CHAPTER 1

INTRODUCTION

The structural carbohydrates of plants constitute the most abundant, renewable, nutritive energy source on earth, but their nutritional value is denied to most species of animals because of the ß-1, 4-glucosidic bond for which no monogastric enzyme exists. Thus ruminants and other herbivorous species have a unique position in the food chain by being able to utilise these structural carbohydrates of plants.

The ability of ruminants to utilise low quality roughages for growth, work and reproduction ensures their place as major meat/milk/wool producing commodities in the world. Ruminants are able to do this because of their unique digestive tract - the rumen, a fermentation chamber in the foregut where roughage is broken down by microbes which, in turn, contribute high quality protein that can be digested in the ruminant's small intestine.

Due to the demands on land for cereal and vegetable production as well as human occupation it is often necessary for ruminants to obtain their feed from cereal byproducts and low quality forages. It is therefore imperative that ruminant nutritional requirements are investigated so that in each environment maximum production can be attained using the resources available in the locality. This demands an intimate knowledge of the biochemical and physiological pathways that determine the use of feedstuffs for the nutritional requirements of ruminants.

Traditionally animals fed low quality forages were believed to be energy deficient and supplementation strategies involved 'high-quality' concentrates. However, results of work during the last two decades have shown that supplementation strategies must consider the two systems operating in ruminants, i.e. the microbial ecosystem and the animal system (see Preston and Leng 1987). Supplementation needs to provide nutrients for each system.

As more of the prime grazing lands become dedicated to primary food production ruminants will increasingly have to be confined and fed byproducts of agriculture. Alternatively they will be forced onto marginal grazing lands that are subject to periodic drought and scarcity of forage. It is important, therefore, to concentrate efforts to obtain the maximum amount of benefit from the available resource rather than resorting to 'blanket' supplementation with high energy cereals.

Critical supplements, i.e. those that have a large affect relative to the amounts fed and are referred to here as having catalytic effects on the efficiency of feed utilisation, need to be identified. One of the critical supplements that has been identified is bypass protein, i.e. protein that escapes rumen fermentation to be digested in the small intestine. Supplementation with bypass protein increases the efficiency of feed conversion and at times will stimulate dry matter intake by the animal. However the feed intake response to bypass protein supplementation has been variable and reasons why this occurs needs to be elucidated.

It is becoming increasingly apparent that other considerations have to be taken into account when formulating livestock rations. Increasing world temperature, i.e. the greenhouse effect, is becoming a very serious problem. Methane is one of the gases contributing significantly to the greenhouse effect, and arises largely from natural anaerobic ecosystems such as rice paddies and ruminant animals. Methane production from ruminants fed low quality feed may be double that of ruminants fed high quality feeds (Leng 1991). This is because in poor quality feed a number of essential microbial

nutrients are deficient resulting in low an inefficient microbial growth rates and high methane production. Under these circumstances methane production may represent 15 - 18 % of the digestible energy of the feed (Leng 1991). Providing the essential nutrients for efficient microbial growth as supplements to the feed may reduce methane production to 7 - 12 % of the digestible energy of the feed. Research is needed to determine methods that can be used to decrease methane production from ruminants.

As ruminants on low quality feeds in the Asia/Pacific region have been estimated to produce up to 60 percent of the methane from the world's population of ruminants (Leng 1991) nutritional scientists in Australia should have a mandate for investigating and applying methods to (1) increase productivity of these animals using the available feed resources, and (2) to be aware that environmental considerations must be taken into account in any development program.

The research reported in this thesis is part of the continuing programme of research being carried out in this laboratory on methods aimed at increasing the efficiency of feed utilisation of ruminants on roughage based diets. The major objective of the studies reported here was to examine factors that affect the feed intake response to supplementation of bypass protein and the interactive effect of temperature.

CHAPTER 2

LITERATURE REVIEW

2.1 Scope of the review

Ruminants on low quality forages are dependent on the products of fermentative digestion in the rumen for their energy (the volatile fatty acids) and protein (contained in microbial cells that flow from the rumen) supply. Factors which affect the efficiency of rumen fermentation on poor quality forage diets largely influence microbial growth. This in turn affects the balance of volatile fatty acids (VFA) to microbial protein availability (which is synonymous with the protein/energy ratio). The protein to energy (P/E) ratio of the nutrients absorbed appears to be the primary factor influencing the efficiency of feed utilisation for body tissue deposition (see Leng 1990a). In addition to ensuring an efficient rumen fermentation which optimises the P/E ratio from this rumen, supplementing forage diets with small amounts of protein that bypasses rumen fermentation will further improve the P/E ratio.

The research reported in this thesis relates to the effectiveness of adjusting P/E ratios in the nutrients absorbed for improving ruminant livestock production from low quality forage diets. The factors that influence P/E ratio, intake and efficiency of feed utilisation of forages are discussed in the following review to establish the background to the research.

2.1.1 Definition of low quality forages

Ruminants given low quality forages are often deficient in a number of critical nutrients including minerals, trace elements, soluble nitrogen and bypass protein. For the purpose of this review, low quality forages are defined as those forages which are less than 55% digestible and contain less than 8% crude protein and 10% soluble sugars and starches (Leng 1990b). In many systems of ruminant production in tropical and subtropical countries, the available forages are often less than 45% digestible and contain less than 3% crude protein.

2.2 Digestive physiology of the ruminant

The unique aspect of the ruminant digestive tract is the rumen - a relatively large fermentation chamber which, when full comprises 10-20% of the liveweight of the animal. The large volume of the rumen allows feed to be retained for sufficient time to ensure exposure of feed particles to fermentative digestion by the resident microbes. Production of saliva ranges from 33 to 200 litres/d in cattle and 6 to 16 litres/d in sheep and provides most of the salts and more than 70% of the fluid entering the rumen (Pond *et al.* 1990). The rumen provides a stable anaerobic environment for the microbes. The pH normally ranges from 5.5 and 7.0 and the temperature from 39^{o}C to 41^{o}C (Church 1976). The food supply is periodic with muscular contractions of the rumen bringing the microbes in contact with freshly ingested or ruminated feed. The ability to masticate and remasticate feedstuffs in combination with high salivary secretion rates sets the ruminant apart from other herbivores (Pond *et al.* 1990). Build-up of products that may be inhibitory to microbial growth is prevented by absorption or by movement along the intestinal tract. The microorganisms secrete cellulases and other enzymes required for the hydrolysis and breakdown of the ingested feed particles. The products of fermentative breakdown are the VFAs (mainly acetic, propionic and butyric), methane and carbon dioxide. The ATP that is generated during fermentation of feed to

VFA is coupled to the synthesis of cellular constituents and is also available for maintenance of microbial cells.

