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CHAPTER 3
DIGESTIVE PHYSIOLOGY OF RUMINANTS

3.1 INTRODUCTION

The main renewable carbohydrate resources in the world are cellulose, hemicellulose and pectin which occur in all plant cell walls in association with lignin. Lignin strengthens the plant's structure, but is often present in high concentrations and physically protects the cell-wall material from degradation by bacteria. Lignin is broken down by microbes under both aerobic and anaerobic conditions and lignin builds up to high concentrations only under certain conditions, eg. in acid conditions such as occur where peats accumulate. Lignin is broken down steadily in most soils by microbes.

Microbes in the rumen degrade lignin slowly and in general feed does not remain in the digestive tract long enough for lignin degradation to contribute nutrients to the animal.

The quantity of lignin is the major factor that limits the utilisation of many plants by ruminants. In general trees and tall-growing plants such as sugarcane and elephant grass come into this category.

Ruminants can digest relatively unlignified plant cell-wall materials through microbial fermentation in the rumen, which places them in a particular niche in the food chain.

The continued use of all ruminants for meat, milk, hide and wool or hair production is justified by:

- Their ability to digest carbohydrate sources not digested by monogastric species
- Their ability to use non-protein nitrogen (NPN) to supply themselves with protein through microbial growth in the rumen
- Their efficient utilisation of dietary protein, provided that it is protected from rumen fermentation
- Their highly efficient use of dietary lipids for productive purposes.

This does not mean that ruminants should never be given feeds that can be readily digested by monogastrics, but their use of such feeds should be minimal. An example is the supplementation of ruminants on high-fibre diets with small amounts of protein meals, which correct imbalances in nutrients available for production and generally have `catalytic roles' in stimulating feed intake and often rumen function. As a corollary to this it is equally important that the breakdown of protein into non-protein nitrogen in the rumen should be minimised.

>From the above introduction, it is obvious that the key to feeding ruminants is an understanding of the mechanisms involved in the fermentation of feed and the availability of end-products from that fermentation. The balance of end-products of digestion in relation to the requirements imposed by the physiological state of the animal affects the efficiency with which the end-products are utilised. Equally, an understanding of the rumen ecosystem and its inefficiencies provides the knowledge required to develop methods for manipulating the end-products of digestion to match the needs of the animal. This information can be used in a systems approach to animal production which aims to optimise the use of the available resources and to match livestock production systems to the resources available locally.

In order to discuss appropriate strategies for manipulating the rumen system and for providing dietary supplements that are largely fermented in the rumen, it is important to present an overview of rumen digestion and the associated constraints.

The feed resources that are used as the basis of diets for ruminants in developing countries (particularly those in the tropics) are:

- Fibrous residues from cereal production, particularly from rice, wheat, maize and sorghum
- Fermentable carbohydrate-rich byproducts from agro-industries, such as molasses from sugar extraction and the brans from processing of cereals
- Pastures.

Fibre and sugars are fermented at different rates in the rumen. However, the end-products of the fermentation are the same but vary in their proportions. A knowledge of the end-products of fermentation of different feeds is necessary in order to develop efficient supplementation of these diets. In this presentation the interactions within the rumen that lead to these variations in end-product production are discussed.

3.2 THE DIGESTIVE TRACT OF HERBIVORES

The dominant feature of the digestive tract of all herbivores is an enlarged region(s) which provides an environment that is capable of supporting a dense population of micro-organisms that ferment carbohydrates and other plant materials to produce mainly volatile fatty acids (VFAs), methane and carbon dioxide and the energy (ATP) for the growth of the micro-organisms.

The digestive tracts of the sheep (or cow) and the horse (hind-gut fermenter) are shown in Figure 3.1. The digestive tract of the pig is included for comparison since the pig is an omnivore which, under some circumstances, may obtain a significant proportion of its nutrients from fermentative digestion in the caecum and large intestine.

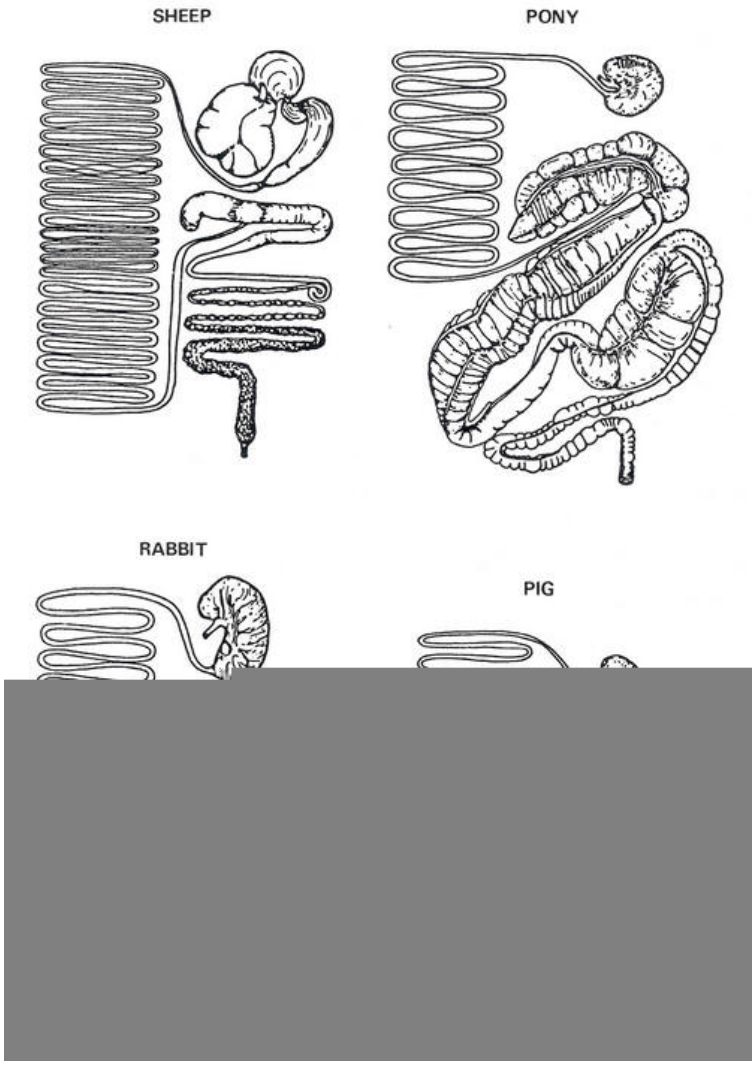


Figure 3. Diagrammatic representation of the digestive tracts of the sheep, horse, pig and rabbit (Source: Dukes 1977).

In many herbivores, particularly the ruminant, there are two fermentation sacs, one before and one after the true stomach. The quantity of material fermented varies in proportion to the relative sizes of these organs and the length of time the digesta are retained in each organ. Fermentative digestion which precedes gastric and intestinal digestion is more easily buffered by salivary secretions than post-gastric and intestinal fermentation, which may lead to more efficient microbial growth. Fermentation in the caecum is buffered by intestinal secretions and ammonia from plasma urea. The rumen micro-organisms receive substrate (forage) directly and are capable of fermenting a wide range of materials. The digesta reaching the caecum are much less varied and the proportion of fermentable dietary carbohydrate and nitrogen is much lower. Microbes in the caecum depend mainly on endogenous nitrogen, particularly urea from blood.

Although fermentations in the rumen and in the caecum or large intestine are probably stoichiometrically similar, it is unlikely that the microbes responsible in the two regions are the same.

3.2.1 Ruminant digestive tract

The mouth and teeth of ruminants are well adapted for the prehension and grinding of plant parts and there are well developed salivary glands in the mouth. A large volume of saliva is secreted even under lush pasture conditions, and this aids in mastication of the feed.

The true stomach or abomasum is preceded by three divisions or diverticula which are lined with a stratified squamous epithelium. The rumen and reticulum are connected by a large orifice and the movement of digesta between these two regions is relatively unrestricted. The rumen and reticulum together with the omasum are referred to subsequently as the rumen. The reticular groove (the oesophageal groove) extends from the cardia to the omasum. It is formed by two muscular folds which can close to direct material from the oesophagus into the abomasum, bypassing the rumen. The groove is less functional in adult ruminants than in suckling animals unless the stimulus has been maintained into adult life by providing nutrients by suckling from a bottle (see Orskov 1983).

The reticulo-omasal orifice is a `valve' which retains feed particles within the rumen until they are reduced to 1 to 2 mm in diameter. Comminution of feed particles depends upon the extent of chewing, the rumination cycle, the rate of fermentation and physical breakdown through mixing. The particles leaving the rumen are therefore usually less than 1 mm in diameter and most of the fermentable carbohydrate has been solubilised.

The omasum is spherical and covered with short blunt papillae arranged in such a way that digesta move between the laminae to the abomasum. Much of the water and electrolytes are absorbed in the omasum.

The abomasum (or stomach), duodenum, jejunum and ileum (the small intestines) seem to have similar functions to those in monogastric animals. It is in these organs that the rumen micro-organisms and the unfermented but digestible residues of the feed are subject to enzymatic digestion and their products absorbed. The large intestine (which consists of the caecum and colon) is posterior to and joins the ileum at the ileo-caecal orifice. The caecum has one blind sac that projects caudo-laterally. The caecum and colon are areas of microbial colonisation and fermentation occurs in these areas. Under most dietary conditions in ruminants fermentation in the large intestine contributes little to digestion of a feed (5-10%).

Blind sacs are present in many of the fermentative organs, particularly those that are tube-like and in which little mixing occurs. The blind sac of the caecum is a reservoir of micro-organisms, which `seed' the digesta thus ensuring further fermentation in the large intestine. The persistence of fungi in the tract may depend on the presence of a blind sac with a slow rate of turnover of the contents.

3.2.2 The rumen environment

The rumen environment appears to be controlled by:

- The type and quantity of food eaten
- Periodic mixing through contraction of the rumen
- Salivation and rumination
- Diffusion or secretion into the rumen
- Absorption of nutrients from the rumen
- Passage of material down the digestive tract.

Only under abnormal circumstances is this environment drastically perturbed. For instance, if grain is suddenly introduced into the diet, lacticacidaemia may occur because of a drop in ruminal pH, growth of *Streptococcus bovis* and the accumulation of lactic acid.

Saliva is continuously added to the rumen and maintains the contents in a fluid state, so facilitating access of micro-organisms to the plant materials. The volume of saliva secreted by ruminants is dependent on diet. The microbial community also affects salivary flow, which may be reduced by the presence of a population of protozoa. These rapidly assimilate starch and sugars and remove the need for copious salivation to maintain rumen pH.

The saliva is a buffered bicarbonate solution of about pH 8 containing high concentrations of sodium and phosphate ions. The saliva and the movement of bicarbonate ions across the rumen epithelium maintain the pH within narrow limits. The buffered rumen liquor is a favourable medium for growth of anaerobic bacteria, fungi and protozoa and allows VFAs to accumulate in the fluid (up to 0.2 molar).

Neutral conditions in the rumen are maintained by continual adjustment of the pH of the ruminal fluid by the above processes and by absorption of VFAs, thus ensuring continuous fermentation. The biomass of microbes in the rumen is maintained at a constant level by the passage of microbes down the digestive tract, and also by death and lysis of the micro-organisms within the rumen. Methane and carbon dioxide are produced as end products of fermentation. At low rumen pH, carbon dioxide comes out of solution and accumulates in a pocket in the dorsal sac. Methane and carbon dioxide are largely eliminated by eructation (Dougherty et al. 1964). At high rumen pH most of the carbon dioxide produced by fermentation or entering in saliva is absorbed and excreted via the lungs.

3.2.3 Rumination

Regurgitation of a `bolus' of rumen digesta is a reflex mechanism that is superimposed on the cyclic contractions of the rumen. Generally, feeds are eaten with only a small amount of mastication and are regurgitated and masticated later. Recent work has demonstrated that on grass-based diets about twice as much dry matter passes through a rumination cycle as is consumed (Ulyatt 1982) (see Figure 3.2). On ground diets or ground and pelleted diets rumination is absent or much reduced.

