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Ruminant Metabolism

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IT has been stated in a previous paper that pasture quality can only be assessed in terms of the thrift and productivity of the animal which eats that pasture. In the past those concerned with pasture production have of necessity thought chiefly of achieving greater production over as great a period of the year as possible. They have been interested in quantity not quality. The animal man has taken the new strains of pasture plants provided by the plant breeder and found that with greater herbage yield he has had to change his ideas on how to utilise it and has also found in some cases that livestock troubles have increased. Greater carrying capacity is not just the simple procedure of achieving more dry matter per acre. In order that the Grasslands worker can achieve quality as well as quantity in his product, the animal man must be able to tell him what is wrong with the animal's diet and what is the ideal balance of nutrients for maximum animal production and thrift.

This, we realise, is a very tall order and I hope to be able to show you that though a great deal of work has been done on non-ruminants, quality of food for these animals has a very different meaning from food quality for ruminants.

The common ground for the plant and animal man is the digestive system of the ruminant. It is only of recent years that the importance of the study of ruminant physiology has been realised but even now there are many aspects that could be more actively pursued.

In a monogastric animal such as ourselves, the digestive system breaks down the ingested food into compounds of lower molecular weight for absorption into the blood stream. The complex substances are broken down to their simpler components and no conversion into other compounds takes place. A small amount of bacterial digestion of food residues occurs in the alimentary tract but normally is of little importance. The usefulness of protein to such animals as the rat, chicken, pig, and man is now known to depend chiefly on the amino acid composition and particularly on the content of about ten so-called "essential" amino acids. Leaf protein is a valuable and well balanced source of amino acids for these animals. Its main drawback as a source of protein is the large quantity of indigestible material that accompanies it and this is the main factor limiting its consumption by non-ruminants. The structural carbohydrates of the plant are not broken down by digestive enzymes; only the soluble carbohydrate is broken down to glucose in the stomach and absorbed as such.

Ruminants living for the most part on leaves have achieved a great modification of the intestinal tract above the stomach into three additional compartments. Immediately on ingestion the food undergoes digestion by bacteria and other micro-organisms in the first two of these. The first stomach, the rumen, is in effect a large fermentation vat (40-60 gallons in a cow) into which food and saliva pass and a vigorous fermentation takes place (in the absence of air). There is no secretion of digestive juices in the rumen.

The ruminant digestion of hexose sugars and starch (the chief carbohydrates of monogastric nutrition) is less economical in terms of carbon and hydrogen than is normal enzymatic digestion. Part of the carbohydrate is lost as carbon dioxide and methane in producing the compounds which are absorbed into the blood stream and part is lost as heat. However, when we consider coarse fodders containing cellulose and pentosans, materials which are indigestible except by the aid of bacteria, the ruminant mode of digestion makes available to the animal sources of energy that are not available to other animals.

The food that the ruminant actually obtains is not in the main the grass that it eats but the micro-organisms that have fermented it and the soluble products of their metabolism. These soluble compounds are absorbed chiefly through the rumen wall and the micro-organisms pass on to be digested in the fourth stomach.

The main products of the fermentation of the carbohydrates are (1) the lower fatty acids, acetic, propionic and butyric, (2) gas, principally carbon dioxide and methane, (3) bacteria, and vitamins of the B complex.

The rate at which fermentation proceeds in the rumen may be assessed either by the quantity of gas produced or by the rate of appearance of the acids in the rumen fluid. Cole (1942) estimated that the volume of gas produced by cattle (fed on alfalfa hay) was in the region of 5 litres in the half hour before feeding, an hour after feeding the volume increased to 20 litres per half an hour. This was followed by a rapid decline during the next three hours. This indicates how rapid is the onset of fermentation and the vigour with which it proceeds.

It is small wonder than the rumen distends so rapidly when the animal is unable to get rid of this gas produced during fermentation by the normal means of belching, as in bloat.

The lower fatty acids are absorbed through the rumen wall into the blood stream and carried to the liver. Schambye and Phillipson (1949) have shown by determining venous and arterial blood glucose and total volatile acids at regular intervals after feeding, that considerably more volatile acid than glucose enters the blood as it circulates through the stomach and intestines. The experiments leave no doubt that as a result of bacterial fermentation in the rumen and the large intestine, the host obtains very little glucose and a large amount of short chain fatty acids. Of these acids, acetic predominates with lesser amounts of propionic and butyric. The adaption of the alimentary tract of the ruminant to allow bacterial digestion on a large scale suggests that in turn the metabolism of the animal may be modified to utilise the products of fermentation rather than glucose

This is supported by the work of Popjak, French, and Folley (1951), who have shown that acetate is used as a precursor of milk fat in the cow.

