Dietary-induced thermogenesis and feed evaluation in ruminants

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In simple-stomached animals it is still uncertain if the composition of absorbed nutrients affects dietary-induced thermogenesis. For instance MacLeod et al. (1989) found no change in percentage energy retention in poultry that were given different amounts of protein, carbohydrate and fat. In ruminants, however, it is generally recognized that the heat produced from similar amounts of metabolizable energy (ME) is greater from a diet based on cellulosic roughage than from one based on concentrates. The recognition of these differences is not new and not in dispute but sometimes heated debates have taken place as to the exact cause of the differences.

HISTORICAL PERSPECTIVE

First indications of the effect of roughages on dietary-induced thermogenesis can be gleaned from early feed evaluation systems. Initially feeds in Europe were evaluated relative to straw or meadow hay (see Tyler, 1975). Morton (1855) lists several authors’ estimates of the value of grain relative to good-quality meadow hay and most of the authors estimate 50–60 kg grain to be equal in nutritive value to 100 kg meadow hay. Since grain is likely to be about 80% digestible and meadow hay 50–60% digestible the greater value given to grain is apparent. When Kellner (1926) proposed a new feeding system based on pure nutrients, because of the variability in previous standards, he compared feed values relative to pure starch for fattening of steers. With use of respiration calorimetry Kellner (1926) observed differences in heat production between cellulosic roughages and starch when a similar amount of ME was given. Kellner (1926) attributed these differences to variation in work of digestion (‘Verdaurungsarbeit’) and devised correction factors based on crude fibre.

Kellner’s (1926) explanation was generally accepted, although the American feed evaluation system which was developed later simply compared feeds on the basis of total digestible nutrients and this is still largely used in the USA today.

When the team in Cambridge led by Sir John Barcroft (Barcroft et al. 1944) proved clearly that the main source of energy for ruminants consisted of volatile fatty acids (VFA) formed during anaerobic fermentation, not as previously thought digestible microbial polysaccharides (Baker, 1942), other reasons were put forward to explain the differences between roughage and concentrate diets. The establishment of the importance of VFA and the development of chromatographic methods to separate VFA soon led to the general finding that the proportion of acetic acid was highest on roughage diets while the proportion of propionic acid was highest on concentrates. Table 1 compares fermentation patterns from different nutrients (Ørskov & Oltjen, 1967). A hypothesis was put forward initially by McClymont (1952) that the higher heat losses with roughage diets could be associated with the higher proportion of acetic acid in the fermentation end-products. Consideration of oxidative metabolism based on Krebs citric acid cycle indicated that successful oxidation of acetyl-CoA depended on continuous regeneration.
Table 1. **Effect of type of carbohydrate on molar proportion (mmol/mol) of volatile fatty acids in the rumen of two steers receiving purified diets (Ørskov & Oltjen, 1967)**

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Acetic acids</th>
<th>Propionic acid</th>
<th>Butyric acid</th>
<th>Higher acids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cellulose</td>
<td>737</td>
<td>183</td>
<td>48</td>
<td>32</td>
</tr>
<tr>
<td>Starch</td>
<td>604</td>
<td>247</td>
<td>104</td>
<td>45</td>
</tr>
<tr>
<td>Starch + glucose</td>
<td>571</td>
<td>289</td>
<td>99</td>
<td>41</td>
</tr>
<tr>
<td>Sucrose</td>
<td>496</td>
<td>232</td>
<td>202</td>
<td>70</td>
</tr>
<tr>
<td>Glucose</td>
<td>380</td>
<td>223</td>
<td>258</td>
<td>139</td>
</tr>
<tr>
<td>SE</td>
<td>28</td>
<td>29</td>
<td>10</td>
<td>—</td>
</tr>
</tbody>
</table>