2.2.1 Rumen microorganisms

The microbiology of the rumen is complex with large numbers of species of organisms being present. The *milieu* that develops is largely dependent on diet. Recent studies using scanning- and transmission-electron microscopy have shown that the rumen microflora is compartmentalised; different populations being associated with feed particles, the rumen wall and the liquid phase of the rumen contents (Czerkawski and Cheng 1988). Three main groups of microorganisms exist in the rumen: bacteria, protozoa and fungi. Of these, bacteria play a dominant role with a population density of greater than 10^{10} per g of digesta (Hungate 1966). Protozoa occur in smaller numbers (10^6 per g) but, because of their size, may constitute more than fifty percent of the microbial biomass in the rumen (Clarke 1977). Information on fungal numbers is relatively scarce due to the close association of the fungal rhizoid with plant material and the irregular production of zoospores. Zoospore population densities (estimated at 10^3-10^5/ml) can only give an approximate indication of the total fungal biomass present (Fonty *et al.* 1990).

The primary sources of carbon and energy for the rumen microorganisms are the dietary polysaccharides. The fibrolytic microorganisms produce small molecular weight carbohydrates from large molecular weight polymers. Extracellular enzymes hydrolyse the polymers and the products are then transported into the interior of cells and fermented (Wolin 1990). Species of microorganisms that are incapable of directly using cellulose utilise the products of cellulose hydrolysis. In addition some rumen microbial species synthesise vitamins which are then available for use by other species that require them for growth (Wolin 1990).

2.2.1.1 Bacteria

Bacteria are the principal organisms in fermenting plant cell wall carbohydrates. *Bacteroides (Fibrobacter) succinogenes, Ruminococcus albus* and *Ruminococcus flavefaciens* are generally accepted as the most important cellulolytic bacteria and are distinguished by their activity, numbers and their close association with plant cell walls (Van Gylswyk and Schwartz 1984, Martin 1990, Wolin 1990).

Most ruminal species of bacteria use ammonia as their main nitrogen source (Hespell and Smith 1983, Wolin 1990).

2.2.1.2 Protozoa

The important protozoa in the rumen are ciliates, entodiniomorphs and holotrichs (Hungate 1966) and are found both in the rumen fluid and attached to (or associated with) feed particles. The holotrich species ferment soluble sugars such as glucose, fructose and sucrose and are relatively large with the cell surface being covered with cilia. The entodiniomorphs, which have tufts of cilia on the anterior parts, can ferment soluble sugars but tend to derive their energy from the digestion and metabolism of fibre or starch (Schwartz and Gilchrist 1975). The population densities of protozoa are greatly influenced by the animals' diet. Low population densities of ciliates occur in the rumen on diets of poor quality forages (Jouany 1989). Addition of starch favours populations of entodiniomorphid ciliates whilst holotrichs respond more to fresh grass or sugar/fibre diets (Hungate 1966, Coleman 1975, Clarke 1977).

The role of protozoa in fibre degradation is not totally clear (Jouany 1989, Williams 1989, Jouany and Ushida 1990) but it is now generally accepted that the efficiency of microbial growth is enhanced and more microbial and dietary protein flows from the rumen when protozoa are not present (Bird *et al.* 1990).

2.2.1.3 Fungi

Fungi were first recognised as inhabiting the rumen in the mid 1970's (Orpin 1975, Bauchop 1979). They were classified by Heath *et al.* 1983, and placed in a new family (Neocallimasticaceae). So far the following list the genera and species of monocentric fungi: *Neocallimastix frontalis, Neocallimastix patriciarum, Piromyces* (formerly *Piromonas) communis, Caecomyces (*formerly *Spheromonas) communis,* and *Caecomyces equi* (Akin and Borneman 1990).

The life cycle of the anaerobic fungi consists of a stage involving a non-motile, vegetative, reproductive form and a stage where a motile flagellated cell is produced (Bauchop 1988). It is during the vegetative stage that attachment to plant material occurs. Scanning electron microscopy has shown that a large population of fungi is present when fibrous diets are fed, but not when the animals are on lush pasture or receive concentrates (Bauchop 1981).

Rumen fungi extensively colonise the lignin-containing tissues of forages and are active in fibre degradation (Bauchop 1979, 1981). The extent to which fungi can degrade plant walls may be limited by interactions with other rumen microbes (Akin and Borneman 1990, Joblin 1990).

It appears that a major role in fibre degradation might be played by fungi in their ability to penetrate the cuticle of grass leaf blades, thus enabling attachment and invasion of the plants by colonising bacteria and protozoa (Orpin 1977, Bauchop 1981, Akin and Rigsby 1987). In addition, the attachment of fungi to the plant structure weakens the structure so that less effort is expended by the animal in rumination of the feed (Gordon 1980).

2.3 Stoichiometry of rumen fermentation

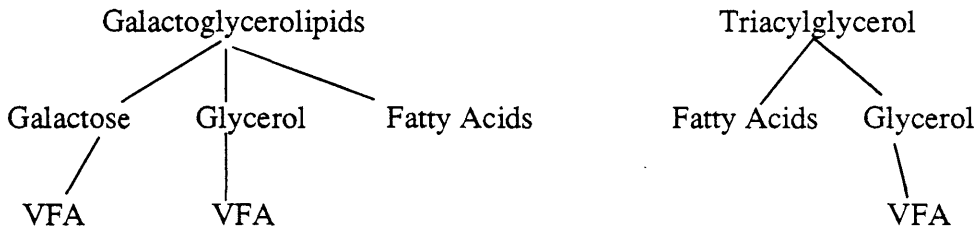
2.3.1 Carbohydrate metabolism

Dietary carbohydrates fermented in the rumen include soluble sugars, starch, pectin, hemicellulose and cellulose. They are hydrolysed to small saccharides that are then fermented to several products. Numerous intermediates may be formed but the final fermentation products that accumulate within the rumen are the VFAs acetate, propionate and butyrate. Carbon dioxide and methane are also produced and either absorbed or excreted by eructation. The ratios of these products vary with diet and frequency of feeding and their balance is dependent on the microbial mix within the rumen. On certain feeds, some carbohydrate(s), mainly starch, may pass from the rumen unfermented. Starch reaching the small intestine in this way is largely hydrolysed enzymatically and absorbed. Other complex carbohydrates escape the rumen and pass to the caecum and large intestine where they are either fermented by microbes or excreted in faeces. The VFAs produced in the caecum are absorbed and contribute usually 10-20 % of the total fatty acids absorbed, although in certain circumstances this figure may be nearer to 30% (Harfoot 1978). The microbial cells produced in the caecum, are largely excreted in the faeces and thus lost to the animal as a source of amino acids.