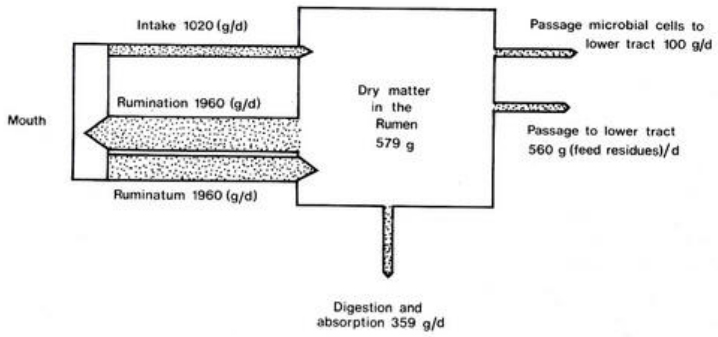


Figure 3.2 The rumination-digestion cycle. The diagram shows the flows of dry matter through the rumen of a sheep fed at hourly intervals a total of 1020g chopped lucerne hay over 24 hours (Source: Ulyatt 1982).

3.2.4 Rumen microbial ecosystem

The microbial ecosystem in the rumen is complex and highly dependent on diet. The vast majority of ruminants consume a mixture of carbohydrates, of which cellulose and hemicellulose are the largest components. However, at times the diet can contain large amounts of soluble carbohydrates or starch (eg. molasses or grain).

Plants have developed molecular structures in their cell walls specifically to deter invasion by micro-organisms. In the rumen the main agents that break down carbohydrates are anaerobic bacteria, protozoa and fungi. The anaerobic bacteria are the principal agents for fermenting plant cell-wall carbohydrates but the anaerobic phycomycetous fungi, discovered simultaneously by Orpin and Bauchop (see Bauchop 1981 for a review) may, at times, be extremely important.

There appears to be a close relationship between fungi and the other microbes in the rumen since the fungi appear to be the first organisms to invade plant cell walls, which allows bacterial fermentation to start and to continue.

Some rumen microbes synthesise enzymes that degrade the most complex plant structures, whilst others use only simple compounds such as cellobiose or glucose. Some bacteria in the rumen assume a syntropic association, where one organism uses the products of fermentation of another and the removal of the end-product allows further fermentation of the primary feed resource by the first organism.

3.3 RUMEN ORGANISMS

The phycomycetous fungi

The anaerobic fungi of the rumen have only recently been isolated and cultured from the rumen. Anaerobic fungi have been shown to be present in the rumen of a number of animal species--- including sheep, goats, cattle and members of the deer family. They have also been found in the caecum of horses and elephants and in the `pseudo-rumen' of kangaroos (Bauchop 1980). Thus they are probably present in all herbivorous animals and may exist in anaerobic environments such as occur in deep-sea sludges and in slurry in methane digestors.

For many years the flagellate organisms observed in the rumen, particularly in defaunated sheep (ie. no protozoa in the rumen), were described as protozoa. These were probably the motile infective stage of fungi (zoospores). Although flagellate protozoa occur in the rumen, the zoospores can be identified by the more rapid movement of their flagellae. The anaerobic roll tube (Hungate 1966) is now used to culture the zoospores, which gives an estimate of their numbers and is more reliable than counting live zoospores.

The vegetative state of the fungi consists of a sporangium arising from rhizoids (similar to hyphae) which grow through the plant tissues. Sporangia growing on lucerne hay and meadow hay are shown in Plate 3.1 and Plate 3.2. Sporangia protruding from the surface of plant particles release zoospores shortly after the food is consumed. These are able to reach newly ingested fibre and invade the tissue, usually via damaged parts of the plant or through the stomata of leaves. They then encyst, germinate and grow through the plant particles. Refractory materials, such as the leaves of wheat straw, when suspended in nylon bags in the rumen of sheep or cattle are heavily colonised by anaerobic fungi, with the areas around the leaf ribs the most densely populated (Plate 3.3). The life cycle of the anaerobic fungi is shown in Figure 3.3.

Plate 3.1 Scanning electron-micrographs of sporangia of rumen anaerobic fungi attached to lucerne stem from rumen digesta of a steer 24 hours after feeding. Bar marker = 50mum (Source: Bauchop 1985).

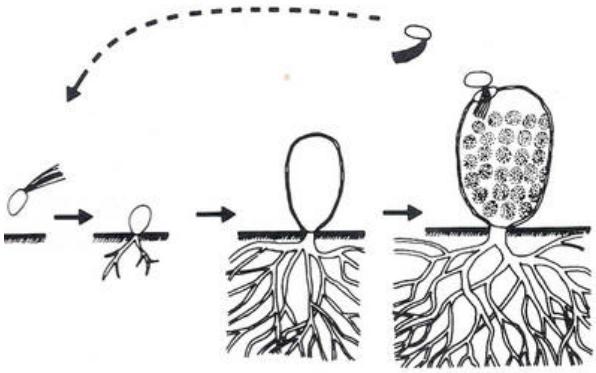


Figure 3.3 Life cycle of the anaerobic fungi in the rumen showing the release of the zoospores from the sporangia and re-infection of particulate digesta (Source: Bauchop 1985).

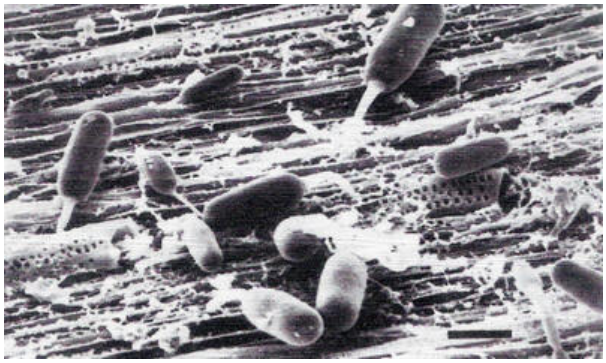


Plate 3.2 Scanning electron-micrographs of sporangia of rumen anaerobic fungi on red clover fragments from the digesta of a steer 24 hours after feeding with meadow hay. Bar marker = 50mum (Source: Bauchop 1985).

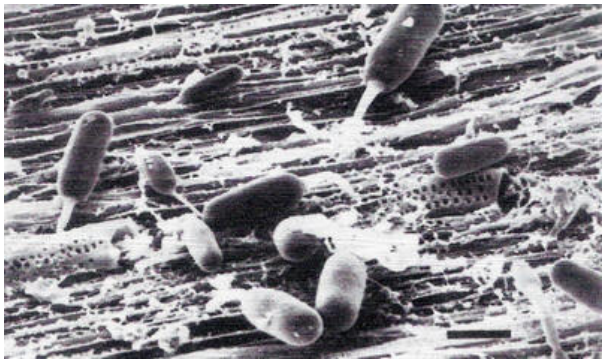


Plate 3.3 Rumen anaerobic fungi colonising wheat straw leaves that had been incubating in a nylon bag in the rumen for 24 hours. Bar marker = 50mum (Source: Bauchop 1985).

The fungi appear to be the first organisms to invade and commence digesting the structural plant components, beginning from the inside. They reduce the tensile strength of these particles (Akin et al. 1983) and thus increase particle breakdown in rumination. The damage to digesta particles by fungi allows bacteria to colonise the cell materials. They are thus extremely important initiators of fermentative breakdown of insoluble plant cell wall materials and their presence must reduce any lag-phase of fibre digestion.

The species of fungi isolated from the sheep's rumen include Neocallimastix frontalis, Piramonas communis and Sphaeromonas communis (Orpin 1975, 1976, 1977) but more are being discovered. These fungi digest some of the plant structural components. It appears to be a reasonable assumption that fungi break hemicellulose-lignin complexes and solubilise lignin but that they do not actually degrade the lignin. This may allow fibre that is physically protected by lignin to be fermented by rumen bacteria.

3.3.2 Protozoa

Protozoa occur in the rumen of sheep and cattle on fibrous diets (which are low in soluble sugars) but their population densities are low (less than 100,000/ml) whereas on diets high in starch or sugars they can reach densities of 4,000,000/ml of rumen fluid. The diet also determines the species of protozoa in the rumen but little is known about the factors that determine the balance of protozoal species or their biomass. For the purpose of this presentation protozoa are divided mainly into the small entodineomorphs (largely *Entodinia* spp.) and the large holotrich protozoa (mainly *Isotricha* or *Dasytricha* spp.). The former occur in animals fed starch-and/or fibre-based diets, whereas the latter have been mainly reported to occur in animals fed sugar/fibre diets (sugarcane) and on fresh grass pastures, which are usually a combination of soluble and insoluble carbohydrates.

Some protozoa are cellulolytic but the major substrates appear to be sugars and starches, which are rapidly assimilated and stored as poly-dextran; this is mobilised as required to provide energy for the growth and maintenance of the protozoa. In this way they often `buffer' the pH of the rumen. Volatile fatty acids are also made available over a more prolonged period. When the population of protozoa is high they may constitute up to 70% of the biomass of the organisms in the liquor with bacteria comprising only 30%.

Protozoa are preferentially retained in the rumen, as indicated by the results of studies comparing the numbers of protozoa in omasal fluid relative to rumen fluid (see Table 3.1) and isotope studies which indicate substantial lysis of protozoa in the rumen (Leng 1982b).

Table 3.1: The presence of protozoa in rumen fluid relative to omasal fluid in sheep and cattle.

Rumen fluid (10^{-5}/ml)	Omasal fluid (% of RF)	
1.4 – 3.8	6 - 29	Weller and Pilgrim 1974
7.2 - 28.4	11 - 42	Nakamura and Kurihara 1978
3.5 – 8.4	30 - 40	Jouany 1978
5.0*	10	Bird *et al. 1978*
7.5	8	Bird *et al. 1978*
2.5 – 5.9#	0- 28	Minor *et al. 1977*
0.5 – 1.3#	41 - 52	Punia *et al. 1984*

#Cattle.

There are a number of possible ways in which protozoa are preferentially retained in the rumen. These include:

- Sequestration to large particles. This seems likely since protozoa are attracted to the highest concentration of soluble carbohydrates which, some time after feeding, is likely to be close to large feed particles. Also electron micrographs prove conclusively that protozoa adhere to feed particles (Bauchop 1980). The photographs show Epidinium spp. (Plate 3.5) or Dasytricha spp. attached to the ends of plant stems in rumen digesta (Plate 3.4) (Bauchop 1980)
- Sequestration onto the rumen wall: Abe et al. (1981) found clusters of holotrichs on the reticulum wall of cattle that had been starved for one day. This is a most interesting finding as it suggests that there is communication between protozoa---how else could they come together in such highly concentrated groupings? Perhaps chemical secretions by protozoa result in groupings of protozoa, as occurs in free-living paramecium (Peres Miravete 1973)
- Increased density of protozoa: Protozoa that have stored starch or sugars become dense and settle in the rumen. Experiments showed that samples taken through the rumen cannula had lower concentrations of protozoa than those taken from mixed rumen contents

after slaughter (Minor et al. 1977)

- Retention of protozoa in the bolus: In rumination, a bolus containing bacteria, protozoa and food particles is regurgitated into the oesophagus and reflexly squeezed as it moves up to the mouth. The liquid and small particles that are separated in this way are swallowed and immediately enter the reticulum and quickly move to the omasum. The protozoa, because of their size, cilia and attachment to large particles, are likely to be retained in the bolus, which when re-swallowed pitches onto the rumen pillar to re-enter a cycle of digesta movement through the rumen.

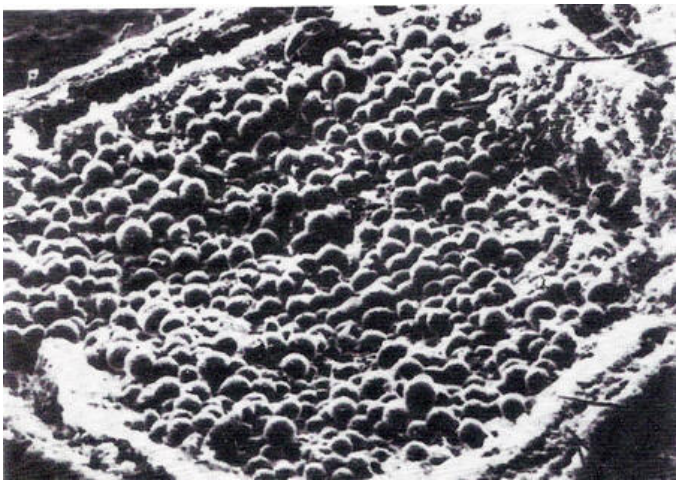


Plate 3.4 Electron-micrograph of Dasytricha spp attached to plant fibres in the rumen (reproduced with kind permission of Dr T Bauchop).