of oxaloacetic acid. Oxaloacetic acid, if deficient, could only be generated from glucose or glucose precursors such as propionic acid and not from acetic acid. Thus, the term futile cycling was coined in the belief that a relative glucose deficiency would lead to an inefficient capture of ATP from acetate oxidation and be responsible for the differences between roughage and concentrate diets. The development of techniques of rumen cannulation and respiration calorimetry led to a test of the hypothesis by Armstrong & Blaxter (1957a,b) and Armstrong et al. (1957, 1958). They carried out a series of experiments in which VFA singly or in mixtures were infused into the rumen of sheep. They observed that while infusion of the different VFA into the rumen of fasted sheep gave similar increases in heat production, differences were seen when fed sheep were given infusions above energy maintenance; greater increases in heat production were observed when acetic acid was infused (67 kJ/100 kJ total VFA) than with propionic and butyric acids (44 and 38 kJ/100 kJ respectively). They also postulated that there was a linear relationship between heat production and proportion of acetic acid in the rumen fluid by infusing two mixtures varying in the proportion of acetic to propionic acid. However, this assertion was based on a miscalculation between molar and energy proportions. Nonetheless, findings presented by Blaxter (1962) and Agricultural Research Council (1965) do demonstrate a general relationship between molar proportions of acetic acid and dietary utilization of ME. There were, however, a couple of problems in accepting a causal basis for this relationship. First if the problem was due to inefficient utilization of acetic acid or so-called futile cycling then a curvilinear relationship should be expected between utilization and acetic acid production, since there was no evidence for inefficient utilization when the supply of C3 or oxaloacetate was adequate. Second since butyric acid is also utilized as C2, a similar efficiency to acetic acid might have been expected. Following these observations a great many large-scale experiments were conducted to test these ideas. Ørskov & Allen (1966a,b,c) and Ørskov et al. (1966) conducted comparative slaughter experiments with lambs given dietary supplements of acetic, propionic and butyric acids. They found no differences at all in energy retention between the different salts added at a level of 15% of ME. In one experiment there was some evidence that when acetate was added to a low-roughage diet it was utilized better than when added to a high-roughage diet, thus providing some evidence of curvilinearity. Similar results were shown by Bull et al. (1970) using triacetin. Hovell et al. (1976), again using VFA salts, showed some evidence of curvilinearity with levels of acetate incorporation, but otherwise no consistent difference in utilization between acetate and
propionate. Ørskov et al. (1969) infused acetic and propionic acids into the rumen of dairy cows and found no difference in heat production but differences in the partition of energy between tissue and milk. Tyrrell et al. (1979) observed a slightly more efficient utilization of acetic acid when it was infused into the rumen of cows receiving a low-rather than a high-roughage diet. Jenkins & Thonney (1988) found a higher empty-body gain when a large supplement of propionate salt was given. This led to high levels of propionic acid in the peripheral circulation which is known to elicit insulin release (Bassett, 1974).

PROBLEMS OF SUPPLEMENTATION

It has generally been observed that levels of VFA infusion above 0.15 of ME created problems of inappetence in the case of VFA salts and digestive problems in the case of acid infusions. This low level of supplementation created difficulties of interpretation. First, as there is a large between-animal variability in intake it is sometimes difficult to detect the effect of a supplement providing 0.15 of energy and even more difficult when the experiment is designed to show possible differences between different VFA. Second, the assumption is made that the salt or acid infusion had no effect on the digestion or utilization of the feed to which it was added. The third difficulty is apparent particularly when acetic acid or acetate is added even at 15% of ME to diets already generating a high proportion of acetic acid. In Table 2 a series of molar proportions are converted to energy proportions and it can be seen that acetic acid due to its low energy value per mole assumes much less importance when converted to energy proportion. In general a molar percentage of 75% of acetic acid is the extreme found even with very-poor-quality roughages. It will then be understood that if 15% of ME is added in the form of acetate or acetic acid, molar proportions are soon reached which are outwith conditions occurring in practice. This criticism of supplementation, however, also applies to the original observation of Armstrong and colleagues. Intravenous infusion of acetate or propionate has also been attempted but since propionic acid is generally metabolized in the liver and elicits an insulin response if it enters the peripheral circulation it is not possible to relate such results to normal diets (Eskeland et al. 1973).