2.3.2 Lipid metabolism

In forage-based diets the main lipids available are largely derived from chloroplast membranes, and the lipids present in seeds. The lipids from the leaves are mainly monogalactosyl and digalactosyl glycerolipids and the lipids from seeds made up

mostly of triacylglycerols. Both are rapidly hydrolysed by the rumen organisms although there is evidence that plant enzymes play some part in the initial hydrolysis (Hawke 1973):



The galactose and glycerol produced by hydrolysis are rapidly metabolised to VFA. Unsaturated long chain fatty acids are extensively hydrogenated by rumen microbes with the formation of stearic, palmitic and oleic acids. Some of the polyunsaturated fatty acids are captured by protozoa in their membrane lipids and some are used by rumen bacteria for growth. Those which leave the rumen are absorbed from the intestine and emerge in the lymphatic and eventually blood circulations as chylomicrons and very low density lipids.

Long chain fatty acids are synthesised by rumen microbes by the condensation of shorter chain acids with 2-carbon units (Goldfine 1972). Rumen microbial lipids are characterised by odd-chain lengths and terminally branched fatty acids (Viviani 1970).

The capacity of rumen microorganisms to digest lipids is strictly limited and reduced fibre digestibility in the rumen has often been observed due to lipid supplementation (Palmquist and Jenkins 1980).

2.3.3 Nitrogen metabolism

Amino acid requirements of ruminants are provided by microbes synthesised in the rumen and passing out into the small intestine and from dietary protein that escapes rumen digestion and is intestinally digested. The proteins and peptides fermented in the rumen are converted mainly to VFA and ammonia. Proteolytic activity in the rumen is

mainly associated with bacteria. Protozoa appear to have little proteolytic activity toward soluble protein (Hespell and Smith 1983, Nugent and Mangan 1981) but ingest and digest particulate protein (Broderic *et al.* 1991). The hydrolysis of proteins by bacterial proteases tends to be sequential with the production of large oligopeptides that in turn are cleaved into smaller peptides and free amino acids (Hespell and Smith 1983). The role of microorganisms in protein metabolism has been reviewed recently (Cotta and Hespell 1986, Wallace and Cotta 1988, Russell *et al.* 1990).

Solubility is an important factor in determining the susceptibility of proteins to bacterial attack in the rumen. The ammonia formed in the rumen is the major nitrogen source for amino acid synthesis by microorganisms. Ammonia is absorbed, particularly at high levels, and converted to urea in the liver. The amino acids valine, leucine and isoleucine are deaminated in the rumen to isobutyric, 2-methylbutyric or isovaleric acids (Wolin 1990). Many rumen species require one or more of these acids for synthesis of branched chain amino acids. The insoluble proteins and some soluble protein that are not fermented in the rumen are washed out into the small intestine where they can be absorbed and contribute directly to the animals' amino acid requirements.

Urea entering the rumen (from dietary addition, saliva or diffusion through the rumen wall) is rapidly hydrolysed to ammonia by bacterial urease and may contribute significantly to the ruminal ammonia pool (Leng and Nolan 1982, Hespell and Smith 1983). The use of urea in this way provides a means whereby N can be conserved and resynthesised into amino acids. This may become important when fermentation and growth of microorganisms is limited by the supply of ammonia, the amount of endogenous N recycled reducing the amount of N required to correct the deficiency (Nolan and Stachiw 1979). However, there are many reports in the literature (Satter and Slyter 1974, Perdok *et al.* 1988) of microbial growth being limited by ammonia deficiency and the low values for recycling obtained by MacRae *et al.* (1977), Norton *et*

al. (1978) and Nolan and Stachiw (1979), indicate recycling is not sufficient to ensure adequate ammonia N. Species differ in the amount of N recycling, for example, *Bos indicus* cattle have been shown to have a greater ability than *Bos taurus* cattle to recycle urea (Hunter and Siebert 1985).

2.4 Means of manipulating ruminant production from low quality forages

When poor quality forages make up the basal diet of the ruminant, it is critical to obtain the highest efficiency of rumen fermentation in order to maximise microbial protein production and digestibility of the forage. Maximising microbial protein production will in turn improve the efficiency of utilisation of the absorbed products. The following section discusses the potentially limiting nutrients for microbial growth in the rumen and how these influence the production from ruminants.

2.4.1 Factors effecting efficiency of rumen fermentation and microbial growth

A recent review of the literature (see Leng 1990b) has indicated that the digestibility of a forage will probably be optimised at a microbial growth efficiency in the rumen which is lower than that which optimises the P/E ratio. It has often been assumed that the yield of microbial protein (i.e. Y-ATP g dry cells produced per mole of ATP available) was fairly constant irrespective of diet. It is now recognised, however, that yield of microbial protein can vary significantly. For example, recent studies by Russell (1990) have shown that *Streptococcus bovis*, treated to inhibit protein synthesis, continued to ferment glucose and produce heat in the absence of growth. He suggested that a futile cycle of protons passing through the cell membrane was responsible for the energy spilling and that, under certain conditions in the rumen when there is a deficiency of nutrients, energy spilling may cause significant reduction in ATP availability and therefore in microbial protein production by increasing the

maintenance requirements of the rumen microorganisms. He hypothesised that the improvements in animal productivity observed with frequent feeding may be due to avoiding situations where the rumen microbes are nutrient limited and energy spilling results.

The rumen microorganisms have definite requirements for both macro and micro-nutrients and microbial growth efficiency in the rumen will be determined by the first limiting nutrient. Several reviews on ways of increasing the efficiency of rumen fermentation are available (Ørskov 1975, Chalupa 1977, Thomas and Rook 1977, Prins 1978, Leng 1982, Chalupa 1984, Owens *et al.* 1984, Thivend and Jouany 1986, Nolan and Leng 1989).