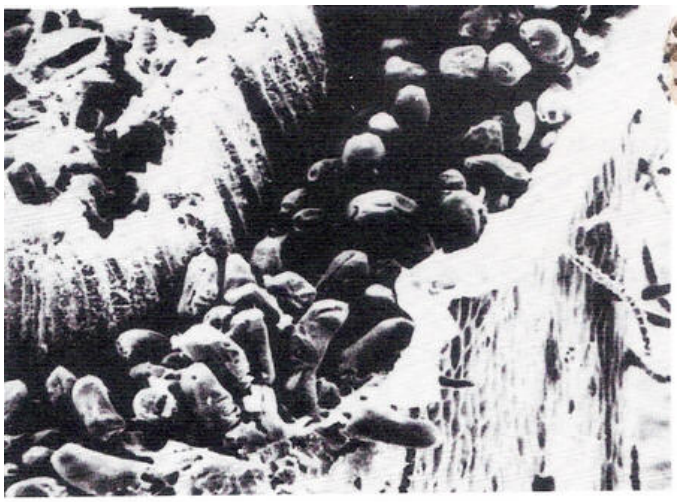


Plate 3.5 Electron micrograph of Epidinia spp attached to plant fibres in the rumen (reproduced with kind permission of Dr T Bauchop).

Although the number of protozoa in omasal fluid is less than that in the rumen (Weller and Pilgrim 1974), this may not be indicative of the number of protozoa flowing down the tract. If protozoa are retained in the rumen, it is likely that they will be also retained in the omasum with its more complex shape. Therefore multiplication of liquid flow rate from the rumen by protozoal concentration in omasal fluid will not give values for protozoa outflow rate. The role of protozoa in the nutrition of the animal and the effects of eliminating them from the rumen (defaunation) are discussed in Chapter 5.

3.3.3 Bacteria

- Bacteria are normally the largest microbial biomass in the rumen. There are a number of distinct groupings of bacteria including:
- Bacteria free in the liquid medium (usually 30% of the total)
- Bacteria attached to feed particles (about 70% of the total)
- Bacteria adhering to the epithelial lining of the rumen
- Bacteria attached to protozoa (mainly methanogens).

The continuous flow of particles out of the rumen necessitates that a proportion of the bacteria detach from particles that have been already largely digested, in order to colonise new material entering the rumen. The number of bacteria in the liquid phase is therefore important in determining the rate of colonisation and therefore the rate of fermentation of feed particles. The bacteria floating free in the rumen are therefore the ones that depend on soluble nutrients but there are also those that are in `transit' between plant particles.

The most important bacteria for fibre digestion are *Ruminococcus flavefaciens, Ruminococcus albus, Bacteriodes succinogenes and Butyrivibrio fibrisolvens*. In some situations *Cillobacterium cellulosolvens* and various *Clostridium* spp. become revalent. Hungate (1966) isolated *Clostridium lochhaedii* from the rumen of cattle fed salt-treated forages. In addition to being a spore former (in contrast to normal rumen bacterial species), this organism has cellulolytic activity many-fold greater than that of the average rumen organism. The major species of rumen bacteria that degrade cell wall polysaccharides are shown in Table 3.2. In general, the bacteria need to be attached in order to digest fibre, although some organisms appear to secrete extracellular enzymes.

Table 3.2: Major species of rumen bacteria degrading cell-wall polysaccharides.

Cell wall polysaccharide	Species
Cellulose	*Bacteroides succinogenes* *Ruminococcus flavefaciens* *Ruminococcus albus* *Butyrivibrio fibrisolvens* *Cillobacterium cellulosolvens* *Clostridium lochheadii* *Cellulomonas fimi* *Eubacterium* spp.
Hemicellulose	*Butyrivibrio fibrisolvens* *Ruminococcus albus* *Ruminococcus flavefaciens* *Bacteroides ruminacola*
Peptic substances	All the cellulolytic and

	hemicellulolytic species plus: *Lachnospira multiparus* *Streptococcus bovis* *Succinovibrio dextrinosolvens*

Source: Cheng et al 1984

The attachment of rumen bacteria to lucerne leaves is shown in Plate 3.6.

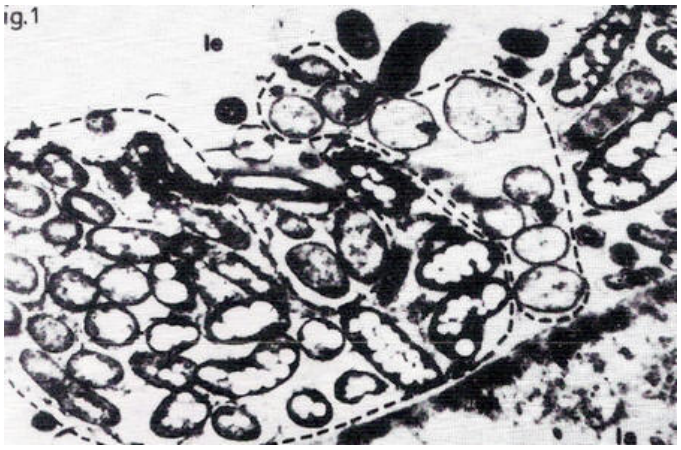


Plate 3.6 Transmission electron-micrograph of a ruthenium red- stained preparation of a whole leaf of lucerne exposed to colonisation by a mixed population of rumen bacteria in vitro. Very extensive microcolonies (delineated by dotted lines) of bacteria have adhered to the cell walls in the intercellular spaces (1e) of this tissue, but the plant cell walls are intact and the intracellular spaces (1a) have not been invaded by the bacteria. The bar in the lower right hand corner in the micrograph indicates 0.1mu. (Source: Cheng et al. 1984).

Information now suggests that cellulolytic organisms produce a raft of enzymes which is often associated with a capsule. These enzymes attack the complex carbohydrate degrading it to cellobiose, glucose or VFAs. The relative distribution of some important microbes on fibre or in the fluid phase is given in in Table 3.3.

Table 3.3: Proportion of bacteria associated with plant cell wall material and liquor in rumen digesta of cows fed straw-based diets.

	Composition (%)	
Genera	**Plant cell wall material**	**Rumen liquor**
Butyrivibrio	32	7
Selenomonas	14	10
Unnamed spirochaete	8	0
Lachnospira	8	1
Megasphaera	0	11
Streptococcus	3	12
Rumenococcus	16	6
Bacteroides	11	38
Others	8	15
Total number of isolates	368	292
Viable count (cfu ml-^{1} x 10^{7})	230	201

Source: From Phillips B and Latham M J, unpu b-lished data (Quoted by Cheng et al. 1984.)

On sugar-based diets, the population of viable bacteria floating free in solution seems to be small (Table 3.4). It is possible that the large populations of protozoa in the rumen of animals fed these diets have displaced the bacterial biomass. However, it seems reasonable to suggest that many of the bacteria that use sugar are attached to the fibrous part of the digesta.

Table 3.4: Viable counts of bacteria, lactobacilli and streptococci ($x10^{-8}$/ml) in rumen contents of cattle fed diets based on grain, hay or molasses

	Grain	**Poor quality hay**	**Molasses**
Viable bacteria	95.8	2.3	3.75
Lactobacillus	34.0		

Streptococcus	15.6	0.05

Source: Preston 1972

Support for this is given by the recognised need (see later) for high-quality fibre in these diets as a support medium. The rumen bacteria present in animals on molasses diets were *Bifidobacterium bifidus, Catenabacterium catenaforme* and other species, as well as *Butyrivibrio* spp. and *Peptostreptococcus provistii* (see Preston 1972).

On diets based on a large proportion of grain, Streptococcus bovis predominates, particularly at low pH. The counts of bacteria in rumen fluid from cattle on starch, sugar or fibre-based diets and their VFA end-products are shown in Table 3.4 and Table 3.5.

3.3.4 Other organisms in the rumen

Mycoplasmas, viruses and bacteriophages are all present in the rumen, probably being infective agents of the major species.

3.4 MICROBIAL INTERACTIONS IN THE RUMEN

Rumen microbial populations vary within an animal, with time after feeding, between days in the same animal and, apparently, in animals in different countries on similar feeds (see Hungate 1975). The end-products of fermentation, however, are virtually the same. For this reason, only the interactions between the major groups of organisms and their involvements in rumen fermentation are discussed.

3.4.1 Bacteria-bacteria interactions

Both on particulate digesta and on rumen epithelial tissue, bacteria associate with related organisms and function as a consortium, one organism growing on the end-products of metabolism of another. The sequential fermentation process involving different species of organisms converting cellulose to VFAs is well recognised, as are the interrelationships between hydrogen-producing and hydrogen-utilising organisms (see Wolin 1979). Within the rumen there are often very close associations of bacterial species, dependent on simple materials liberated by each to the mutual benefit of both (syntropic associations). These interactions of rumen bacteria appear to be highly beneficial and there appears to be little that can be done to manipulate these associations, other than inhibition of methanogenesis.

3.4.2 Protozoa-bacteria interactions

There is conclusive evidence that there are marked interactions between protozoa and bacteria. Protozoa ingest and digest bacteria and reduce the bacterial biomass floating free in solution in the rumen (Hungate 1966; Coleman 1975), and thus they may reduce the rate at which bacteria colonise ingested food particles. With readily digestible feeds this may not be significant but with refractory feeds, predation may increase the lag phase of degradation of particles.

Protozoa effectively compete with bacteria for the soluble sugars and starches, storing these carbohydrates within their cells. In this way the protozoa reduce the severity of acidosis on some diets. On sugar-based diets (eg. sugarcane) the protozoal biomass is probably larger than the bacterial biomass.

3.4.3 Interactions of bacteria, fungi and protozoa

Eadie and Gill (1971) found that the number of flagellate protozoa (motile zoospores?) increased following defaunation of the rumen. If these flagellates were zoospores, then it suggests that protozoa either `compete' for nutrients with fungi or reduce fungal growth in other ways. For instance Orpin (1975) observed predation by protozoa on the non-motile flagellates (zoospores).

To investigate these interactions, studies have been made on the effects of defaunation on fungal growth and digestibility of feed in the rumen. The digestibility of fibrous feeds in nylon bags in the rumen of sheep that were faunated, then defaunated (and remained unfaunated) and then refaunated showed that the unfaunated state of the rumen resulted in an increased rate of disappearance of straw dry matter (by 6-10 units/24 h). This was associated with more zoospores in rumen fluid (Table 3.6) and a greater growth of fungi as indicated by the numbers of sporangia on fibre that had been incubated in the rumen in nylon bags for 6-12 hours (see Bird and Leng 1985).

Table 3.5: Patterns of rumen fermentation in cattle given diets based on grain, hay or molasses.

	Cereal grain#	**Forage@**	**Molasses***
No. of calves	4	3	4
Rumen pH	6.1	7.1	6.6
Total VFA, mEq/litre	57#	82	32#
Molar % of VF A			
Acetic	44.9	76.2	49.7
Propionic	42.7	]5.2	21.3
Butyric	5.8	7.4	25.7
Iso-butyric	1.3	0.4	0.3
Valerie	2.2	0.2	2.8
Iso-valerie	2.0	0.3	0.2

Caproic	0.7	0.7

*#. Flaked cooked maize (40 %) and rolled oats (40 %) @Poor-quality hay *Approximately 80% molasses and 15 % dried grass*
Source: Preston (1972)

Table 3.6: The interactions of protozoa and fungi in the rumen; the indices of fungal populations in faunated and unfaunated sheep fed wheat straw, ammoniated wheat straw (NH_3-straw) or native pasture.

	Viable zoospores (10^3/ml)	
Diet	**Faunated**	**Unfaunated**
Wheat straw	3	17
NH_3-straw	7	16
Wheat straw	4	12
Native pasture	7	30

Soetanto 1986; Leng 1984b, 1985.

Elimination of protozoa in the rumen leads to an increase in the number of bacteria in the liquid pool. In studies with sheep using total faecal collection procedures, the apparent digestibility of dry matter was increased by 18% when protozoa were not present (Soetanto 1986). From these preliminary studies (see Table 3.7) it is apparent that defaunation may lead to large increases in productivity of ruminants fed fibrous diets.