Table 2. Molar proportions and equivalent energy proportions for different mixtures of volatile fatty acids and efficiency of utilization above maintenance (Kf) determined with intragastric nutrition of lambs (Ørskov et al. 1979)

<table>
<thead>
<tr>
<th>Molar proportions (mmol/mol)</th>
<th>Energy proportions (J/kJ)</th>
<th>Determined Kf values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acetic acid</td>
<td>720  590  480  390  300</td>
<td>0.59  0.61  0.61  0.57  0.64</td>
</tr>
<tr>
<td>Propionic acid</td>
<td>70   210  330  430  530</td>
<td></td>
</tr>
<tr>
<td>Butyric acid</td>
<td>210  200  190  180  170</td>
<td></td>
</tr>
</tbody>
</table>

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Table 3. *Effect of grain processing on proportions of volatile fatty acids (mmol/mol) and feed utilization by groups of eight early-weaned lambs (Ørskov et al. 1974)*

<table>
<thead>
<tr>
<th>Type and form of grain</th>
<th>Acetic acid</th>
<th>Propionic acid</th>
<th>Higher acid</th>
<th>Digestibility</th>
<th>Food conversion (kg dry matter/kg gain)</th>
<th>Live w gain (g/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole barley</td>
<td>525</td>
<td>301</td>
<td>174</td>
<td>81.1</td>
<td>2.75</td>
<td>340</td>
</tr>
<tr>
<td>Ground barley</td>
<td>450</td>
<td>453</td>
<td>97</td>
<td>77.2</td>
<td>2.79</td>
<td>347</td>
</tr>
<tr>
<td>Whole oats</td>
<td>650</td>
<td>186</td>
<td>164</td>
<td>69.9</td>
<td>3.07</td>
<td>241</td>
</tr>
<tr>
<td>Ground oats</td>
<td>532</td>
<td>375</td>
<td>93</td>
<td>67.5</td>
<td>3.33</td>
<td>238</td>
</tr>
</tbody>
</table>

Although the evidence for no difference in efficiencies of utilization of the VFA is overwhelming, commercial companies competed to find products which could decrease acetate and increase the proportion of propionic acid in the rumen. Here it must be pointed out that if the assessment of ME utilization was based on a single factor of converting digestible energy to ME then some relationship between utilization and proportion of acetic acid would be found; on grounds of stoichiometry the disposal of hydrogen to produce methane is positive while acetic acid is produced

\[ C_6H_{12}O_6 + 2H_2 \rightarrow 2CH_3COOH + 2CO_2 + 4H_2 \]

while the production of propionic acid would act as a H sink

\[ C_6H_{12}O_6 + 2H_2 \rightarrow 2CH_3CH_2COOH + 2H_2O \]

and reduce CH₄ production. Thus, some relationship between utilization and digestible energy can be expected to relate to proportion of acetic acid due to the implication of CH₄ production (Hungate, 1966; Ørskov et al. 1968). Such differences are, however, small and difficult to detect. It is, for instance, possible to change the type of fermentation by cereal processing without any detectable change in feed utilization. For example, Table 3 shows the effect of feeding whole or processed oats or barley to early-weaned lambs. In spite of large changes in type of fermentation there were no significant differences in digestibility and feed utilization.