2.4.1.1 Minerals

Mineral requirements of ruminants are affected by many factors, including kind and level of production, age, the level and chemical form of the elements, interrelationship with other nutrients, mineral intake, breed and adaptation (McDowell *et al.* 1984). Requirements for minerals are notably dependent on level of productivity, with mineral availability becoming more crucial at higher levels of productivity (McDowell *et al.* 1984). Several reviews are available on the influence of mineral deficiency in ruminant nutrition (see Durand and Kawashima 1980, Ammerman and Goodrich 1983, McDowell *et al.* 1984, Smith 1984, Durand and Komisarczuk 1988).

Moderate mineral deficiencies may reduce feed intake by ruminants through, at least in part, the impaired activity of rumen microbial growth (Durand and Komisarczuk 1988). Grazing ruminants are often susceptible to mineral deficiencies or toxicities with soil type, water source, plant species and climate influencing availability of minerals (Ammerman and Goodrich 1983). McDowell *et al.* (1984) observed that for grazing cattle in tropical areas the mineral most commonly deficient is phosphorus, followed by copper and cobalt.

The effect of a mineral deficiency on the rumen microbes is a decreased growth efficiency which results in a decrease in cell production thereby reducing the P/E ratio in the products for absorption in the animal. If the deficiency is severe, digestibility of the forage will be affected and the microbial population will decrease, leading to a decrease in feed intake (Leng 1990b). It is usual when mineral deficiencies are suspected to provide a 'blanket' mixture in the form of a salt lick or a molasses urea block fortified with minerals (McDowell *et al.* 1984, Kunju 1986, Suttle 1987, Leng 1990b).

2.4.1.2 Rumen ammonia

As most rumen bacteria use ammonia as their main nitrogen source it is essential to ensure adequate levels of NH_3-N in the rumen fluid in order to optimise microbial growth. Using continuous-culture fermenters charged with ruminal contents obtained from steers, Satter and Slyter (1974) found that increasing the ammonia concentration beyond 50 mg NH_3-N/l had no effect on microbial protein production. Excessively high levels of ammonia, up to 800 mg NH_3-N/l, did not inhibit microbial growth (Satter and Slyter 1974). On the basis of this work, they suggested that addition of non-protein nitrogen supplements to ruminants was warranted only if the ruminal concentration of ammonia was less than 50 mg NH_3-N/l. However different laboratories have obtained different values of the optimum rumen ammonia level for maximising dry matter digestibility. For example, *in vivo* studies by Mehrez *et al.* (1977) on sheep fed whole barley fortified with graded levels of urea, indicated that ammonia concentration for optimum DM digestibility was 235 mg NH_3-N/l rumen fluid. However this value was based on a barley diet and these authors suggested that optimum ammonia concentration for maximal digestibility of roughage may be different since it could be dependent on the pH of rumen fluid and on the availability of energy-yielding substrate. Recent

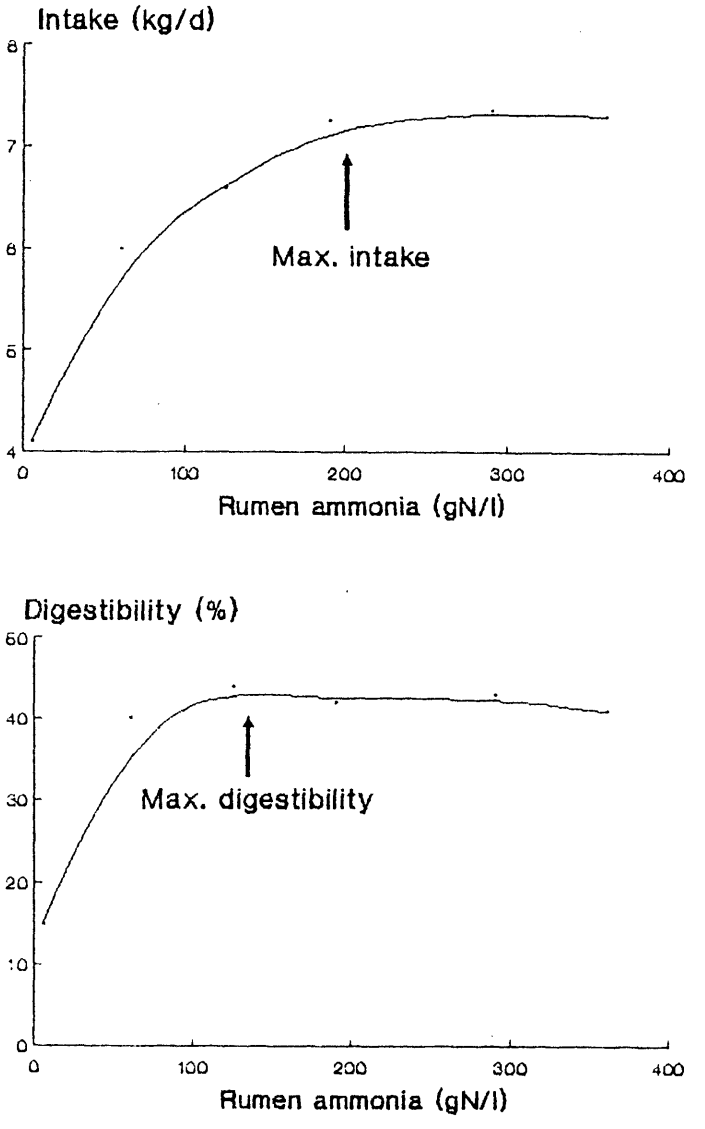


Figure 2.1 *The effects of the concentration of ammonia in the rumen on the intake and digestibility of straw by cattle (Perdok et al. 1988).*

studies in Australia (Boniface *et al.* 1986, Perdok *et al.* 1988), with cattle fed low quality roughages, have shown that digestibility was optimised at a rumen ammonia level below 100mg NH_3-N/l whilst intake was optimised at about 200 mg NH_3-N/l (see Figure 2.1). It has been hypothesised (Leng 1990b) that, on low quality roughage diets, provided the rumen microorganisms have sufficient nitrogen, it is the P/E ratio absorbed from the intestines that is critical in determining intake by the animal. Leng suggests

that when bypass protein is supplemented and thus the P/E is adjusted then maximum intake of the basal diet should occur at rumen ammonia levels of 100 mg NH_3-N/l.

