the present prediction.

In the hindquarters, energy expenditure appeared to increase with the dietary CP level (Table 1, equation 7); however, this was associated with a large standard error which limits quantitative interpretation. This trend parallels that for blood flows. There is no experimental evidence of an effect of dietary CP content on hindquarters energy expenditure and this point would warrant confirmation.

Overall, the responses predicted here do not clarify the small and variable effects of CP on the efficiency of energy utilization by the growing ruminants (Ortigues *et al.* 1990).

CONCLUSIONS

The approach used here attempted to build a generalized quantitative picture of the influence of nutritional factors on net nutrient fluxes through tissues and tissue energy expenditure in the fed growing ruminant. The hypotheses involved in establishing the data-set and the type of data available suggest that the outcome of this work could be considered as a research tool to identify areas of research where information is scarce. For example, studies on concentrate diets using grain sources other than maize, or diets based on forages other than lucerne would be necessary, as well as more systematic studies on level of intake, CF and CP contents. The quantitative influence of nutrition on nutrients such as L-lactate, β-hydroxybutyrate, NEFA and other lipid constituents also remains unclear. Nutritional influence on the energy metabolism of peripheral tissues, especially muscles, is also a key area to explore.

Finally, it has established general trends, even though only the most significant effects could be detected because the origin of the data was wide ranging and interpretation was limited by both the small number of observations and involvement of the most commonly used feed ingredients. A more detailed analysis would be necessary to improve this interpretation. Nevertheless, some questions were raised, such as the role of PDV in determining the difference between the efficiency of energy utilization of forage and concentrate diets in relation to acetate absorption. The possibility of altering the partition of nutrients in favour of muscle by nutritional means seemed limited. It is probably highly dependent on the rate and distribution of blood flows to tissues and would need to be tested, especially in the context of growing ruminants raised for meat production. Finally the exogenous supply of nutrients to tissues appeared to be greatly diluted by the arterial blood supply, leading to smaller changes in blood metabolite concentrations and in nutrient balance, thus raising the issue of what controls changes in nutrient use by tissues. Combined investigations on the role of splanchnic-released hormones on the control of nutrient partition and use would seem particularly appropriate.

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