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SOME ASPECTS OF RUMEN METABOLISM INFLUENCING INTAKE AND PRODUCTION IN SHEEP

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SUMMARY

A brief account is given of present knowledge of some of the factors which influence intake, the proportion of volatile fatty acids formed in the rumen and the efficiency of their utilization by the sheep. This information is used to explain the differences in weight gains obtained in animals pastured on short-rotation ryegrass, perennial ryegrass, both alone and with white clover. With both ewes and lambs, short-rotation ryegrass gave considerably better weight gains than perennial ryegrass. The addition of clover gave improvement in weight gains with both grass varieties. The data obtained on rumen fill, papillary development and proportions of volatile fatty acids indicate that the differences in weight gains could be explained on the basis that short-rotation ryegrass is less fibrous and higher in soluble carbohydrate than perennial ryegrass.

THE breeders of pasture plants are often criticized for not taking the feeding value of their product into consideration when evaluating the progeny of their hybridization programmes. They can, with some justification, throw the problem back to the animal nutritionist and chide him for not providing a reliable yardstick with which to judge their new plant material. The reason for the gap between the plant breeder and the nutritionist is that in the past not enough was known about the metabolism of the ruminant to be able to produce other than empirical formulae with which to make predictions about the nutritive value of herbage.

With ruminants, even the determination of dietary deficiencies or toxicities in the feed, though usually giving rise to spectacular syndromes that are easily recognized, is not always the simple problem of direct determination of the offending substance. The transformations that take place in the rumen have to be considered. Two examples are:

- (a) New Zealand white clover contains cyanogenetic glucosides. The animals ingesting white clover are protected from poisoning because the cyanide released in the rumen is rapidly absorbed into the blood stream and converted into non-toxic thiocyanate in the liver. This can lead to an elevated blood level of the goiterogenic thiocyanate in sheep but not in cattle. Hence, in sheep, the cyanide of clover can inhibit the uptake of iodine by the thyroid gland, an effect not known in other animals.
- (b) The study of oestrogenic substances in clovers, their isolation, estimation and the determination of their biological activity might well appear to be a problem of organic chemistry allied with small animal testing. However, it has recently been shown that interconversion of less potent to more potent oestrogens can occur in the ruminant's paunch, and so one is immediately concerned with the biochemistry of their interconversion by the micro-organisms.

Important though these problems may be, it is probable that shortage of dietary energy is a far more serious cause of low productivity in farm livestock than are deficiencies or toxicities associated with pasture plants. It is in this field that fundamental knowledge has been lacking which would enable the usefulness of food as an energy supply for the animal to be predicted from the chemical composition of food.

The Weende system of proximate analysis, developed last century, in which determinations of water, ether extract, crude fibre, nitrogen-free extract, crude protein and ash were made, has stood the passage of time well. It has been the basis for determining and describing the energy value of feeds, on which the livestock feed industry in the Northern Hemisphere has been based. However, the proximate system of analysis does not define the nutrient contents of feeds. It is an index of nutritive value because the fractions that it isolates are correlated with some properties of the feeds that have nutritional significance. It is now possible to advance beyond these limits, (a) by fractionation and measurement of the constituent parts of the materials grouped within the older analyses, (b) by studying the fate of these materials in the rumen and (c) by determining the pathways of utilization by the ruminant animal of the products of their fermentation. In this paper, (b) and (c) will be considered, together with some experimental results with ryegrass varieties.

VOLATILE FATTY ACID PRODUCTION AND UTILIZATION
IN THE RUMINANT

The mixture of acids found in ruminal ingesta consists of acetic, propionic, butyric and higher acids. There is now little doubt that the animal obtains the major portion of its total energy requirements by the absorption from the gut of these products of microbial digestion of carbohydrate.

With diets consisting entirely of hay (relatively high in fibrous cellulose) the mixture of acids found in the rumen usually consists approximately of acetic 76%, propionic 15%, butyric 12% and trace of higher acids 3%. The addition of concentrates rich in starch or soluble sugars tends to lower the proportion of acetic acid and raise that of propionic and butyric acids. The grinding of hay also brings about a similar change in the ratio of acids. This trend is accentuated when cooked starch is added to ground hay, and under these conditions the proportion of propionic may equal or exceed that of acetic.