With the development of the technique of intragastric nutrition (Ørskov et al. 1979; MacLeod et al. 1982) it became possible to nourish ruminants totally on VFA infused into the rumen and protein to the abomasum. This alleviated the problems referred to earlier, on control of VFA composition absorbed with respect to basal diet. A large-scale trial involving forty-eight cannulated sheep was carried out with a wide range in VFA proportion covering almost any conceivable composition of VFA, and even unphysiological ones with molar percentages of propionic acid varying from 5 to 45% and acetic acid from 45 to 85%. The heat production was measured both at an estimated maintenance energy input (450 kJ/kg W₀.75) and at twice the maintenance energy input. The calculated efficiencies of utilization above energy maintenance \((K_f)\) are given in Table 2. As can be seen there was no consistent difference in utilization over the large spectrum of VFA proportions tested, the average utilization of VFA being in the region of 60%. It is interesting that almost the same efficiency of utilization was observed by caecal infusion of VFA or fermentable carbohydrates in pigs reported by Gadeken et al. (1989) and Muller et al. (1989) respectively.
Recently, trials with cattle have further substantiated the results using indirect open-circuit calorimetry to measure heat production. Here, the molar percentage of acetic acid was varied from 30 to 92. The molar percentage of butyric acid was held constant at 8. The molar percentage of propionic acid varied from 0 to 60. Still higher proportions of propionic acid resulted in several metabolic problems including haemolysis and blood in urine. The most important results are presented in Fig. 1 (E. R. Ørskov and N. A. MacLeod, unpublished results). The level of energy input was kept here at 675 kJ/kg $W^{0.75}$ or equal to an estimated 1.5 times maintenance energy expenditure. It can be seen that at about 75-80 molar % of acetic acid in the infusate there is an increase in nitrogen excretion which suggests a deficiency of gluconeogenic compound resulting in some oxidation of amino acids in the process of protein turnover. This is followed by an elevation in the blood concentration of β-hydroxybutyrate which indicates also glucose deficiency as it can be reduced to normal levels by infusion of small amounts of glucose. The metabolic crisis finally results in a reduction in heat production accompanied by an excretion of acetic acid in the urine. Thus, at the extreme acetic acid proportions, far beyond physiological levels, the animal does not resort to wasteful oxidation of acetate or futile cycling but excretes acetic acid in the urine.

The biochemical evidence for acetate cycling or cycling between acetate and acetyl-CoA which could theoretically lead to heat losses when the utilization was blocked or inhibited is also very limited. Crabtree et al. (1987) showed convincingly in sheep muscle that the rate of cycling was very limited. Even with a twofold increase in acetate concentration the heat produced in that reaction could account for no more than 0.5% of...
basal metabolic rate. In spite of little or no evidence that a wasteful utilization of acetate
was occurring in ruminant tissue, Ortigues et al. (1989), for instance, interpreted live
weight responses to fish meal in lambs given straw-based diets as being due to glucogenic
precursors from fish meal causing a ‘reduction in wasteful oxidation of acetate’.

PROBLEMS OF FASTING METABOLISM

In the foregoing section it was argued that evidence for inefficient utilization of ME from
roughages being a result of the high proportion of acetic acid was very sparse. Consequently
one should seek an alternative explanation. First of all the concept of
differences in the so-called efficiency for maintenance ($K_m$) and $K_f$ efficiency for
production, will be dealt with.

Determination of the efficiency for utilization of ME below energy maintenance
depends on measurement of fasting metabolism in animals. This measurement has been
criticized on several grounds in recent years (see Marston, 1948; Webster et al. 1974). In
addition Koong et al. (1985) and Burrin et al. (1989) showed clearly that the numerical
value of fasting metabolism depended to a large extent on the feeding level received
before fasting, and that these differences could largely be attributed to differences in
organ size such as liver and intestine, etc. Another problem with fasting metabolism is
that it gives rise to a substantial increase in N excretion (about 40% above basal levels)
indicating protein oxidation due to deficiency of glucose precursors. In addition the
blood β-hydroxybutyrate is elevated. Based on these observations Ørskov (1982)
suggested that it was conceptually incorrect to use fasting metabolism as this represented
the metabolism of a glucose-deficient diet, i.e. body fat, to estimate the efficiency of
utilization of nutritionally-balanced diets. He suggested the hypothesis depicted in Fig. 2
in which the accepted concept according to Agricultural Research Council (1965, 1980) is
shown; the more likely situation is also indicated. Evidence to support this hypothesis

![Graph of Metabolizable energy intake vs. Energy retention](https://www.cambridge.org/core/terms).