2.4.1.3 Amino acids and peptides

Work by Maeng *et al.* (1989) has shown that, at times, the addition of preformed amino acids and peptides to a diet adequate in non-protein-nitrogen (urea) increased microbial growth efficiency. The source of carbohydrate in the basal diet determined the need by the microbes for amino acids or peptides. A greater response to these additions was found when the basal carbohydrate was either starch or sugar as compared with cellulose. Hence, in some situations, increased microbial cell production per unit of carbohydrate fermentation will be obtained by the addition of a small amount of supplementary protein in addition to non-protein nitrogen.

2.4.2 Methods to increase the efficiency of utilisation of poor quality roughages by ruminants

Once the basic requirements of the rumen microorganisms have been met, there appears to be considerable scope for manipulating the efficiency of utilisation of poor quality feed by ruminants. This may be by manipulating the microbial mix that exists in the rumen or by supplementing the diet with certain key supplements to meet the need of the animal for specific nutrients. The phrase 'balance of nutrients' was first used by Preston and Leng (1987) for ruminants to describe this matching of requirements of the animal with specific nutrients. The following section highlights the main methods used to manipulate feed utilisation efficiency.

2.4.2.1 Bypass protein

It was assumed that the animals' need for protein was met by the outflow from the rumen of microbial amino acids. However, Ørskov (1970) proposed that it was most logical to consider host animal and rumen microbial requirement separately. He described the net amino acid needs of host animals during early and late growth, pregnancy and lactation and then superimposed on the graph the potential net contribution of microbial amino acid outflow from the rumen (Figure 2.2). It can be seen from Figure 2.2 that there are large gaps in the sufficiency of microbial amino acid production to meet the host animals' need. Bypass protein was then suggested as a means of satisfying the animals requirement for amino acids surplus to that provided by the rumen microorganisms.

Bypass protein is defined as that portion of a dietary protein which passes intact from the rumen to the abomasum (Hungate 1966). On most diets some feed protein escapes rumen degradation and flows out to the abomasum. The potential for bypass of a protein depends on several factors. The two most important ones being solubility and outflow rate of the protein from the rumen. For example, Ørskov *et al.* (1983) calculated that the proportion of linseed meal degraded within the rumen would be reduced from 87% at a fractional outflow rate of 0.01/h to 40% at a fractional outflow rate of 0.10/h.

Responses to supplementation with bypass protein reported in the literature include increases in (1) feed intake (Ørskov *et al.* 1971, Kempton and Leng 1979, Hennessy and Williamson 1990); (2) wool growth (Reis and Tunks 1969, Ferguson 1975), Leng *et al.* 1984, (3) liveweight gain (Faichney 1971, Ørskov *et al.* 1971, Chalupa 1975, Preston 1976, Perdok and Leng 1990), (4) feed conversion efficiency (Egan 1965, Preston 1976, Kempton and Leng 1979). (5) milk yield (Clark 1975), and (6) nitrogen retention (Black 1970, Faichney 1971).

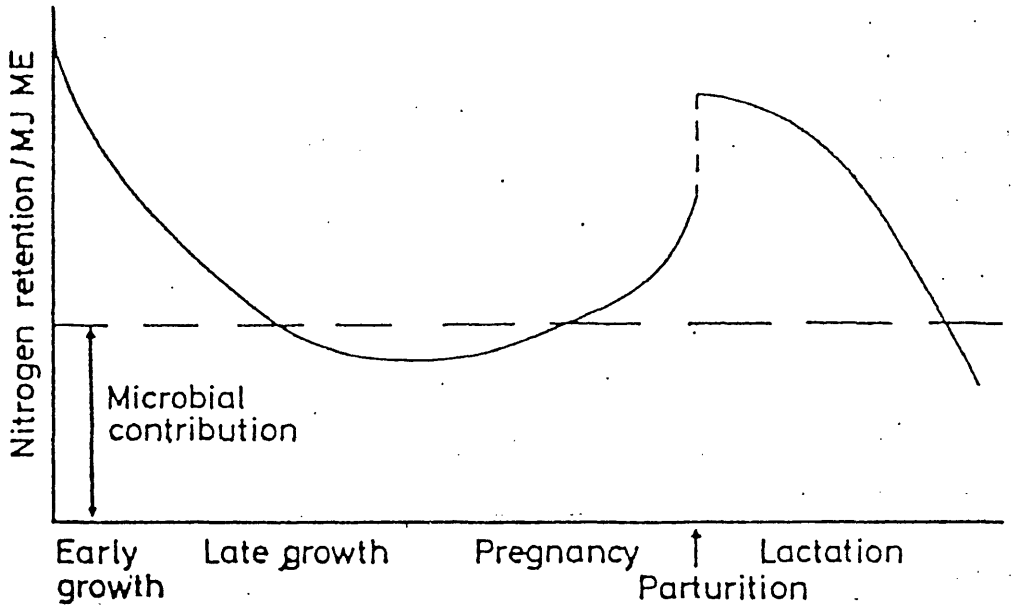


Figure 2.2 *The effect of age and production on potential nitrogen retention in relation to ME intake (Source Ørskov 1970)*

Egan (1977) reported a strong relationship in sheep between the P/E ratio in digestion products and the level of voluntary intake. However, there is still controversy reported in the literature as to whether feeding of bypass protein increases intake of the basal diet. Leng (1990b) has suggested that an interaction exists between feeding of bypass protein and environmental temperature. This is discussed more fully in Section 2.6.

When feeding low quality forages the problem of protein supply is exacerbated by lack of sufficient nitrogen for the rumen microorganisms. A typical situation of response to supply of nitrogen for both the rumen microorganisms and to meet the animals requirement is given by Lindsay and Loxton (1981). They showed the effect of the additions of urea/sulphur and urea/sulphur plus bypass protein (500 g/d) to the hay (45% digestible, 0.4% N) diet of growing cattle (170 kg liveweight). The addition of urea/sulphur increased feed intake by 33% and decreased liveweight loss from 410 g/d

to 320 g/d. Addition of the urea/sulphur plus bypass protein further increased intake by an additional 63% and led to a liveweight gain of 220 g/d.

2.4.2.2 Protozoa

There is substantial evidence in the literature that rumen protozoa decrease the amount of microbial and feed protein that reaches the intestines (Bird and Leng 1990). It is known that protozoa engulf bacteria (Coleman 1975) and may therefore decrease the numbers of microorganisms flowing through into the abomasum. *In vitro* studies have estimated engulfment rates of bacteria by mixed rumen protozoa of 150 to 4,290 bacteria per protozoan per hour (Denholm and Ling 1989). Ling (1990) suggests that rumen efficiency could be increased considerably if a way could be found to prevent digestion of bacteria by protozoa.