Large changes can be brought about, therefore, by preparing the food in ways which do not require changes in the amount of the components of the diet. Thus diets with the same theoretical starch equivalent can produce considerable differences in the proportions of individual fatty acids found in the rumen.

An example of this type of experiment is shown in the results obtained by Ensor *et al.* (1959) (Table 1) in which ground and pelleted hay plus heated corn were compared with chopped hay plus ground corn, for fattening steers.

TABLE 1: EFFECT OF TWO METHODS OF PREPARATION OF A FEED
UPON LIVELWEIGHT GAIN AND EFFICIENCY OF FEED CONVERSION

Ration	No. of Steers	Average Gain (lb)	Average Daily Gain	lb Feed D.M./100 lb Gain
2 in. chopped hay + ground corn + pelleted linseed oil meal (1:1:0.02)	8	114.6	2.05 ± 0.14	399.0 ± 28.0
Ground and pelleted hay + heated corn + pelleted linseed oil meal (1:1:0.02)	8	142.9	2.55 ± 0.19	329.7 ± 28.5

It can be seen in Table 1 that the steers receiving the second ration gained 0.5 lb per day more than the steers receiving the first, and required 69.3 lb less feed on a dry matter basis per 100 lb of weight gain. Their rumen contents showed

a marked fall in acetate and an increase in propionate content, and they digested protein more efficiently than the controls.

That the second type of ration which gave increased weight gains is not suitable for milk fat production was demonstrated by the same authors by comparing long hay (38 lb) with ground and pelleted hay (28 lb), and 4 lb of heated corn. The latter ration caused a 53% drop in fat content of the milk and a 7% drop in milk production when compared with the first.

This emphasizes the fact that the nutritive value of food may differ according to the type of physiological function it supports. Lactation is, in general, a more efficient process than fat deposition. This means that a food will have a higher absolute value as an energy source for supporting lactation than for fattening the same animal when dry.

RUMEN FERMENTATION IN RELATION TO MAINTENANCE AND PRODUCTION

There appear to be two main considerations in the utilization of different feeds for animal production. These are dealt with in turn.

THE EFFICIENCY OF UTILIZATION OF THE ENERGY OF FEEDS

Blaxter and his associates have carried out most of the work in determining the calorimetric efficiency for maintenance and fattening of the end products of ruminant digestion. Respiration experiments have been conducted with sheep receiving intra-ruminal infusions of fatty acids, individually or as mixtures, both below maintenance and during fattening. In the fasting animal, it has been found that acetic acid alone is poorly utilized with the production of a large amount of heat. Butyric acid alone or in combination with acetic is also very inefficiently utilized for maintenance. The addition of propionic acid and butyric acid to varying amounts of acetic acid results in mixtures that can substitute for body fat as an energy source at a constant efficiency of about 85%. This compares with an efficiency of 100% for glucose, the major end product of carbohydrate metabolism in the non-ruminant animal. In other words ruminants, while having the ability to digest feed constituents which are unavailable to animals with simple digestive tracts, utilize the energy they obtain from feed with a lower efficiency.

This is more pronounced when the volatile fatty acids are considered as sources of energy at above maintenance levels of feeding. In this case, the energy of glucose is utilized with an efficiency of about 70%, while that of acetic is only 33% efficient, propionic 55% and butyric 62% efficient.

Mixtures of the acids give results which are to be expected from the results for individual acids—*i.e.*, a mixture high in acetic acid is less efficiently utilized than one in which propionate and butyrate predominate. The overall process of storing excess food is about 50% efficient in the ruminant.