Table 3.7: Effects of the faunated (+ P) or the un-faunated (-P) state of the rumen on dry matter loss (%) from nylon bags in the rumen of sheep# fed wheat straw or ammoniated wheat straw (NH_3-straw). Materials in the bags were straw or NH_3-straw or cotton wool (CW).

Host diet	**NH_3 straw**		**Straw**	
Material in bag	**Straw**	**CW**	**Straw**	**CW**
4 h incubation				
+P	15	4	5	12
-P	20	6	6	12
48 h incubation				
+P	50	63	32	74
-P	55	72	37	88

 # See Table 3.6

Veira (1986) has recently reviewed the literature on the effects of the faunated state on apparent digestibility of dry matter in ruminants over a wide range of diets. He found that digestibility is generally higher in the animals that are faunated as compared to their pen fed counterparts. However, the diets were mostly of high digestibility (ie. greater than 60%) whereas data in Table 3.7 comes from animals on diets of 45-55% digestibility and which did not contain starch. The effects of the unfaunated state on digestibility may be reversed when soluble sugars and/or starches are in high concentrations in a diet.

Any manipulation of a diet (Chapter 5) must be viewed in the light of the interactions among protozoa, bacteria and fungi. For instance, feeding concentrate supplements to ruminants on roughage-based diets often decreases the intake of roughage. The net effect of adding concentrates (and also molasses blocks) to a roughage diet may be to increase protozoal numbers. The interactions are obviously complex and the results of any research into manipulation of the rumen that does not measure responses in the biomasses of protozoa, bacteria and fungi will be difficult to explain. There is an urgent need to develop simple methods for estimating the biomass of the bacteria (in fluid and on particles), protozoa and fungi in order to explore these interactions more fully.

3.4.4 Conclusions

Interactions among micro-organisms within the rumen are complex and not always to the advantage of the host. Large protozoal populations in the rumen have been shown to decrease animal productivity, apparently largely through lowering the amino acid to energy ratio in the absorbed products of digestion. However, possibly of more importance, it appears that protozoa reduce the biomass of bacteria and of fungi in the rumen of animals on diets high in fibre, and thus may reduce the rate of digestion of fibrous feeds (see Chapter 5).

The interactions of diet with the faunated or unfaunated state are not well understood and fibrous diets low in bypass protein are the ones on which ruminants are likely to be more efficient in the unfaunated state.

3.5 ENERGY TRANSACTIONS IN THE RUMEN

3.5.1 Fermentation of carbohydrate

The universal end-products of fermentation of all diets in the rumen are the VFAs (acetate, propionate, butyrate), carbon dioxide and methane. Energy is lost as both heat and methane. The ATP produced by conversion of feed to VFAs and intermediary compounds used in cell growth is the main source of energy for the growth of micro-organisms. A simple scheme for rumen fermentation is shown in Figure 3.4.

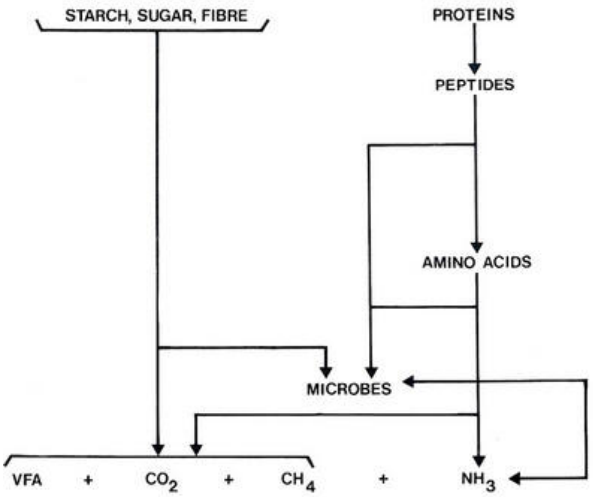


Figure 3.4: Outline of the pathways of carbohydrate and protein degradation in the rumen (Source: Leng 1982a).

The overall reactions within the rumen are shown in Figure 3.4 and Figure 3.5. Details of the reactions are shown in Figure 3.6 which is presented to emphasise the detailed knowledge that exists on the pathways by which the micro-organisms convert carbohydrate to VFAs, carbon dioxide and methane.

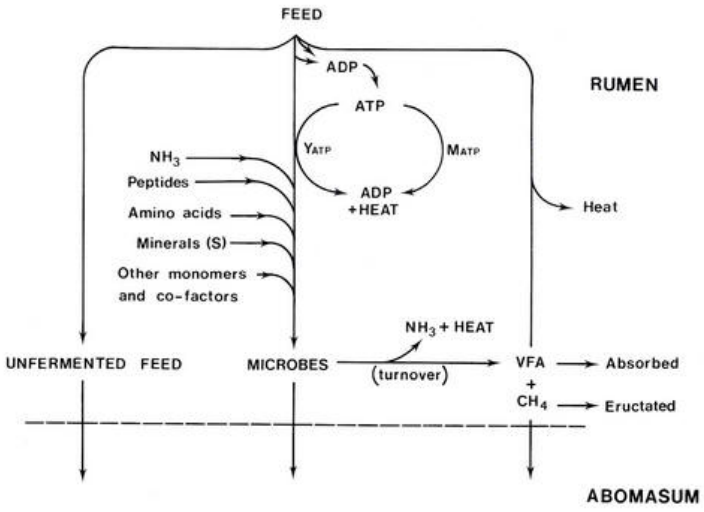


Figure 3.5 Energetics of rumen fermentation (Source: Leng 1982a).

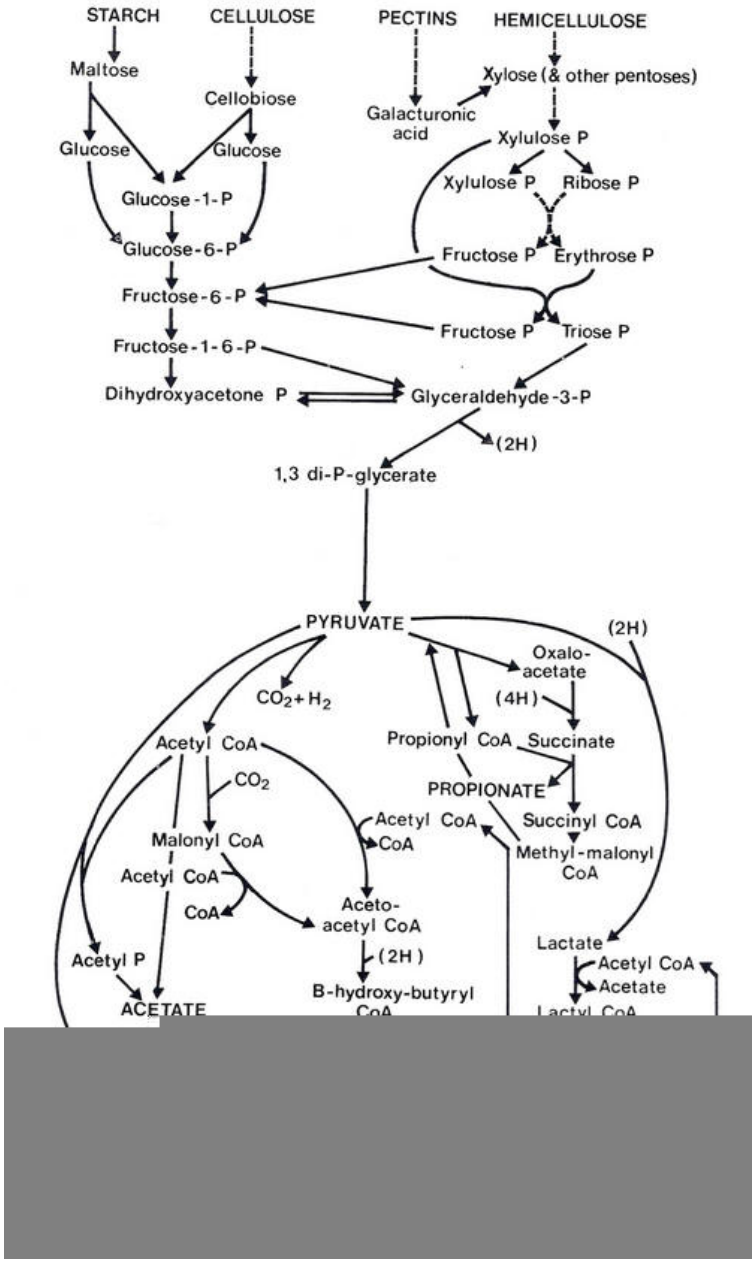


Figure 3.6. Outline of the pathways of fermentation in the rumen (Source: Leng 1970a).

A more quantitative approach to rumen fermentation is illustrated in Figure 3.5. The diagram shows that the digestible components of ingested feed are:

- Converted to VFAs
- Broken down to intermediate components that are the monomers for microbial growth
- Avoid fermentation and move to the lower digestive tract where they may be digested.

Some of the potentially fermentable feed will inevitably escape fermentation and will be digested in the intestines. Recent research has demonstrated that a proportion of some feeds invariably escape intact to the lower tract (eg. maize grain). Others can be manipulated relatively easily (eg. protein meal) to avoid the fermentative processes in the rumen. Feeds that escape fermentation are described as bypass nutrients. The terms that are used in other countries to describe bypass protein (ie. rumen undegraded proteins) are not descriptive of all forms of bypass protein. Suckled milk for instance, is a form of both bypass protein and bypass carbohydrate (lactose). Both these components of milk are readily fermented in the rumen when they enter, but because of the reflex closure of the oesophageal groove while suckling these bypass the rumen and become available for digestion in the intestines.

- Bypass protein is defined as any portion of a protein meal that escapes the rumen intact and is available for digestion in the intestines
- Bypass energy (mainly starch) is that part of the feed that escapes fermentation and is digested and absorbed from the small intestine.

One of the costs of the ruminant mode of digestion is that fermentation of readily digestible feeds results in up to 20% of the metabolisable energy intake being lost as heat and methane. A second major disadvantage is that proteins that are fermented in the rumen are lost as sources of essential amino acids. In subsequent chapters it is argued that in the developing countries protein is too valuable to be fermented

since protein fermentation is inefficient as a source of ATP for microbial growth (about half that of an equivalent weight of carbohydrates). Also the N for microbial growth can be supplied in more elemental form (ie. as non-protein nitrogen-urea).

3.5.2 Fate of dietary fat in the rumen

Fat in the diet of ruminants varies from negligible amounts to levels in excess of 10% of the dry matter in leafy forages or where animals are able to select leaf-tip materials (Hawke 1973). Most of the lipids in pasture plant materials are phospholipids and glycolipids. The major long-chain fatty acid components of these are linolenic (50%), linoleic (10%) and palmitic (15%) (Hawke 1973).

The complex lipids of plants are rapidly hydrolysed in the rumen by bacterial lipases to fatty acids, galactose and glycerol; the last two are fermented to volatile fatty acids. The long-chain fatty acids are largely unsaturated and as soon as they are released they are adsorbed onto particles in the rumen where they are hydrogenated by microbes (Reiser 1951). These long-chain fatty acids (now largely stearic, palmitic and oleic acids) are absorbed only from the intestines. Rumen bacteria incorporate some of the long-chain fatty acids into their cellular components.

3.5.3 Microbial growth and fermentation

Anaerobic conditions of the rumen limit the availability of ATP for microbial growth. In aerobic microbial systems the carbohydrate is converted to carbon dioxide and water with a yield of 36 moles ATP/mole of glucose oxidised. By contrast, anaerobic fermentation yields only about 4 moles ATP/mole of glucose converted to VFAs.

Rumen micro-organisms use ATP for essentially two purposes:

- For the energy to synthesise their own cells
- To provide the energy for maintenance.

The ATP available for microbial growth depends on that required to maintain the organisms. The efficiency of ATP generation and cell growth also depends on the substrates that provide the `building blocks' of the micro-organisms. The composition of bacterial cells is fairly uniform and the cost (in ATP terms) of synthesis of the individual components of cells can therefore be calculated (Table 3.8).

Table 3.8: The composition of bacterial cells and the ATP requirements (req) for microbial cell synthesis from glucose (Glu) or pyruvate (Pyr) or acetate (Ac). Y_{ATP} is in g dry cells/mole ATP.