Protozoa have an affect on the amount of feed protein that flows through into the abomasum. For example, Ushida *et al.* (1986) showed that 13-20% more protein was degraded in the rumen of faunated sheep than in fauna-free sheep. Michalowski (1988) observed that the most important factor affecting the utilisation of proteins by ciliates was the solubility of proteins in the culture medium. Proteins of low solubility were degraded most intensively by ciliates and were most effective in supporting ciliate growth. This finding supports the work by Bird and Leng (1984) that defaunation of sheep is equivalent to the use of a bypass protein supplement.

It is now possible to maintain fauna-free flocks and herds at pasture and in feedlots (Bird *et al.* 1990). Bird and coworkers have summarised the advantages of replacing the protozoa population with bacteria in the microbial ecosystem as increasing the utilisation of non-protein nitrogen by bacteria, increasing microbial outflow from the rumen and reducing the amount of dietary protein degraded in the rumen. They have emphasised that the P/E ratio in the nutrients available to ruminants on low quality

roughages is critical and that by reducing or eliminating protozoa the P/E ratio is increased.

2.4.2.3 Catalytic effect of a green forage

Silva and Ørskov (1988) have suggested that it might be possible to improve the digestion of low quality roughages by adding a source of easily digestible cellulose and/or hemicellulose. In line with this suggestion, the work by Krebs *et al.* (1989) indicated that freshly ingested material in the rumen is seeded with bacteria from existing feed particles. In view of this, the stimulus frequently found by the addition of a small amount of green forage to straw or other low quality forage diets may be in the provision of a substrate that, because of its high digestibility, provides a source of bacteria with which to seed other less digestible feed sources (Leng 1990b).

2.4.2.4 Glucose availability

In ruminants, the lack of glucose precursors has been linked with inefficient feed utilisation (Bergman 1973, Preston and Leng 1987). The thesis that the availability of glucose and/or glucogenic compounds is essential for efficient production of ruminants was first proposed by Leng and Preston (1976). However, since then, there has been considerable controversy in the literature (ARC 1980) concerning this perceived need and part of the research in this thesis is in response to this controversy. The background information to gluconeogenesis and its importance is dealt with in the following section.

2.5 Glucose metabolism in ruminants

Ruminants, like monogastrics, have an obligate requirement for glucose, however, because of pregastric fermentation, ruminants have to rely on gluconeogenesis from propionate and other substrates for their glucose supply. Therefore, gluconeogenesis is a continuous and important process in ruminants (Bergman 1963, Ballard *et al.* 1969, Leng 1970, Yost *et al.* 1977, Young 1977, Lindsay 1978). Glucose

is required by a minimum of five areas of the body: (1) nervous system, (2) for turnover and synthesis of fat, (3) muscle, (4) foetuses, and (5) mammary gland (Bergman 1973). The amount of glucose required by the animal is therefore variable and dependent on the physiological state of the animal.

2.5.1 Glucose absorption on grain based diets

It has been estimated that in nearly all feeding circumstances most of the blood glucose of ruminants is derived by gluconeogenesis (Lindsay 1978). Ruminants given large amounts of grain (largely maize and sorghum grains) may obtain some of their glucose requirements from starch that escapes ruminal fermentation to be digested and absorbed as glucose from the small intestine (Waldo 1973). For example, Armstrong and Beever (1969), using the data of Tucker *et al.* (1968) for sheep fed a ration containing 40% ground maize, estimated that 5.3 $g/W^{0.75}$ of glucose would be absorbed from the small intestine. This figure is above the requirement of 4.4 $g/W^{0.75}$ calculated for the non-pregnant animal (Armstrong 1965). Fine grinding of grain may result in a faster rate of passage through the rumen and lead to escape of starch from rumen fermentation (Bergman 1973). Ruminants given low quality roughages have little or no glucose absorbed from the digestive tract (Bergman 1963, Leng 1970).

2.5.1 Gluconeogenesis

In roughage fed ruminants, only propionate and amino acids serve as significant precursors for gluconeogenesis (Leng 1970, Bergman 1983). The synthesis of glucose takes place in the liver (85%) and the kidneys (15%) (Annison *et al.* 1957, Ballard *et al.* 1969, Leng 1970, Bergman 1983). Glucose synthesis occurs from endogenous substrates produced originally from glucose, for example, from alanine and glutamine formed in muscle and from glycerol mobilised from adipose tissue or lactate formed by nearly all tissues when glucose is metabolised (Bergman 1983). When these

compounds return to the liver through the blood circulation they can be resynthesised into glucose.

2.5.2.1 Propionate

Propionate is a major source of glucose and glycogen (Leng 1970, Yost *et al.* 1977, Bergman 1983). The liver removes 90% of the absorbed propionate and only small amounts reach general blood circulation. Propionate production rates from the rumen vary with diet and level of feeding and this will effect glucose synthesis (Yost *et al.* 1977, Preston and Leng 1987). Bergman *et al.* (1966) showed that in sheep the percentage of glucose originating from propionate markedly increased as more propionate was absorbed. In sheep fed a maintenance ration of pelleted alfalfa hay (18% protein) 25 to 30% of the glucose was derived from absorbed propionate whilst in sheep fed half maintenance the percentage fell to 13%. These authors postulated that the amount in starved sheep would decrease to zero and that in grossly overfed sheep it would not account for more than two thirds of the total glucose produced. One difficulty in estimating the amount of glucose derived from propionate is the metabolic crossover of the radioactive label that arises from cycling in the TCA cycle (Krebs *et al.* 1966). Cridland (1984) has shown that crossover can be considerable and may account for the low apparent proportion of glucose derived from propionate in some situations.

Annison and White (1961) showed that under starvation, there was a relatively small decline in glucose entry rate in sheep indicating that glucogenic substrates other than propionate are important since the concentrations of VFAs in the rumen of starved sheep are low. In lactating cows, between 45-60% of blood glucose has been estimated to be formed from propionate (Wiltrout and Satter 1972). These authors have suggested that the balance must come from direct absorption of glucose from the intestine or synthesis from glucogenic amino acids.