These differences in the efficiency of utilization of the energy of glucose and the volatile fatty acids for maintenance and for synthesis are explained by biochemical research over the last twenty years. Oxidation of nutrients in all species is accompanied by the transfer of part of the free energy of dissimulation to the adenosine phosphates. This energy stored in the pyrophosphate bond of A.T.P. can be used for maintenance purposes in the animal—*i.e.* in the maintenance of osmotic gradients, for transport of substances within the body and for muscular contraction. If nutrients are supplied in excess of maintenance requirements, the excess can be used for growth or stored as fat. This involves the stepwise synthesis of long chain molecules from smaller units and the energy required must be supplied from that stored in the A.T.P. pool originally captured in the oxidation of the absorbed nutrients.

It is now known that the biochemical pathways of synthesis of fat, protein and carbohydrate are not exactly the reverse of the energy yielding oxidation steps and that more energy is required for the synthetic steps than is required for maintenance.

THE FACTORS WHICH CONTROL MAXIMAL FOOD INTAKE

It seems likely that the regulation of food intake is based on opposing reflex mechanisms which aim at maintaining a state of constancy within the body. In simplest form the basic ones are probably "hunger" (which induces feeding behaviour) and the mechanism of "satiety" (which is inhibitory to feeding behaviour).

The main consideration in connection with feed capacity as a determinant factor in efficiency for ruminants is evidently the factors which limit intake. There is considerable evidence with non-ruminants to show that appetite for food is determined by both the physical distension which it causes in the gut, and by homeostatic mechanisms whereby the animal equates its intake of energy to its particular needs. That is, the non-ruminant tends to eat to a constant energy intake unless, of course, the stage is reached where it is physically incapable of consuming enough of poor quality rations.

Blaxter *et al.* (1961) have pointed out that the reverse is true for ruminants which eat more of high quality diets than low quality and have suggested that the mechanism concerned is purely one of digestive tract distension which is a function both of the digestibility of the food and its rate of passage through the gut. Blaxter *et al.* (1961) believe that homeostatic regulation of feed intake comparable to that seen in poultry and pigs operates in ruminants only when the feed given has an apparent digestibility of over 80%. So, for practical purposes, increase in the nutritive value of a ration for ruminants should lead to a more spectacular improvement of total efficiency of feed conversion for ruminants than it does for non-ruminants. It enables the ruminant to eat more of a ration that is more efficiently utilized. Blaxter *et al.* (1961) have shown that an increase in digestibility of a fodder from 50 to 55% results in an increased liveweight gain of 100%, made up of an increased intake and increased energy digested.

Blaxter *et al.* (1961) have suggested, as a result of these studies, that voluntary intake of a fodder by an animal can be used as an index of its nutritive worth over a wide range of fodder quality. Crampton *et al.* (1957) also found that voluntary intake of fodders was a better index of their nutritive value than either their chemical composition or TDN content.

EXPERIMENTAL RESULTS

In order to obtain herbage with which to attempt to correlate chemical composition and rumen fermentation pattern with weight gains in sheep, ryegrass strain trials have been run in three successive years as a joint project by Massey College and the Grasslands and Plant Chemistry Divisions of D.S.I.R. (described in detail Rae *et al.*, 1961). Sheep were pastured on either perennial ryegrass, short-rotation ryegrass, perennial ryegrass and white clover, or short-rotation ryegrass with white clover.

Two varieties of ryegrass were chosen for comparison as it was felt that the number of variables from the point of view of chemical composition would be less than between two distinct species of plants. The objective in stock management was to ensure that sufficient pasture was available at all times so that growth rate was not limited by pasture scarcity.

In the first trial, ewe hoggets were put on all plots in May, 1957, and body weights taken at approximately monthly intervals. Rams were put with the ewes in March, 1958. The lambs

TABLE 2: AVERAGE LIVeweIGHTS, FROZEN CARCASS WEIGHTS, WEIGHTS OF RUMEN CONTENTS, VOLATILE FATTY ACID LEVELS FOR GROUPS OF EWES FED ON FOUR DIFFERENT TYPES OF PASTURE FOR 18 MONTHS (1959-60).