		ATP required (10^4 mole/g cells from different substrates)		
Macromolecule synthesis	**Bacterial composition (g/100 g cells)**	**Glu**	**Pyr**	**Ac**
Polysaccharide	16.6	20.6	71.8	92
Protein	52.4	204.9	339.4	427
Lipid	9.4	1.4	27	50
RNA	15.7	43.7	71.2	101
DNA	3.2	24.4	29.8	19
Transport of nutrients into cells		52	200	306*
Total ATP req		347	740	995
Y_{ATP}		28.8	13.5	10

Adapted from Stouthamer (1979)

The point being stressed in this table is that if the microbial cell components are synthesised from the glucose (eg. from cellulose), then growth is highly efficient. If, however, the end-products of fermentation (ie. VFAs) are used, the synthesis of microbial cells is much lower per unit of organic matter fermented. The estimates of microbial cell yields in terms of carbohydrates fermented indicate that it is the intermediates in the breakdown of glucose in the rumen that are used to synthesise microbial cells. Microbial growth efficiency is expressed in terms of YATP:

- YATP is defined as the weight (g) of dry cells that is produced per mole of ATP available. The ATP available is usually calculated from a knowledge of the reactions in the fermentative pathways.

3.5.4 Factors affecting the quantities of rumen microbes available for digestion in the small intestines

- The major factors that affect microbial cell synthesis in the rumen are:
- The availability and/or concentration in rumen fluid of precursors (eg. glucose, nucleic acids, amino acids, peptides, ammonia and minerals (including S, K and P))
- The maintenance requirements of the microbes
- The turnover of microbial cells

- The destruction of bacteria by predatory protozoa.

Availability of substrates for microbial cell synthesis:

A continuous supply of fermentable carbohydrates to maintain both fermentation and the supply of precursors for cell growth is paramount to efficient use of ATP. The rate of fermentation must be synchronised to the rate of uptake and therefore availability of ammonia, sulphur and/or peptides, amino acids,and other microbial nutrients.

Role of ammonia in rumen fermentation:

Forty to 60% of the dry matter of the microbial cells is protein and therefore the synthesis of amino acids and proteins are the main reactions that require ATP. The pathways of synthesis of amino acids in rumen microbes are not clearly defined. It is however, abundantly clear that ammonia is highly important for the efficient synthesis of amino acids and therefore microbial protein. At low ammonia levels in rumen fluid, reactions that fix ammonia into amino acids require ATP whereas, when ammonia levels are above a certain optimum, the ammonia is incorporated into amino acids without using ATP.

It has been suggested that maximum microbial synthesis rate occurs at ammonia concentrations between 5 and 8 mg N/100 ml (Satter and Slyter 1974). Different optima have been found by other researchers, suggesting that diet influences the optimum ammonia level. Recent studies suggest the value may be as high as 15-20 mg N/100 ml depending on diet (see Leng and Nolan 1984). The high ammonia concentration needed for maximum cell growth suggests that the rumen micro-organisms probably have similar mechanisms for incorporation of ammonia to those in soil microbes, which assimilate ammonia via glutamate dehydrogenase. However bacteria grown under low ammonia concentrations fix ammonia in a two-step process involving glutamine synthetase and glutamate synthase. These reactions involve conversion of glutamate to glutamine and then a reductive transfer of the amide-N of glutamine to 2-oxoglutarate and this step requires ATP (Meers et al. 1979; Tempest et al. 1970; Brown et al. 1974) (Figure 3.7).

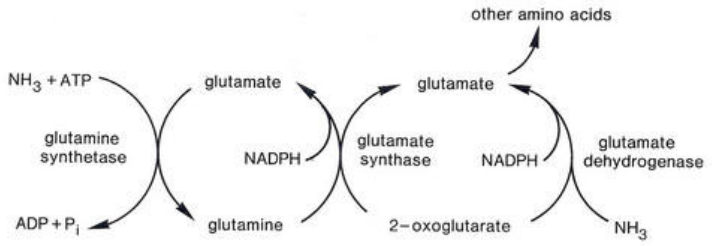


Figure 3.7 Two-step process by which ammonia is assimilated by bacteria (Source: Leng and Nolan 1984).

Role of other nutrients in microbial cell synthesis:

Hume (1970) reported that synthesis of microbial protein in the rumen of sheep on semi-purified diets was more efficient when casein was the nitrogen source than when urea was the N source.

The efficiency of microbial protein synthesis in washed micro-organisms is increased by amino acids and peptides (Maeng et al. 1976). This has led to the suggestion that one of the roles of protein supplements is to increase the efficiency of microbial protein synthesis in the rumen through the slow release of amino acids, in addition to the beneficial role of the portion that bypasses the rumen. However, the relative supply of amino acids or ammonia-N has little effect on microbial yields since, at high ammonia concentration, synthesis of amino acids from the corresponding keto acid and ammonia does not require ATP.

The moderately high milk yields of cows fed semi-synthetic diets containing starch, sugar, cellulose and urea (Virtanen 1966) indicates a high efficiency of microbial protein production in the rumen with urea as the sole source of nitrogen. The high apparent efficiency may be due to: (i) using carbohydrate sources with differing rates of fermentation thus ensuring a relatively constant supply of precursors for microbial synthesis; and (ii) the absence of protozoa (see Chapter 5).

Figure 3.5 illustrates the role of other nutrients required to maximise the efficiency of microbial growth. These include amino acids and peptides, most of the macro and trace minerals (with emphasis on sulphur and cobalt) and other, as yet, unidentified compounds that increase microbial growth efficiency. An example of the presence of possible unidentified growth factors is seen in the stimulation of production that occurs when chicken litter is used to supplement urea as a source of nitrogen in molasses-based diets (see Chapter 5) suggesting that there are compounds in the litter that stimulate certain groups of micro-organisms.

3.5.5 Maintenance-ATP (MATP) requirements of rumen micro-organisms

- MATP is defined as the ATP that is directed from growth to utilisation in other processes, for instance osmo-regulation (Leng 1982a).

The effects of a large increase in MATP of micro-organisms in the rumen is a small increase in heat production, a large increase in VFA production and a large decrease in cell yield (ie. a decrease in YATP). MATP has a number of components including:

- ATP needed for motility of microbes
- Requirements for ATP and nutrients to replace turnover of components of the micro-organisms (ie. the dynamic state)
- ATP for production of extracellular proteins (mainly enzymes) and polysaccharides
- ATP for active transport.

Microbial cell turnover in the rumen:

The rate of growth of microbes in the rumen is always greater than the rate at which microbes flow from the rumen. This is because:

- Protozoa are retained and only a small proportion move down the tract (see earlier). Those retained apparently lyse in the rumen and are fermented (Leng 1982b)
- Protozoa engulf and digest quite a proportion of the bacterial pool (Coleman 1975)
- Bacteria and protozoa spontaneously lyse either due to the action of infective agents, lack of substrate or a change in the environment, such as a reduction in the pH of the rumen fluid.

The net effect of these interactions is considerable recycling of nitrogen within the rumen. Nolan and Stachiw (1979) found that up to 50% of the microbes that were produced were lysed in the rumen of sheep on a straw-based diet.

Periodic fasting of animals may also result in lysis of a large proportion of the microbial pool in the rumen. Hespell (1979) showed that 60% of rumen bacteria died and 30% lysed when they were without substrate for 2 hours.

Influence of rumen protozoa on bacterial cells available for digestion:

At high population densities of protozoa in the rumen, a considerable proportion of the bacterial pool is engulfed and digested by the protozoa. At high population densities of *Entodinia* species of protozoa (ie. 2,000,000/ml) Coleman (1975) calculated that all the free-floating bacteria in the rumen may be engulfed, removing some 30% of the total biomass. Recent studies have indicated that 16-30% more protein enters the duodenum of sheep when they are unfaunated than when they contain high population densities of protozoa (see Table 3.9).

Table 3.9: A comparison of post-ruminal flows of non-ammonia N (microbial and bypass protein) in faunated and and unfaunated sheep.

Diet#	N-intake	No. of animals	N-compound entering small intestine	Faunated sheep (g/d)	Unfaunated sheep (g/d)	Author
la	25.2	2	Total NAN	18.3	21.3	Lindsay and Hogan (1972)
			Bacterial-N	12.0	14.0	
Ib	34.0	2	Total NAN	29.4	31.7	Lindsay and Hogan (1972)
			Bacterial-N	18.0	19.3	
2	25.2	5	Total NAN	18.0	19.3	Bird and Leng (1985)
			Microbial-N	14.7	16.7	
3	20.0	4	Total NAN	17.0	24.8	ICl/UNE (1980, unpublished)
			Microbial-N	15.4	19.2	
4	25.0	3	Total N	19.0[a]	22.0[b]	Rowe *et al.1981*
			Microbial-N	11.8	15.0	
5	13.0	3	Total NAN	*15.6[a]*	*17.4[b]*	Veira *et al.1983*
6	22.5	6	Total NAN	*23.4[a]*	*32.8[b]*	Ushida *et al.1984*
			Microbial-N	15.3	18.1	

Source: After Bird and Leng (1985)

#1a: 1000g lucerne hay (1b) 1000g red clover; 2. 430g oaten chaff, 430g sugar, 35g urea, 35g fish meal; 3. 720g oaten chaff, 100g casein, 80g lucerne, 100g molasses 4. 500g medium quality hay, 225g oats, 115g sugar, 70g fish meal, 30g urea; 5. 48% corn silage, 47% shelled corn, 1 % urea, 4 % mineral mix; 6. 67% lucerne hay, 30% barley, 3% wheat straw.

The effects of defaunation are discussed in Chapter 5. The net effect of a large population of protozoa in the rumen is to decrease the protein-to-energy ratio in the end-products of fermentative digestion that are available for absorption. For example, if the YATP of the rumen fermentation was 14, the ratio of microbial protein synthesised to VFAs produced would be 25g protein/MJ VFA energy, but predation by protozoa reduces the actual availability of protein to between 12 and 14g protein/MJ VFA energy. The VFA energy available would be increased by some 25-30% and the protein available for digestion decreased by about the same amount.

3.6 MODEL OF FERMENTATION IN THE RUMEN

3.6.1 Stoichiometry

For the purposes of the present discussion, a model for a 200 kg steer will be used to illustrate the quantitative availability of nutrients from rumen fermentation. The steer consumes 4kg (25 mole anhydroglucose, molecular weight 160) of organic matter, which is

completely fermented in the rumen.

It is assumed:

- That the fermentation of 1 mole of carbohydrate gives rise to either 2 moles of acetate, 2 moles of propionate or 1 mole of butyrate, according to the following stoichiometry:
  - hexose 2pyruvate + 4[H] + 2ATP
  - pyruvate + 2H2O 2HAc + 2CO2 + 2H2 + 2ATP
  - 2pyruvate + 8[H] 2HPro + 2H2O + 2ATP
  - 2pyruvate + 4[H] HBu + 2H2 + 2CO2 + 2ATP
  - CO2 + H2 CH4 + 2H2O + ATP

In the stoichiometry, [H] indicates reduced co-enzymes and HAc is acetic acid, HPro is propionic acid and HBu is butyric acid

- That the production rates of individual volatile fatty acids are proportional to their concentrations (Leng and Brett 1966) (see Figure 3.8)
- That one-third of the organic matter fermented is converted to microbial cells
- That 2 moles of ATP are generated per mole of acetate, 3 for butyrate, 3 for propionate, and 1 mole of ATP per mole of methane (Isaacson et al. 1975).

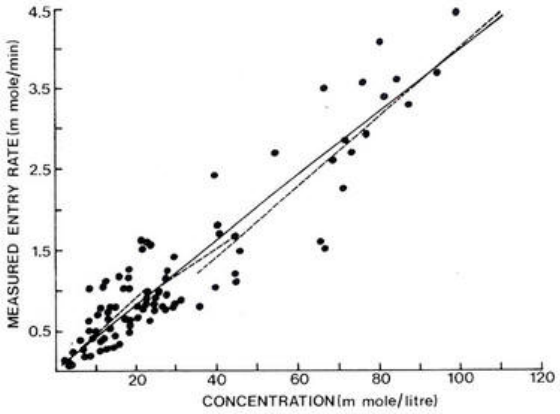
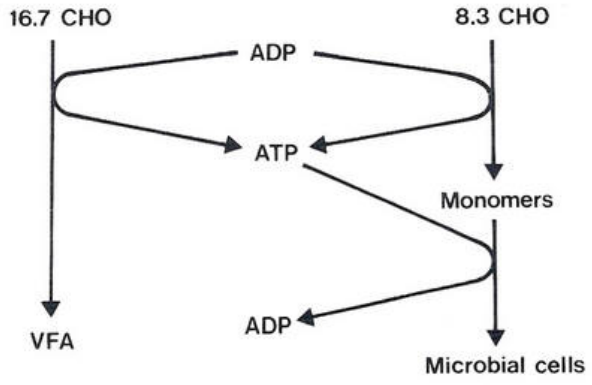


Figure 3.8 Relationships between measured VFA entry rate and concentration of VFA in ruminal fluid. The broken lines indicate the relationships between production and concentration for the individual VFA; the unbroken line is for the combined data (Source: Leng 1970a).