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Fig. 2. The effect of energy input on efficiency of energy utilization below and above energy maintenance. 
(---) The probable course of events. F. fasting heat production.

https://www.cambridge.org/core/terms
was recently presented by KuVera et al. (1989). They showed that glucose infused at low levels into the abomasum of fasting steers did not result in an increase in heat production, but in some cases even a decrease, and always a decrease in urinary energy due mainly to reduction in excretion of urinary N to levels similar to basal N excretion. KuVera et al. (1987) also noted that a mixture of VFA given at about 0.2% of energy maintenance was sufficient to reduce fasting N excretion to that observed at energy maintenance. Thus, it seems that the concept of differences in utilization of ME below and above energy maintenance needs to be reconsidered. It can at least be postulated from the evidence that assessment of energy utilization in response to energy supply should, perhaps as a starting point, use about one-third of an estimated energy maintenance rather than fasting so that the requirement for glucose precursors is likely to be met. Similar conclusions could be drawn from the results of Gill et al. (1989).

**PROBLEMS OF DIFFERENCES IN UTILIZATION BETWEEN FIBROUS ROUGHAGES AND CONCENTRATE**

In the previous section evidence was given showing that the differences in utilization of ME from concentrate and roughage diets appeared not to be related to the composition of absorbed nutrients, and that the differences observed had been exaggerated by allocating the differences to $K_f$. It was also argued that differences between $K_f$ and $K_m$ were dubious. It follows, therefore, that the century-old realization of differences in utilization of ME between such diets still needs an explanation. Having, so to speak, disposed of differences between $K_m$ and $K_f$, it is necessary to consider actual differences in heat production from animals receiving roughage or concentrate diets. It will be appreciated that if the concept of $K_m$ and $K_f$ is maintained and if it is assumed that differences in $K_m$ are small then differences in $K_f$ could be very much dependent on the production level achieved and on the point determined as the maintenance energy level. For instance, if heat production in cattle is either 45 or 50 MJ/d when 60 MJ ME is given and the estimated maintenance energy need is either 30, 35 or 40 MJ energy the corresponding values for $K_f$ can be calculated as in Table 4. It can be seen that relatively small changes in heat production, here 10%, can result in large differences in the value for $K_f$. It can also be seen that both $K_f$ itself and the differences between diets depend on the maintenance level. If the maintenance need is not determined in the experiments reported it becomes possible to be somewhat subjective as to the desired results. Such problems of errors and subjectivity of interpretation was recently discussed in an interesting letter to the editor by Graham (1986) and also dealt with in some detail by Hovell et al. (1976).
ACTIVITY ASSOCIATED WITH FOOD CONSUMPTION

It is perhaps to be expected that if the increased heat production was associated with activity to do with eating and rumination, the differences in utilization would decrease with increasing feeding level since time spent eating and ruminating is not necessarily increased in proportion. Adam et al. (1984) showed that the cost of eating was related to time spent eating and not to dry matter consumed. This is, indeed, supported in work reported by Flatt et al. (1967) who in dairy cows did not observe differences in heat production between diets varying from 200 to 600 g roughage/kg in the form of lucerne (Medicago sativa) hay. Yet comparisons between roughage and concentrate diets are often made at a low level of feeding, if for no other reason than that a high level of intake of pure-roughage diets is difficult to achieve.

CAN THE DIFFERENCES BE EXPLAINED BY COST OF EATING AND RUMINATING?

If the maximum time spent eating and ruminating is assumed to be about 8 h for each activity when long roughages or grass diets are consumed, and 1 h for each activity when pelleted diets are given, the differences in energy cost can be estimated. With cattle Holmes et al. (1978) and Adam et al. (1984) observed the cost of eating to average 32 J/kg live weight per min. There is very little work reported on the cost of rumination in cattle, but KuVera et al. (1989) recently recorded a tentative value of 9.3 J/kg live weight per min. While the physical work associated with the two activities is likely to be similar, the blood flow etc., to the viscera is increased during eating and probably accounts for the higher observed cost of eating above ruminating.