2.5.2.2 Amino acids

The production of glucose from amino acids in ruminants may vary considerably depending on the nutrition and physiological state of the animal (Leng 1970, Bergman 1973). Amino acids are absorbed from the intestines via the intestinal villi into the portal blood and are carried to the liver where they enter the amino acid pool to be used for protein synthesis, glucose synthesis or in energy metabolism. Glucose may be formed from the carbon skeletons of the amino acids in the liver and the nitrogen is metabolised to urea and either recycled back to the rumen and intestines or excreted in the urine.

Leng (1970) on the basis of Krebs' work (Krebs 1964), assumed that a maximum of 55 g of glucose can be synthesised from 100 g of protein. Using this value, 70% of the glucose production for non-pregnant sheep could have arisen from amino acids in the studies of Hogan and Weston (1967). They showed that in sheep given alfalfa chaff at 90% of *ad libitum* intake, 100-120 g of digestible protein passed through the abomasum. However, Tagari and Bergman (1978) have shown that actual absorption of amino acids into the blood can be considerably less than its disappearance from the gut lumen and hence the previous estimate of 70% may be an overestimation. Bergman (1983) summarised that ruminants fed at maintenance levels derived a minimum of 15% of their glucose from amino acids and that the maximum figure was 36%.

Amino acids vary in their gluconeogenicity (Bergman 1983). For example, it has been shown that the essential amino acids threonine, methionine, isoleucine, valine and phenylalanine play little part in glucose synthesis (Black 1968, Black *et al.* 1970, Egan *et al.* 1983, Wilson *et al.* 1983) whilst the non-essential amino acids such as glutamate, aspartate, alanine, serine and glycine play significant roles in gluconeogenesis (Egan *et al.* 1970, Wolff and Bergman 1972, Heitmann *et al.* 1973, Bergman and Heitmann 1978).

2.5.2.3 Glycerol

Glycerol exists in the body mainly in combination with fatty acids and is stored as triglycerides in peripheral tissues (Bergman 1983). When the stores of triglycerides are mobilised to provide energy, glycerol is released into the blood. It is removed primarily by the liver and kidneys where it is used for glucose synthesis and oxidation to CO_2 (Bergman 1983). Under normal feeding circumstances, circulating glycerol contributes only 5% of the total glucose produced but in starved sheep, propionate absorption is negligible and glycerol may replace propionate as an important glucose precursor (Bergman *et al.* 1968).

2.5.2.4 Lactate

Lactate may be absorbed from the intestines or may be formed during the anaerobic metabolism of glucose. Its concentration in the blood is usually low but it may increase tenfold during periods of exercise. Once in the blood, it is largely converted to glucose in the liver and kidneys. This glucose, when released into the blood, may return to the muscles to be converted to glycogen. This cyclic process is known as the Cori cycle (Cori 1931). The Cori cycle has been estimated to account for no more than 5% of the total glucose formed in ruminants (Judson and Leng 1968). However the contribution of lactate to gluconeogenesis during exercise has not been measured and may be important under certain circumstances.

2.5.2 Importance of glucose precursors in effecting metabolic heat production

It has been the basis of the metabolisable energy system that the heat produced from the same amount of metabolisable energy is greater from a diet based on cellulosic roughage than from one based on concentrates (see ARC 1980). However, recent studies have challenged this concept (Leng 1990b). In support of this challenge, Leng (1990b) provided data to show that where a forage based diet is supplemented to

provide a high P/E ratio, the efficiency of use of ME becomes similar to that of a concentrate based diet.

When the VFA patterns in the rumen of sheep or cattle are examined, it is found that cellulosic roughage diets result in a fermentation pattern in which the proportion of acetic acid is high whilst concentrate diets result in less acetate and higher levels of propionate. There has been a considerable amount of research effort directed towards determining whether the high acetate proportions in the rumen produced by roughage feeding leads to a futile cycle of metabolism within the animal (in order to reduce the acetate levels) and the subsequent increase in heat production (Ørskov *et al.* 1966, Tyrell *et al.* 1979, MacRae and Lobley 1982). The theory proposed is that, when there is an imbalance in the acetate to propionate ratio, there is a lack of glucose to produce the necessary NADPH for conversion of the excess acetate into triglyceride in adipose tissues. In forage-fed ruminants, it appears that glycogenic amino acids are diverted away from protein synthesis into glucose synthesis to provide the NADPH required for acetate utilisation (Butler-Hogg and Cruickshank 1989). Several studies have suggested that the utilisation of absorbed amino acids in forage-fed animals is only 40-45% (Lobley *et al.* 1987, Butler-Hogg and Cruickshank 1989) which indicates that the amino acids are used for a different purpose than protein synthesis.

Armstrong and Blaxter (1957a) stated that acetic acid when given to fasting sheep is less efficiently utilised than either propionic or n-butyric acids . These authors hypothesised that, in fasting sheep given acetic acid as the sole energy source, metabolic blocks occurred at 3 points: the supply of oxaloacetic acid to maintain the TCA cycle, the supply of the reduced coenzymes for lipogenesis and possibly the supply of ATP for the initial acetylation of Coenzyme A. They suggested that these blocks probably resulted from the low supply of glucose in the fasting animal.

Acetic acid when given alone to fasting sheep caused an increase in nitrogen excretion whilst n-butyric acid had no effect and propionic acid exerted a marked

nitrogen sparing effect (Armstrong and Blaxter 1957a). These results indicated that amino acids were deaminated, possibly to supply substrate for gluconeogenesis when acetate was the sole energy source. The heat increment (i.e. the extra heat produced by the animal when given VFA salts) of acetic acid was 41%, propionic acid 13% and n-butyric 16%.

In subsequent experiments, Armstrong *et al.* (1957) showed that only very small quantities of propionic and n-butyric acids were needed to facilitate the dissimilation of acetic acid by way of the TCA cycle and allowed about 85% of its energy to be used by the fasting animal to prevent body fat mobilisation and protein for oxidatative purposes. When the acids were present in mixtures representing the normal range of molar proportions found in the rumen, they exhibited similar heat increments of between 14-15%. Further work by this group (Armstrong and Blaxter 1957b) showed that, when the acids were added singly to rations of fattening sheep on a diet of dried grass, the individual acids were utilised for liopogenesis with much lower efficiencies than in the fasting animal and marked differences in the utilisation of the individual acids were found. Under these circumstances the heat increments were 67% for acetic acid, 44% for propionic acid and 38% for butyric acid. The acids were primarily used to synthesise fat and the high heat increments suggested that the efficiency of conversion was low. The heat increment of carbohydrate in the ruminant originate from four areas (Armstrong and Blaxter 1957b): (1) heat of fermentation (i.e. during bacterial oxidation), (2) metabolism of the fatty acids in the tissues, (3) metabolism of energy absorbed as hexose - from 'bypass nutrients' or from the bacterial polysaccharide synthesised, and (4) the physical work used in ingesting and chewing the food and propelling it through the gut.