The first evidence of the utilisation of acetate for fat synthesis by the lactating mammary tissue was obtained by Folley and French who studied the respiration in vitro of slices prepared from the lactating mammary gland of ruminants and non-ruminants. They showed that slices from the glands from non-ruminants utilise glucose, and acetate only in the presence of glucose. Fat synthesis in animals is an energy requiring process and it seems possible that in the ruminant in which carbohydrate is being assimilated as acetic acid, a cellular adaptation has taken place in such a way that the oxidation of acetate is the primary energy source. In non-ruminants the energy is derived from the metabolism of carbohydrates. Propionic acid is the only acid of the three formed that is a producer of increased glycogen in the liver.

As might be expected from this work the amount of acetate produced in the rumen appears to be linked to the percentage of butterfat appearing in the milk.

Tyzink and Allen (1951) found that by reducing the roughage intake of cows in the form of hay to 3lb. per day and giving them as much concentrates as they could eat, the fat percentage was depressed in two weeks by 1-2%. The ratio of volatile acids in the rumen was determined and the animals on normal roughage had levels of acetic 65%, propionic 20%, butyric 15% which is fairly normal. On the low roughage diet acetic acid was decreased and propionic increased to a level higher than acetic with butyric staying about the same. Four of the low roughage cows were fed sodium acetate. Milk fat increased within 24 hours of the first feed of acetate and reached normal level when given at 1lb. daily. When acetate feeding was discontinued the milk fat returned to the sub-normal low roughage level. Administration of propionic acid did not correct the depression of milk fat. With high propionate in the rumen the animals put on weight. It was found in earlier work that the low roughage high concentrate diet gave a raised iodine value and a lowered Reichert value for the butterfat. This may be the result of less acetate being available for the synthesis of the saturated fatty acids of butter fat.

In New Zealand we have a maximum iodine value in winter and spring (Cox and McDowall) which is the period of lowest roughage. Whether this has any relationship to the acetic acid level in the rumen remains to be seen.

In vitro investigations on the rumen wall have shown (Pennington, 1952) that the rumen epithelium, besides allowing the fatty acids to pass through into the blood stream has the ability to metabolise them.

The rate of utilisation of butyrate far exceeds that of the other acids and 50% of the butyrate carbon which is utilised appears as ketone bodies, of which aceto-acetate predominates.

It appears from the work of Quastel and Wheatley (1933) and Jarrett and Potter that propionate has antiketogenic properties and it will be of interest to see if this applies to the rumen epithelium. If this is so the rumen propionate and butyrate concentrations may well be of importance in ketosis. Schultz (1950) found that feeding sodium propionate (¼lb. daily) gave recovery from ketosis in 18 cows. Appetite returned in two days and the blood picture was normal in 10 days. The feeding of propionate by mouth gives a marked elevation of blood glucose. If glucose is given by mouth the amount available for absorption is very small as it is unlikely that much escapes fermentation in the gut. As Schultz points out it is unlikely that any one ketosis treatment will work on all cows because of the complicated nature of the disease.

Another difference between ruminant and non-ruminant I might point out is that the volatile acid in the peripheral blood of sheep is many times greater than that reported for man or dog while blood glucose in adult sheep is about half that found in most other mammals.

The ruminant is well adapted to the use of carbohydrates not available in other animals but its digestive system is not ideal for making maximum use of the nitrogenous constituents of the herbage.

Protein of the pasture is partly broken down by the micro-organisms and in part passes on to the true stomach for enzymatic digestion. Part of that broken down by the micro-organisms is used by them and built into microbial protein while some is converted to ammonia and absorbed directly from the rumen and excreted in the urine as urea.

The wastage of protein in the rumen is determined by (1) the amount of the protein degraded by the micro-organisms (2) the extent to which this non-protein nitrogen is utilised by the rumen microflora. The bacteria require carbohydrate as their energy source for growth to make use of this non-protein nitrogen. If there is not enough fermentable carbohydrate available for the bacteria to utilise all the ammonia formed, the excess is absorbed and excreted, and is waste as far as the animal is concerned.

It is generally agreed that a fair proportion of the protein digested by the anmial in the abomasum is microbial protein which has been shown experimentally to be a high gade, well balanced protein for rats.

That protein synthesis by the microflora can result in an improvement of the quality of plant proteins for sheep is shown by the synthesis of sulphur containing amino acids. Sulphur can only be utilised by non-ruminants in organic form and it has been considered because some plant proteins are rather low in sulphur-containing amino acids, these may be a limiting factor in wool growth which has a high content of cystine (Marston 1939). However, it has been shown by Block and Stekal (1950) using radioactive sulphur that the rumen organisms synthesise sulphur containing amino acids from inorganic sulphate and so make up for the deficiency of the plant protein.