Steers weighing 300 kg and receiving long roughage would expend 6 MJ/d on the activities of eating and ruminating compared to 0.8 MJ/d for the pelleted diets. Thus, the differences in $K_f$ for concentrates and roughage can easily be explained by these activities (Table 4). Whether standing time is also increased when longer time is spent eating is uncertain. If it is, this would further lower the apparent efficiency of roughage utilization as the cost of standing relative to laying is about 10 J/kg live weight per min (KuVera et al. 1989). At a low level of production (e.g. 0–600 g gain/d) such differences would contribute to substantial differences in the rate of live-weight gain. For example, if the energy value of gain is 15 MJ/kg (Agricultural Research Council, 1980) then a higher heat production with roughages of 5 MJ/d could amount to a reduced live-weight gain of almost 200 g/d.

Kellner (1926) used the term 'Verdaurungsarbeit' or work of digestion to explain differences in utilization between concentrate and fibrous roughage diets. If with this we understand cost of eating and rumination, then Kellner's (1926) observations were probably correct and all we have done during almost a century is to confirm his deduction that efficiency of utilization of absorbed energy would be increased if the 'Verdaurungsarbeit' or work of digestion were reduced, for example, by grinding and pelleting long roughages to reduce time of eating and rumination. Evidence for this can be found in the review and summary by Agricultural Research Council (1980). They showed no differences in $K_f$ between concentrates and roughages when the roughages were ground and pelleted. However, while grinding and pelleting is costly and generally not economic for roughages. It also has the problem that outflow from the rumen would be increased.
due to low particle size so that digestibility and, thus, ME concentration in the feed could be decreased.

IMPORTANCE OF VFA IN FEED EVALUATION AND ANIMAL NEED

The knowledge of VFA production in the rumen has contributed greatly to the qualitative understanding of rumen fermentation and use of energy by the host animal. To use information on VFA produced from a given feed as a contributor to feed evaluation seems of dubious value. First, the type of fermentation produced from a feed is by no means constant (see Table 3); among other aspects it varies with rumen pH and, thus, with eating and salivation behaviour of individual animals. In addition, due to different absorption rates the VFA proportions found in the rumen most often do not represent the proportions in which VFA are produced (MacLeod & Ørskov, 1984). Second, as can be seen from Table 3 and Fig. 1, over the physiological range of VFA proportions (450–750 mmol acetate/mol VFA) the animal metabolism is similar. An exception appears to be that of dairy cows which respond to acetate proportions of less than about 0·50–0·55 and propionate proportions greater than 0·35–0·45 by decreasing milk energy and increasing body energy accretion. This is particularly important when large amounts of concentrate containing starch or soluble sugars are fed twice daily and when the starchy feeds are overprocessed (see Table 3). In this instance, propionate absorption may exceed the ability of the liver to metabolize it so more enters the peripheral blood. High concentrations of propionic acid elicit an insulin response which then changes the proportion of energy for milk relative to body tissue production. Such knowledge can be used to aid general management strategies, or to identify specific problems in particular situations. However, information on the type of fermentation to expect from feeds is imprecise, subject to large between-animal variation and is so influenced by level and pattern of feeding that satisfactory prediction models currently seem unlikely. Furthermore, as the present paper has attempted to show, variation in the supply of different VFA within the normal range has no effect on net utilization so that even if it were possible to describe VFA availability to the animal, such information is unlikely to add precision to feed evaluation. On the other hand, time spent eating, rumination time, degradation rate and outflow rate are important factors in determining feed intake and feed utilization in ruminants and better knowledge of these factors is likely to offer more to animal production than concern about VFA proportions.

REFERENCES


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