The equation for fermentation of 4kg of carbohydrate is as follows:

- 16.7CHO 21HAc + 6HPro + 3HBu + 7.5CH4 + 78ATP
- 8.3CHO 1.4polysaccharide + 13.8pyruvate + 2CH4 + 17ATP
- Overall:
- 25CHO 21HAc + 6Pro + 3HBu + 9.5CH4 + 1300g dry cells

In the example, one-third of the carbohydrate provides the precursor for microbial cells and about 1300g dry cells (assuming that 1g of fermentable carbohydrate is converted to 1g of bacterial cells) are produced at a YATP of about 14.5. At YATP higher than this, VFA production is decreased and cell production is increased. The model is shown in Figure 3.9.



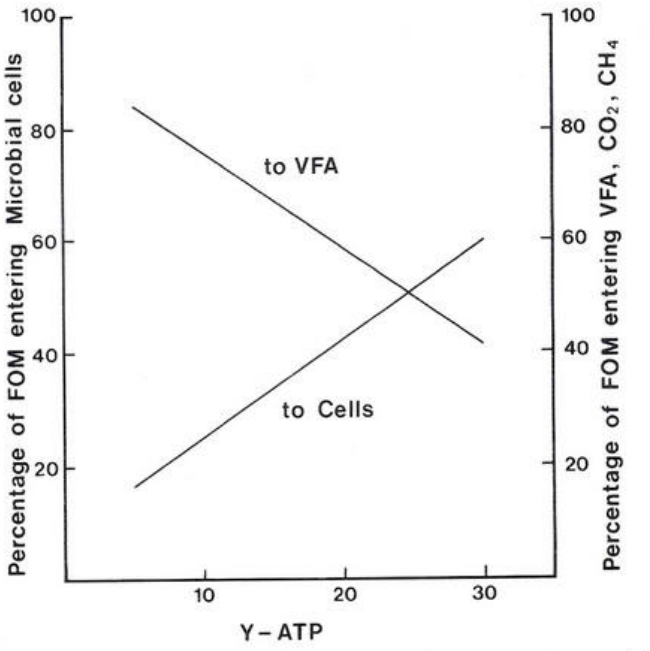


Figure 3.9 The partitioning of carbohydrate fermentation into microbial constituents or VFA plus methane and carbon dioxide (Source: Leng 1982a).

Figure 3.10 Relationship between microbial growth efficiency (YATP) and the percentage of the fermented organic matter that is partitioned into VFAs and gases (methane and carbon dioxide) and that entering into microbial cells (Leng 1982c)

Using this model but allowing YATP to vary, the percentage of the carbohydrate metabolised in the rumen that is converted to microbes or VFAs and methane is shown in Figure 3.10. At YATP 0 the microbial cell production should be zero but in the figure some discrepancy from this is apparent, indicating that microbial cell production is overestimated by the model. The point to be stressed here is that, depending on the efficiency with which ATP is used, the amount of carbohydrate converted to microbial cells can approach that fermented to VFAs. These relationships were derived from the above stoichiometry assuming that 1g of cells is formed from 1g of carbohydrates fermented. However, it fits exactly the value found by Baldwin (1970) using a more detailed biochemical approach.

3.6.2 Energy losses in fermentation

Energy is lost as heat in the rumen when carbohydrate is fermented to VFAs and microbial cells. The energy losses as heat are always small but influenced by YATP. To demonstrate this, the partitioning of carbohydrate into VFAs and cells was estimated from Figure 3.10. The productions of VFAs, methane and cells were then calculated from the stoichiometry given earlier. The energy balance in the rumen was then calculated (see Table 3.10).

Table 3.10: The influence of the efficiency of microbial cell synthesis in the rumen on the balance of end-products available from fermentation in a steer consuming 4 kg organic matter that is completely fermentable.

	***YATP* 8**		***YATP 14***		***YATP 10***		***Y ATP* 25**	
	Moles	**MJ**	**Moles**	**MJ**	**Moles**	**MJ**	**Moles**	**MJ**
Carbohydrate fermented								
to VFA	19.7	55.5	16.6	46.8	14.5	40.8	12.4	34.9
to cells	5.25	14.8	8.33	23.4	11.5	29.5	12.1	35.4
VFA produced								
HAC	25.3	22.2	21.6	18.7	18.5	16.3	15.9	14.0
HProp	7.1	10.9	6.0	9.2	5.2	8.0	4.5	6.9
HBut	3.6	7.8	3.0	6.5	2.6	5.7	2.2	4.8
Methane	10.1	9.4	9.4	8.5	8.9	8.0	8.5	7.6
Total methane + VF A		50.3		42.9		38.0		33.3
Approximate energy in microbes #		13.5		22.2		28.1		33.7
Microbial cells produced (kg)		0.83		1.33		1.68		2.02
Heat of fermentation (MJ)		6.4		5.1		4.3		3.1
Indigestible energy of microbes (assuming 80% digestible) (MJ)		2.7		4.4		5.6		6.7
Total energy loss (MJ)		9.1		9.6		9.9		9.8
Metabolisable energy (ME) (MJ)		61.2		60.7		60.4		60.5

Source: Leng 1982a
#Assuming 20.9 kJ/g of organic matter

These calculations show that as the efficiency of cell synthesis increases methane production and heat of fermentation decrease. Thus any factors that increase microbial cell yield may increase the availability of metabolisable energy. However, microbes are between 75 and

95% digestible (Roy et al. 1977; Hagemeister et al. 1980). If the digestibility of microbes is considered to be 75%, the extra losses of energy as microbial residues in the faeces would remove any energetic advantage. However, protein-to-energy ratios (P/E) in the nutrients available for digestion would be increased markedly. If, however, the rumen microbes were 100% digestible, as suggested by recent isotope studies (J V Nolan, personal communication), then an increase in YATP results in a significant increase in metabolisable energy of a diet. If different physiological states (eg. pregnancy and lactation) result in increased digestion of microbes or increased absorption of amino acids (because of hypertrophy of the intestines and/or increased enzyme secretion) an increase in microbial cell yield would be highly beneficial, increasing the efficiency of feed utilisation considerably.

3.6.3 The balance of microbial protein to VFA energy (P/E ratio)

To facilitate translation of YATP values into P/E ratios, the latter were calculated (Table 3.11) and the relationships are shown for two distinct fermentation patterns in the rumen (Figure 3.11).

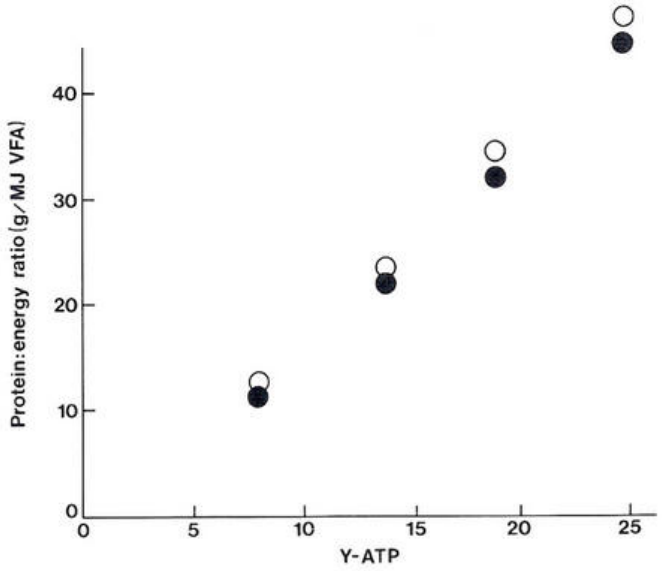


Figure 3.11 The relationships between YATP and the protein-to-energy ratio in the products of fermentation.

The effect of different efficiencies of microbial growth on the ratio of protein to VFA energy (P/E ratio) available from the rumen of a steer consuming 4kg of organic matter which is totally fermentable.

Table 3.11: The effect of different efficiencies of microbial growth on the ratio of protein to VFA energy (P:E ratio) available from the rumen of a steer consuming 4kg of organic matter which is totally fermentable.

	Y_{ATP}			
	8	**14**	**19**	**25**
Microbial protein# synthesised (g/d)	500	800	1010	1212
VFA produced (MJ/d)	41	34	30	26
Methane produced (MJ/d)	9.4	8.5	8.0	7.6
Heat (MJ/d)	6.4	5.1	4.3	3.1
P/E ratio (g protein/MJ)	12	25	34	47

#Microbial protein may be only 75-85% *digestible and* ***th****is will change the P/E ratio markedly in the animal*

If YATP can vary from 8 to 25, then, in animals dependent on rumen fermentation, the protein available for digestion in the intestines relative to the energy absorbed as VFAs (the P/E ratio) can be as low as 9g protein/MJ of VFA energy or as high as 34g protein/MJ of VFA energy. This highlights the problems of a system for calculating recommendations for N requirements when the efficiency of microbial growth is assumed to be constant (ie. 30g N/kg of organic matter apparently digested in the rumen).

In all situations, if a nutrient needed for microbial growth is limiting, the P/E ratio will decrease irrespective of which nutrient is limiting (eg. ammonia, sulphur etc).

The P/E ratio in the absorbed products is of applied significance as will be demonstrated later. It can be markedly altered by the incorporation in a diet of protein which bypasses the rumen fermentation and provides amino acids for absorption. When the objective of a feeding strategy is the production of milk, meat, hair or wool then microbial protein output from the rumen should be at a maximum relative to the energy in VFAs. The more microbial protein that is produced from a low-cost carbohydrate source, the less will be the requirements for supplementary bypass protein (which is usually the most expensive portion of a diet).

3.6.4 Protein fermentation and P/E ratio

Protein that is fermented in the rumen is largely wasted because:

- Dietary protein is fermented and essential amino acids are deaminated
- Fermentation of 1g of protein generates only half the ATP that would be produced from 1g of carbohydrate.

This means that only 30 to 60g of microbial protein become available to the animal for digestion for every kilogram of dietary protein that is fermented in the rumen.

3.6.5 Significance of P/E ratio

Is the protein to energy ratio important in terms of applied animal production? With the exception of the working animal almost always it will be biologically beneficial to maximise the amount of amino acids absorbed relative to energy.

The amino acid supply affects a large number of biological functions within the animal. Obviously where products containing protein are the objective of the feeding system, the amount of protein absorbed relative to energy will be highly related to the level of production achieved. For example, wool growth, milk production and growth in young animals will respond to increases in P/E ratio.

Considerable research has demonstrated that in animals fed low nitrogen diets, supplementation with fermentable nitrogen stimulates rumen function which stimulates feed intake. On many diets low in protein, supplementation with bypass protein stimulates feed intake. This appears to hold for a wide variety of diets from fibrous cereal residues through to diets based on starches (barley) and sugars (molasses) (see Chapter 8). Amino acids absorbed from the digestive tract provide essential amino acids for synthesis of tissues, and in addition provide precursors for other compounds required in tissue growth. They also provide a proportion of the glucogenic precursors to the animal and in this way have an effect on hormonal secretions, which influences the animal's reproductive capacity (see Chapter 7).

3.7 N-TRANSACTIONS IN THE RUMEN

3.7.1 Dietary nitrogen

In the industrialised countries, only relatively small amounts of urea are fed to ruminants and protein provides most of the dietary nitrogen. The non-protein-nitrogen fractions of such feeds include amides, amines, amino acids and nitrate; the last mentioned may be present in significant quantities in immature pasture. In the developing countries, where crop residues are fed to ruminants, urea or ammonium salts and materials such as chicken manure are the most appropriate sources of fermentable N. The major non-protein-nitrogen component in chicken manure is uric acid.