Criteria	P	Pasture Type		
		P+C	SR	SR+C
Final liveweight (lb)	97	125	120	137
Frozen carcass weight (lb)	40.9	59.1	61.2	69.1
Rumen contents weight (lb)	11.7	10.5	8.1	8.1
Rumen contents weight/100 lb body weight	12.10	8.4	6.75	5.9
Volatile fatty acid (mM/100 ml)	11.81	13.40	12.26	14.67

were weaned early December, 1958, and the ewes slaughtered. The growth curves of the animals on the different treatments separated very early and at slaughter the ewes on short-rotation ryegrass (SR) averaged 25 lb liveweight heavier than those on perennial ryegrass (P). The addition of clover (C) to the grass species resulted in advantage of 16 lb above perennial ryegrass alone and 10 lb above short-rotation ryegrass alone. The average daily weight gains of the lambs on P, P + C, SR and SR + C were 0.30, 0.40, 0.38 and 0.47 lb respectively.

These results were confirmed in the second trial in which the object was to try to obtain an explanation for the differences in weight gains. Animals were slaughtered, four at a time (one taken at random from each treatment), immediately after removal from pasture. Rumen fill was determined as well as volatile fatty acid concentration and, in the case of the P and SR+C treatments, the proportions of the individual acids.

The results of this second trial are shown in Table 2.

The difference in rumen contents weight is even more striking if referred to the 0.734 power of the body weight. In contrast to the negative correlation between rumen contents weight and body weight on different treatments, there is, as would be expected, a positive correlation within a treatment. The individual volatile acids produced in the rumens of the animals were only determined for the two extreme treatments—*i.e.*, P and SR + C. The results are given in Table 3.

SR + C sheep were significantly lower in acetic but significantly higher in both propionic and butyric acids than animals on P.

In ruminants the direct absorption of the volatile fatty acids from the rumen into the blood is facilitated by papillae

TABLE 3: PERCENTAGES OF INDIVIDUAL FATTY ACIDS FROM SHEEP RUMENS OF ANIMALS ON PERENNIAL RYEGRASS AND SHORT-ROTATION RYEGRASS PLUS WHITE-CLOVER

<i>Pasture species</i>	<i>Acetic</i>	<i>Volatile Fatty Acid Propionic</i>	<i>Butyric</i>
Short-rotation ryegrass			
Perennial ryegrass	74.5 \pm 2.4	20.7 \pm 1.4	4.8 \pm 1.6
+ white clover	61.4 \pm 2.2	25.3 \pm 1.4	12.3 \pm 1.6

which cover the inner surface of the rumen. It had been thought that the development of these papillae was the result of the physical nature of the food but it is now known that the volatile fatty acids exert a much greater stimulating effect on the appearance of the papillae examined. Though there was considerable individual animal variation within the four treatments, it was obvious that the papillae from the rumen walls of SR + C animals were much better developed than those from the P fed sheep. This increased papillary development with higher propionate and butyrate levels is in line with the results of Sander (1959), at Cornell, who showed that the infusion of sodium butyrate or propionate into fistulated calves resulted in the growth of papillae; acetate, glucose and sodium chloride were largely ineffective.

The results reported by another member of Loosli's group at Cornell are of interest. Two rations with different ratios of hay to concentrate, 9 : 1, and 1 : 9, were fed for 30 weeks to 7-week-old calves. The high-hay calves (high acetate) had much larger rumens (61 versus 37 litres) and poorer papillary development than those receiving the high concentrate ration (higher propionate).

The results obtained from these two trials appear explainable on the basis that the two grasses differ in fibre content and are both improved by the addition of a supplement of clover, which is relatively high in readily fermentable carbohydrate. The additional improvement in liveweight obtained with clover is less in the case of the better grass (SR 10 and 17 lb) than in the case of the poorer (P 25 and 28 lb). This is in line with observations that go back to the time of Forbes and his associates, that the nutritive value of a feedstuff is not constant. It depends on the ration to which it is added. Corn has a smaller net energy value when added to good lucerne hay than when added to a ration of straw. These observations are readily explained with our present knowledge of the fermentation patterns determined for these feeds.

In a third trial carried out during 1961, it was planned to repeat the above trials and in addition to carry out some treatment reversals, to determine whether similar treatment differences were attained at various seasons of the year. A similar pattern of weight gains was found, as in the first two trials, except in the case of P+C which produced better gains relative to the other species, than previously. This is probably due to considerable contamination of the pasture by other species, and a much higher proportion of clover.