In protein metabolism in the ruminant there are thus two opposing tendencies at work.

(1) Non-protein nitrogen poor in essential acids is converted into high grade protein.

(2) Food protein of good amino acid composition is attacked in the rumen and converted into ammonia which to a great extent is absorbed and excreted as urea.

As an example of the first is the utilization of urea as a partial protein substitute for beef cattle feeding in the States where corn is commonly used for fattening.

An example of the second tendency is demonstrated in the experiments of Cuthbertson and Chalmers (1950) who investigated the nitrogen balance of pregnant ewes maintained on low-plane rations, comparable to those eaten by Scottish hill sheep during the winter months. Ewes in negative nitrogen balance were given a casein supplement by mouth. A large proportion of the additional protein (60-70%) was deaminated in the rumen and most of the ammonia formed excreted in the urine. The ewes remained in a state of negative balance. When the rumen was by-passed and the same quantity of nitrogen added by fistula in the form of a casein hydrolysate the nitrogen was retained by the ewes to a much greater extent.

This emphasises the disadvantages of bacterial digestion when easily available proteins are concerned. Chalmers and Synge (1950) correlated the greater value of herring meal supplements over casein supplements for sheep with the lower production of ammonia in the rumen from the herring meal.

McDonald (1948) has shown that zein, the principal protein of corn, is less completely converted into ammonia in the rumen of sheep than is casein. So the protein zein, together with non-protein nitrogen as in urea feeding, is probably of more use to the ruminant than casein.

This is in direct contrast to the state of affairs in non-ruminants where it was shown many years ago for growth of rats that casein is a very good protein, whereas zein is very poor when fed as the sole source of protein. This is due to zein being deficient in lysine and tryptophane.

We can see that it is not the crude protein determination or even the amino acid analysis that determines the value of protein to ruminants. The solubility of the protein and its susceptibility to microbial degradation, the amount of non-protein nitrogen and the nature and amount of the carbohydrate being simultaneously fermented, are obviously important factors.

The experiments quoted here have been concerned with "artificial diets" and we do not know how these findings apply to animals at pasture. However, we can say that the crude protein figure has very restricted value. We need to know in what form the nitrogen is present and its ratio to the soluble carbohydrate. It may well be that our high producing pastures high in protein in winter and spring could do with supplementary feeding with carbohydrate.

Besides the wastage of protein from the animal point of view we do not know yet what deleterious effects high levels of ammonia in the rumen have on the well being of the animal.

When we come to methods of conservation of pasture Synge (1952) has pointed out that a big mistake may be made in assessing losses on crude protein analyses. The question of hay versus silage is not a matter of quoting results for digestible crude protein. In silage making much of the protein of grass is converted into soluble nitrogenous substances of lower molecular weight and the soluble carbohydrate is fermented to give the desired acidity. Silage making has brought about just the state of affairs we do not want in a fodder for ruminants; an increase in the easily deaminated nitrogenous constituents and a decrease in the fermentable carbohydrate. With hay this worsening effect cannot be so great and even less so with dried grass.

I think that if I have done nothing else I will have shown you how little we know of what constitutes a balanced diet for ruminants. Pasture quality is something we do not yet understand. Crude fibre and crude protein determinations may well lead us astray. There is a great deal of work ahead of us in the fields of plant chemistry, the biochemistry of rumen fermentation and farm animal physiology.

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Discussion

Mr. ANDREWS: Are there any special diets which yield excessive amounts of butyric acids in the rumen?

Dr. JOHNS: Dr. Phillipson at the Rowett has found that sheep fed on flaked maize produced an abnormal microbiological picture in the rumen. **Clostridium butyricum** appeared in large numbers. However, the amount of butyric acid was low. This may have been due to the low pH (less than 5) at which pH it has been found that the rate of absorption is more rapid than at pHs near neutrality. I know of no other work on attempts to produce high butyric acid in the rumen.

Mr. HANCOCK: Would the butyric acid in silage throw these balances out?

Dr. JOHNS: The amount of butyric acid in a poor silage may be deleterious to the animal but it is probable that the important factor is the ratio of butyrate to propionate in the rumen.

Mr. ANDERSON. Would propionate help in the treatment of pregnancy toxaemia?

Dr. JOHNS: I do not know, but if the cause is lack of energy it seems likely that it would.

Mr. EDMOND: What proportion of the animal's intake would be affected by the rumen microflora and how variable is the microflora population over the year.

Dr. JOHNS: Both would depend on the food the animal is eating rather than the season of the year.