3.7.2 Degradation of dietary protein in the rumen

Between 20 and 100% of the protein in many diets based on high-protein forages, protein meals and grains may be soluble. It is assumed, for practical purposes, that the solubility of protein-N in buffer solution indicates the degradability of the protein of a meal in the rumen. However, soluble proteins such as serum albumin, ovalbumin, chloroplast protein extract and soluble proteins from soya bean meal and rapeseed meal have variable resistance to degradation in the rumen (see Mahadevan et al. 1980). The chemical form of protein and the presence of disulphide bonds and perhaps phenolics (tannins) have major influences on degradability of proteins in the rumen.

Degradation of protein to peptides and amino acids is by bacterial (usually surface) proteases and peptidases. Nugent and Mangan (1981) showed that lysis of leaf protein in the rumen was high but affected by diet and that soluble protein was adsorbed rapidly onto the bacterial cell prior to lysis. Small particles such as chloroplasts were engulfed directly by protozoa and then degraded only slowly.

Factors affecting the extent of ruminal degradation of the less-fermentable proteins in food particles have received little study. Fermentation of particulate proteins depends on the length of time that they are in the rumen, and factors such as their rates of solubilisation and enzymatic degradation. In addition to chemical factors affecting rates of degradation of soluble proteins (ie. cross-linking and number of accessible hydrolysable sites in the protein molecules, enzyme concentration, and pH), physical characteristics of particles also affect accessibility of proteins to enzymatic action. The surface area of the protein that is accessible to microbial proteases may be reduced by formation of fibrous proteins by treatment with formaldehyde and by lipids or other water-insoluble substances used to encapsulate the protein. Rates of disruption of these substances are major factors that affect the rate of breakdown of such protected proteins.

3.7.3 Outflow of dietary and endogenous nitrogenous materials from the rumen

The amount of dietary N leaving the rumen is determined principally by the total N in the diet, the rate of its fermentation and its residence time in the rumen. Protein of dietary origin in abomasal digesta is often estimated by an indirect method (ie. from the total flow of N in digesta after the microbial fraction has been identified by microbial markers and an allowance has been made for endogenous N). The endogenous component, however, should not be disregarded. The method of estimating undegraded protein leaving the rumen contains all the inaccuracies of estimating or measuring the other fractions. Degradation of feed proteins seldom has been estimated directly, although techniques for its measurement are available and should be evaluated further. Indirect measures of the dietary protein bypassing the rumen, which relates the amount of supplemental protein in a diet to wool growth of sheep have been reported (Leng et al. 1984).

3.7.4 Peptides and amino acids in rumen fluid

In animals fed high-protein diets, a high proportion of the N in the rumen may be derived from peptides and amino acids in the feed protein. Peptides or amino acids are degraded rapidly by bacterial peptidases and deaminases, and peptides are present in the rumen in significant quantities only when the protein is fermented at high rates.

Amino acids are absorbed from the rumen but probably only in small amounts as the majority of free amino acids are probably deaminated to give rise to branched-chain volatile fatty acids (VFAs), carbon dioxide and methane. The level of branched-chain VFAs in the rumen fluid is an index of amino-acid degradation in the rumen, as these generally arise from the fermentation of valine (isobutyrate), leucine (isovalerate), isoleucine (2-methyl butyrate) and proline (valerate).

3.7.5 Rumen ammonia pool

The sources of ammonia in the rumen include proteins, peptides and amino acids (see preceding section), and other soluble-N materials. Urea, uric acid and nitrate are rapidly converted to ammonia in the rumen. Nucleic acids in rumen fluid are probably also degraded extensively to ammonia. Figure 3.12 indicates possible sources of the ammonia pool.

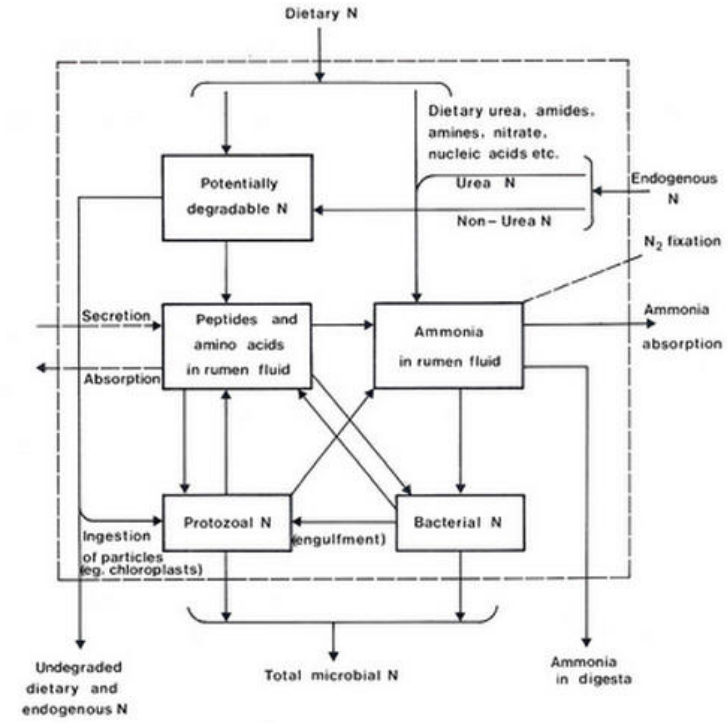


Figure 3.12 A model of the metabolism of nitrogen in the rumen (Source: Leng and Nolan 1984)

The ammonia pool is a focus for studies of metabolism of nitrogen in the rumen, and much knowledge has been gained from measuring fluxes of N through this pool.

Ammonia N is lost from rumen fluid by:

- Incorporation into microbial cells that pass out of the rumen
- Absorption through the rumen wall
- Passing out of the rumen in fluid.

The ammonia pool in the rumen is relatively small and turns over rapidly. The amount of ammonia entering the pool varies over a wide range according to quantity and degradability of protein in the diet and with the extent and method of supplementation of urea. Concentrations of ammonia N in the pool can be expected to change rapidly even when animals have continuous access to food.

The amount of ammonia that flows out of the rumen in fluid is relatively small, and it follows that ammonia produced in the rumen that is not incorporated into micro-organisms is absorbed mainly through the wall of the reticulo-rumen.

To maintain a high level of ammonia in rumen fluid over 24 hours on low-protein diets requires urea to be taken in continuously. This can be ensured by spraying urea on the basal feed or by providing a urea block or liquid mixture which is licked at regular intervals. Urea given in a single meal is unlikely to maintain rumen ammonia levels above the minimum required for efficient fermentation for more than a few hours per day (see Figure 5.1).

3.7.6 Recycling of N to the rumen from plasma urea

Movement of urea from blood into the rumen and conservation of urea in the body by reduced excretion of urea in urine are mechanisms for supporting rumen ammonia levels above a minimum needed by the microbes. Ruminants have evolved these mechanisms to ensure efficient microbial synthesis in the rumen at moderate N intakes. However, studies with cattle and sheep on low-N pastures and straw-based diets have shown that continuous supplementation with urea increased: (i) feed intake; (ii) digestibility of the feed; (iii) N balance; (iv) protein availability from the rumen; and (v) productivity. This demonstrates that N recycled through plasma urea at times cannot meet the N requirements of the rumen organisms for maintenance or production on such diets.

In studies with sheep on straw-based diets, the amounts of urea from blood plasma entering the rumen were relatively small (0.5 to 2.3g N/d) (Nolan and Stachiw 1979). Although urea can enter the rumen through the epithelium (Houpt 1970), it seems probable that for sheep consuming these low quality diets, most of the urea enters the rumen via saliva. In contrast, Kennedy and Milligan (1978) found that considerable amounts of urea (6 to 10g urea N/d) were recycled in sheep given brome grass (*Bromus inermis*), and Potthast et al. (1977) calculated that 9.5g urea N/d entered the rumen of sheep given an N-free basal diet plus 300g sucrose/d. Under these conditions considerable quantities of urea must have entered the rumen by transfer through the rumen wall and the suggestion is that there is a mechanism for this that is ``switched on'' when sugar enters the rumen. This has never been proven. It is possible that a high osmolarity in the rumen through the addition of sugar causes water to flow from the blood into the rumen and this carries with it urea.

It should be noted that these studies generally involve isotope dilution techniques which may not give unequivocal results where the pools of nutrients being investigated are very small (ie. rumen ammonia) and where the samples can be contaminated with extraneous N. Any N contamination would increase the apparent recycling rate.

The applied studies demonstrate responses to urea supplementation of animals fed low-nitrogen diets. This suggests that under long-term nitrogen deprivation, urea recycled to the rumen is relatively unimportant when compared with the effects of urea supplementation.

There are few studies on the movement of urea from plasma into the rumen of cattle. Mugerwa and Conrad (1971) estimated that considerable amounts of urea were transferred to the digestive tract of cattle given grain-based diets containing urea. Norton et al. (1978) found low rates of transfer of urea to the rumen of Zebu and Banteng cattle and buffaloes given roughage diets (mean 4.3g N/d). Kennedy (1980) estimated urea degradation in Hereford steers given low-N hay with and without added sucrose, and found that the rates of transfer to the rumen were 11 to 14g N/d but were increased to 23g N/d by supplementation with sucrose. Urea recycling in this case (10g N/d) may have allowed an extra 300g of organic matter to be digested in the rumen. The transfer of urea to the rumen appears to be increased by increasing intakes of digestible organic matter and was decreased by increasing ruminal ammonia levels (Houpt 1970).

Kennedy and Milligan (1980) reviewed the literature on sheep and showed that urea recycling to the rumen was positively related to the rate of apparent digestion of organic matter in the rumen and to urea concentration in plasma. The last factor may relate to the content of urea in saliva.

The question of whether urea recycling is ``controlled'' to the animal's advantage is still not clear. Although entry of urea from blood plasma into the rumen via the saliva and across the rumen wall appears to be subject to some ``control'' (Allen and Miller 1976), microbial growth and feed digestibility are at times limited by ammonia deficiency (Campling et al. 1962).

3.7.7 Urea (ammonia) toxicity

So called urea toxicity is characterised by neurological symptoms and possible derangement of brain metabolism. In practice, it occurs following rapid intake of urea that could be due to:

- Insufficient mixing of urea in compounded diets
- Sifting of urea to the bottom of a loose feed mixture
- Leaching of urea in troughs, permitting animals to drink solutions containing high concentrations of urea
- Excessive consumption of urea from blocks that have been softened by rain or rain water collecting in holes licked in the blocks or by over-consumption of liquid mixtures.

The likelihood of toxicity is greater in animals that have not been adapted to urea supplements. Animals that have been fasted for a day or more, and in those with liver dysfunction (eg. fluke infestation or damage from toxic plants) that prevent them from converting ammonia to urea, are also at risk.

Urea itself is not toxic; it is the ammonia produced from urea in the rumen that is toxic. When large amounts of urea are consumed, the pH and the concentration of ammonia in the rumen increase, and more ammonia is absorbed which is normally converted to urea in the liver and excreted in the urine. The usual explanation of urea toxicity is that the liver cannot cope with the increased absorption of ammonia; that the level of ammonia in peripheral blood rises; ammonia is carried to the brain in the blood and brings on the clinical symptoms. Any malfunction or inefficiency in the liver obviously increases the likelihood of ammonia toxicity.

An alternative explanation that has recently been put forward is that when ammonia is in high concentrations in the rumen, some diffuses into the peritoneal cavity and from there goes by lymph drainage to the jugular vein, thus bypassing the liver. If this is the case, the efficiency with which the liver removes ammonia is less important than previously supposed.

The clinical neurological symptoms may not be the only manifestation of urea toxicity. Milder forms of toxicity may decrease growth rate without producing any obvious clinical symptoms. If this is so, it is a further reason for not supplying urea in excess of requirements. The implication is that intake of urea should be limited to the minimum needed to make good use of the available feed.

3.7.8 Other sources of non-protein nitrogen (NPN)

Urea is not the only source of NPN. Ammonium salts and biuret are other possible sources. The ammonium salts, like urea, provide ammonia almost instantly for microbial protein synthesis in the rumen. As with urea, large intakes over a short time can lead to toxicity and death. Ammonium salts do not seem to have any other advantages that would warrant their use in place of urea, and in some cases they appear to be more dangerous. Ammoniation of moist feeds high in sugar by injection of anhydrous ammonia creates conditions (high temperature) which favour the formation of toxic imidazole compounds which cause bovine hysteria (see Chapter 8).