Interesting additional information has been gained in that the animals which were switched after four months from P to SR + C, and vice versa, made weight gains similar to those that had been on the treatment all the time. This is demonstrated in Table 4.

TABLE 4: EFFECT ON LIVEWEIGHT GAIN OF SHEEP OF REVERSAL OF FEED FROM PERENNIAL RYEGRASS TO SHORT-ROTATION RYEGRASS AND *Vice Versa*

<i>Treatment</i>	<i>Liveweight Gain Sept. 7 to Nov. 11 (lb)</i>
SR + C, prior to Sept. 7; P from Sept. 7 to Nov. 17 ..	5.1
P continuously	7.3
P prior to Sept. 7; SR + C from Sept. 7 to Nov. 17 ..	19.7
SR + C continuously	20.6

The P (continuously) animals had, as before, considerably larger rumen contents weight in relation to body size than the SR + C (continuously). After the two-and-a-half month change of diet, the animals P to SR + C had rumen contents weights which had decreased significantly and SR + C to P had increased.

These results indicate that rumen fill is by no means a constant feature when once developed, and that factors other than physical distension can limit intake. The fact that the amount of rumen contents of the P sheep have decreased from that typical of the P pasture to that typical of the SR + C, and that the average weight gains have increased to be similar to those that have been on the SR + C throughout the trial, would indicate a greater importance for a homeostatic mechanism limiting intake than has been considered by Blaxter *et al.* (1961).

Further work is planned with fistulated animals to investigate the differences in fermentation patterns and rate of passage of ingesta that must contribute to the differences observed.

DISCUSSION

Whether the differences obtained with the various pastures are entirely due to the differences in the carbohydrate composition of the pastures is still speculation until further chemical work is carried out. Other substances in the plant material could, in addition, influence intake and alter the fermentation pattern.

Recent work (Annison and White, 1961) has indicated that, although little glucose is absorbed from the alimentary tract of the sheep, glucose appears to be only slightly less important in the metabolism of ruminants than in non-ruminants. Propionate is undoubtedly a major precursor of glucose for sheep, but on Annison and White's calculations can supply only 50% of the glucose used per day. Lindsay (1959) believes that gluconeogenesis from protein must be a major source of glucose for sheep. If this is true, this source of energy is obviously of importance under New Zealand conditions of high protein pastures.

It will be realized that work in recent years has greatly increased our knowledge of the metabolism of ruminants. The early excellent work of Kellner and of Armsby which has proved so very useful in developing methods of food evaluation in farm animals is receiving a more logical explanation. This will continue to improve as understanding of the chemical, physical and biological factors that control the bacterial population of the rumen increases, together with knowledge of the energetics of dissimulation of the products of the bacterial fermentation of the carbohydrates in the ruminant's diet.

Shaw (1960) has stated, "It is proposed that a simpler determination of the molar proportions of volatile fatty acids in rumen fluid will suffice to establish the relative production of the rumen volatile fatty acids on any given diet, and will serve as a valuable guide to the efficiency of rations for producing milk of high or low fat content, gains in body weight and even the prevention of bovine ketosis."

This appears to be very true under indoor feeding conditions with standard rations, but in the field additional factors still have to be contended with in evaluating pasture plants, such as change in chemical composition with maturity, at periods of flush growth, "palatability", and, of course, all these must still be related to the plant's production under a particular set of environmental conditions,

In considering the most effective method of co-operation in research aimed to produce the maximum amount of animal product per acre from pasture, it appears that the plant breeder has, in addition to his present responsibilities, to take into account the amount of a particular plant the animal will eat and its fermentation products in the rumen. Rather than having to determine this on all new plant material, some chemical basis for appraisal which correlates with the fermentation pattern must be sought. The animal husbandman should be interested in the efficiency of utilization of the fermentation products for milk, meat and wool production. In effect, the common meeting ground for plant and animal research workers should be the rumen.

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