Biuret as an N supplement should have advantages over urea in that it is degraded to ammonia slowly, and thus provides the micro-organisms with a continuous supply of ammonia. It is relatively non-toxic even when consumed in large amounts and has been used as a substitute for urea.

Biuret is made by heating urea to high temperatures, causing two urea molecules to condense to biuret and ammonia.

- 2urea biuret + ammonia
- $CO(NH_2)_2$ $NH_2\text{-}CO\text{-}NH\text{-}CO\text{-}NH_2 + NH_3$

Biuret is broken down to ammonia in the rumen by the enzyme biuretase. The ruminal micro-organisms will only produce this enzyme when they are presented with biuret regularly over a period. Depending on the protein content of the diet, it may take up to 6 weeks before sufficient enzyme is produced. Moreover, if the supply of biuret is withdrawn from the adapted animal for 2 or 3 days, a readaptation period is needed to regain the same capacity to degrade biuret.

During the adaptation period, much of the biuret is absorbed. It is not metabolised by body tissue, but is excreted in the urine. Even when the rumen micro-organisms are fully adapted to biuret it seems likely that a large proportion of the biuret escapes degradation in the rumen and is either absorbed or passes down the digestive tract. There is thus a considerable degree of inefficiency of utilisation inherent in the use of biuret as an NPN supplement. Another disadvantage is the high cost---about three times that of urea. Moreover, on sugar-based diets, the ammonia from biuret does not become available fast enough to match the rate of fermentation of the carbohydrate.

These disadvantages offset the lower toxicity and the theoretical advantage that the slow breakdown should provide.

3.8 SULPHUR NUTRITION OF RUMINANTS

Animals cannot synthesise the sulphur amino acids cysteine and methionine from sulphate. The ruminant relies on micro-organisms in the rumen to convert sulphate to hydrogen sulphide which is used to synthesise methionine and cysteine for microbial growth. In the industrialised world, sulphur is never likely to be deficient because of the incidence of acid rain which contains appreciable amounts of sulphur dioxide, forming sulphuric acid in the soil. However, in the less industrialised countries sulphur deficiency can be extremely important. Even in countries where the soils are derived from volcanic rock, sulphur may be deficient in the soil. This is mainly because the soils are highly leached and the sulphur salts are highly soluble and are labile in the soil.

Sulphur can be the first limiting nutrient for efficient rumen fermentation, the primary effect being decreased availability of microbial protein and, as a result, loss of appetite.

3.8.1 Sulphur utilisation in the rumen

On protein rich diets, fermentation of sulphur amino acids in the rumen leads to production of hydrogen sulphide, which is absorbed across the rumen wall, converted to sulphate and excreted in the urine. In forage plants the nitrogen-to-sulphur ratio may vary from 4:1 to 55:1, with an average value of about 15:1. The ratio of N:S for efficient microbial growth in the rumen appears to lie between 10 and 14:l for sheep and between 14 and 15:1 for cattle (Bray and Till 1975). If the ratio is greater than these, sulphur supplementation is needed. Sulphur supplements that are commonly used include elemental sulphur, various sulphate salts and, to a lesser extent, the sulphur amino acids of feed proteins. Molasses contains appreciable amounts of sulphur (about 0.3%), because sulphur dioxide is used in the preparation of sugar from the sugarcane juice.

The anaerobic fungi, which appear to be so important in the initial digestion of fibrous feeds, are highly dependent on a source of sulphur for their growth (Akin et al. 1983).

Sulphide production in fermentation:

In general, Desulfovibrio species are responsible for converting sulphate to hydrogen sulphide in the rumen. Desulfovibrio ruminus reduces sulphate at a rate about 20 times that previously recorded for Desulfovibrio desulfuricans. Analysis of microbial protein from the rumen has suggested that there is little variation in the amino acid composition of mixed bacteria and protozoa. However, the amounts of methionine and cysteine in the protein of ruminal bacteria show considerable variation between strains.

The uptake of sulphide by micro-organisms for amino acid synthesis is determined by the size of the sulphide pool. This in turn is determined by the balance between sulphide generation, absorption and incorporation into microbial organic matter. Absorption of hydrogen sulphide is extremely rapid and concentration dependent. Sulphur thus appears to behave similarly to ammonia. The sulphate is very rapidly converted to hydrogen sulphide which is absorbed, in the same way as urea is rapidly converted to ammonia and absorbed. Sulphate recycling via the saliva is an important means of maintaining rumen sulphide levels. If the sulphide level in the rumen falls below l mg/litre of liquor, microbial growth and dry-matter digestibility of the feed are reduced.

Utilisation of cysteine and methionine in the rumen:

Fermentation of soluble proteins containing cysteine and methionine is extremely wasteful. Considerable amounts of S-amino acids are degraded to VFAs, ammonia and hydrogen sulphide when high-protein diets are fed to ruminants. Feeding high levels of cysteine shows that the organisms that use cysteine can be saturated and large amounts of cysteine may flow to the lower digestive tract. For instance, when sheep were fed 5g of cysteine in 800g of feed, 200-400 mg of free cysteine flowed out of the rumen per day (Bray and Till 1975). Such large amounts of free cysteine obviously do not occur in the rumen and normally no S-amino acids per se flow from the rumen to the omasum.

Recycling of sulphur:

Absorbed sulphide is oxidised to sulphate in the liver, enters the blood and is distributed through the extra cellular fluid. Sulphate is recycled to the large intestine via secretions and to the rumen via saliva. Some is lost via the urine. The amount of sulphur returned to the rumen in saliva is related to plasma sulphur levels and in cattle there is a strong positive correlation between salivary and blood sulphate. The direct flow of sulphate across the rumen wall is of minor importance and the majority of sulphur that recycles to the rumen is through saliva. On entering the rumen, sulphate is reduced and made available for amino acid synthesis in much the same way as ammonia released from urea is available for microbial growth.

Sulphur availability in rumen fermentation:

The continuous availability of sulphur for fermentation in the rumen is important. As with urea supplementation, providing a sulphur supplement as a single meal may produce a peak concentration of sulphide in the rumen which is out of phase with the need for sulphur for microbial growth.

Multinutrient blocks based upon molasses and urea may be beneficial to sulphur metabolism by favouring slow and continuous intake of sulphur. Where proteins are being fed to ruminants to provide fermentable nitrogen these also probably provide fermentable sulphur. Therefore sulphur is unlikely to be deficient where large quantities of high-protein meals and concentrates are being fed. Where protein is a small proportion of the diet this source of S is insignificant and the animal must depend on elemental S to support efficient microbial growth in the rumen. Thus S supplementation is likely to be required in feeding systems based on crop residues and byproducts.

3.8.2 Toxicity of sulphur

Kandylis (1984) found that sulphur toxicity occurred where pastures were heavily contaminated with industrial effluent. In the non-industrialised countries sulphur toxicity is rare except where high levels of sulphur are given as feed supplements or are used in agro-industrial processes. The sulphur content of molasses sometimes exceeds the apparently safe levels for ruminants. The effects of this are unknown.

The safe level of sulphur in a diet is between 0.1 and 0.2% and appears to vary between diets. The primary effect of a slight excess of sulphur in the diet is to reduce feed intake. High levels of dietary sulphur lead to the generation of large quantities of hydrogen sulphide gas which when eructated enters the lungs and causes severe nervous and respiratory stress (Dougherty et al. 1964). Rumen stasis is also observed in cases of severe sulphur poisoning in cattle. Concentrations exceeding 0.3 - 0.4% may cause toxic effects leading to death (Kandylis 1984).

A large amount of sulphur in the diet is harmful to cellulolytic organisms in the rumen and reduces fibre digestion (Hubbert et al. 1958). The breakdown of starch by rumen micro-organisms was unaffected by high sulphur levels and the effects on sugar-fermenting bacteria are not known.

3.9 FERMENTATION IN THE LOWER GUT

Residues of feed, bacterial cells and endogenous secretions passing into the intestines are fermented in the caecum and large intestine. The stoichiometric relationship between VFA production and microbial cell synthesis is likely to be similar to that in the rumen. The VFAs produced are absorbed and little VFA appears in faeces. Acetic acid is the main VFA produced in the caecum and large intestine.

Fluid from the caecum and large intestine has a high proteolytic activity. It is therefore probable that the microbes present are degraded by the action of phages or other infective or predatory organisms followed by fermentation of the lysed cells. This suggestion is consistent with the high level of branched-chain VFAs present in caecal fluid relative to that in rumen fluid (Faichney 1969; Orskov et al. 1970).

The main nitrogen source for caecal organisms is almost certainly ammonia, largely from urea entering from blood. However, other endogenous-N materials from gut epithelium cells, enzymes and rumen bacteria may all be degraded to give ammonia. Amino acids from the bacterial cells degraded in the large intestine may be taken up as such, but the apparent production of large amounts of branched-chain and higher VFAs suggests that the degraded bacterial cells are absorbed largely as VFAs and ammonia.

Infusing carbohydrates into the caecum of sheep increased excretion of protein in the faeces (Thornton et al. 1970; Orskov et al. 1970). The increased N excretion appeared to be bacterial cells which were presumably produced from the infused substrate. Caecal digestion of

fibrous feeds may increase where nutritional (eg. sulphur deficiency) or other factors result in considerable amounts of unfermented feed (that requires fermentation for its digestion) escaping the rumen.

The nature of the fermentation in the caecum is likely to influence productivity of the animal because an increased partitioning of fermentative digestion to the caecum will decrease the proportion of essential amino acids relative to energy available for metabolism. The net result of this will be a decrease in feed intake because the P/E ratio will be lowered, particularly where ruminants are fed low-protein/ high-carbohydrate feeds.

3.10 ABSORPTION OF VFAs

The significance of the VFAs as major substrates for ruminants has been stressed earlier. It appears that about 60% of the digestible energy of a feed comes from VFAs and approximately 30% from bacterial cell constituents. If it is assumed that the organisms are digested to the extent of 80% and they are approximately 60% protein, 20% nucleic acids, 10% polysaccharides and 10% lipid, then the absorbed VFAs and products from bacteria may contribute to available substrate in roughly the following proportions: VFAs 60-70%, amino acids 20%, carbohydrate 4%, lipid 8%. To this could be added small quantities of dietary long-chain fatty acids and a variable quantity of dietary protein or starch, depending on the diet.

VFAs are absorbed from the rumen, apparently by diffusion across the rumen wall. About 25% of the VFAs are absorbed from the post-ruminal tract since they leave the rumen in the digesta. A large proportion of the fluid from the reticulum passes unchanged to the abomasum by way of the omasal sulcus (Hill 1961) but most of the water and electrolytes (particularly bicarbonate ions) are absorbed from the omasum.
The VFAs are metabolised in the epithelial wall of the rumen and omasum (Stevens 1970). There are few studies which quantitatively account for the metabolism of VFAs by these organs.

Since the absorption of VFAs from the rumen appears to be by simple diffusion, the requirements for substrate of the rumen wall are mainly to meet (i) the energy requirements for active transport of electrolytes and (ii) the maintenance energy requirements for the turnover of the tissue and the replacement of worn-off rumen epithelium.

The individual VFAs are metabolised by the rumen epithelium. A proportion of the acetate is oxidised to CO_2; propionate is oxidised to CO_2 but, contrary to previous suggestions, little or no conversion to lactate occurs. Butyrate is oxidised to CO_2 and converted mainly to ketone bodies.

The extent to which the VFAs are modified in passing through the rumen wall is not known. It appears that butyrate is converted quantitatively to ketone bodies which account for most of the ketone bodies in circulation in feeding animals (Leng and West 1969). Acetate and propionate appear to be absorbed as such.

Acetate enters the blood of the sheep at up to twice the rate of its production in the rumen. This indicates that quite large amounts of acetate are produced from absorbed long-chain fatty acids or that fat depots are continually turning over giving rise to acetate.

Propionate is removed almost totally from blood by metabolism in the liver. Propionate contributes extensively to glucose synthesis and possibly produces 80-90% of the glucose synthesised.

The formation of B-hydroxybutyrate together with acetate, which pass unchanged through the liver, conserves substrate for oxidation in extrahepatic tissue. The liver probably obtains its substrates from propionate and butyrate and it may also remove some of the long-chain fatty acids that are absorbed from the digestive tract.

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