In an attempt to clarify the situation Ørskov and Allen (1966a,b,c) and Ørskov *et al.* (1966) conducted comparative slaughter experiments in which fattening lambs fed a diet of chopped ryegrass hay and a pelleted concentrate were given sodium and calcium

salts of acetic, propionic and butyric acids. The concentrate consisted of 45% barley, 20% flaked maize, 13% molassine meal, 15% decorticated groundnut meal, 5% white fish meal and 2% dicalcium phosphate. They found no differences in energy retention between the different salts added at a level of 15% of the metabolisable energy (ME) of the diet. From their results, there was some evidence that, when acetate was added to a low roughage diet, it was utilised more efficiently than when added to a high roughage diet. Tyrrell *et al.* (1979) showed that the efficiency of use of metabolisable energy from infused acetic acid in mature, nonpregnant, nonlactating Holstein cows was 27% when they were fed a 100% alfalfa hay diet and 69% when a ration consisting of 30% hay, 57% corn and 11% soybean was fed. The high partial efficiency of acetate use for body tissue synthesis observed in the experiment of Tyrrell *et al.* (1979) in mature cows fed a 30% hay diet was similar to that observed in young growing sheep fed high concentrate of mixed diets (Elliot *et al.* 1965, Ørskov and Allen 1966a,b,c, Ørskov *et al.* 1966, Bull *et al.* 1967, 1970).

Using isolated bovine adipocytes, Yang and Baldwin (1973), demonstrated that fatty acid synthesis from acetate may be limited by glucose availability. In the above diets, the low partial efficiency of acetate use when a diet of hay was fed may be due to lack of glucose precursors whilst when concentrate diets are fed acetate is utilised for fatty acid synthesis.

Data from Tyrrell *et al.* (1979) suggested that cattle oxidise acetate under certain dietary conditions rather than store its energy as body tissue, although the acetate load seemed to decrease nitrogen retention leading to a suggestion that at least part of the heat produced originated from oxidation of amino acids. When acetate was added to the rumen of cows fed a diet of hay, it resulted in a significantly greater heat production than when added to the rumen of cows fed the 30% hay plus 70% concentrate ration. These authors hypothesised that oxidation may simply be a means of disposing of acetate in excess of the animals' ability to use it for synthesis.

When the diets that Ørskov *et al.* (1966) used were examined, it was seen that: (1) the basal ration was fed to obtain a liveweight gain of 113 g/d, (2) the concentrate portion of the basal ration contained flaked maize and white fish meal, both of which are recognised as potentially good sources of bypass nutrients, (3) molassined meal and decorticated groundnut meal (a relatively slowly degraded protein source which can provide a continuous supply of peptides and amino acids) were included in the basal concentrate and would help to ensure high microbial growth efficiency (see Maeng *et al.* 1989). Hence the basal diet ensured a good supply of microbial protein to the small intestine (i.e. a high P/E ratio from the rumen) and in addition the diet was further balanced with the supply of bypass protein and starch to the small intestine. All these factors would ensure a balanced supply of appropriate substrates for the efficient use of any additional acetate. MacRae and Lobley (1982) estimated that there was an adequate supply of protein in the experiments of Ørskov and his colleagues which could be used to supply glycolytic precursors and hence provide enough $NADPH_2$ so that acetate could be used for lipogenesis. These authors have also suggested that there is unlikely to be sufficient protein in many roughage diets to produce $NADPH_2$ and so that, in addition to an excess of acetate, the animal has a reduced ability to convert it to fatty acids. In order to prevent a metabolic embarrassment, it was hypothesised that the excess acetate is metabolised in a futile cycle with the subsequent release of heat (Blaxter 1962, Tyrell *et al* 1979, MacRae and Lobley 1982, Ketelaars and Tolkamp 1991).

In further experiments examining the roles of VFA ratios on animal productivity, Ørskov and colleagues (Ørskov *et al.* 1974) changed the type of fermentation in the rumen, by changing the processing of the cereal component of the diet, without any detectable change in feed utilisation of the basal diet fed *ad libitum.* In these experiments the basal diet consisted of 91% barley, 7.5% white fish meal and 1.5% of a vitamin-mineral mix and would provide sufficient protein and glucogenic

precursors so that the animal would not to be metabolic disturbed by an imbalanced ratio of acetate to synthesis energy (see Preston and Leng 1987).

Ørskov and Macleod (1990) suggested that, at extreme acetic acid proportions in the rumen (far beyond physiological levels), the animal excretes acetic acid in the urine. They based this hypothesis on some of their unpublished data which showed that, at about 75-90 molar % of acetic acid in a VFA infusate into the rumen of cattle, there is an increase in nitrogen excretion and this is followed by an excretion of acetic acid in the urine and a reduction in heat production.

Ørskov and Macleod (1990) suggested that the difference in heat production from high or low roughage diets occurs due to the energy costs of eating, ruminating and moving materials along the digestive tract. Using the data of Holmes *et al.* (1978a), Adam *et al.* (1984) and KuVera *et al.* (1989), these authors estimated that steers, weighing 300 kg and receiving roughage, would expend 6 MJ/d on the activities of eating and ruminating compared to 0.8 MJ/d for pelleted diets. However, studies by Webster and colleagues (Osuji *et al.* 1975, Webster *et al.* 1975) indicated that the heat produced from fermentation and the aerobic metabolism of the gut was only about half of the total heat increment of feeding in sheep. This indicates that the remaining heat increment must be derived from tissues other than those of the digestive tract. These workers concluded that the decline in efficiency with which ME (surplus to maintenance requirements) is retained in the body as foods become more fibrous, must be due to the nature of the substrates made available by digestion and the metabolic reactions for which they are used.

Leng (1990b) has proposed that it is the balance of nutrients which affects the efficiency of feed conversion; the addition of small amounts of bypass protein to basal roughage diets being the catalyst for more efficient feed conversion. It is obvious in the study of heat production from roughage versus concentrate diets that the following factors are extremely important: (1) the physiological state of the animal (maintenance,

growth, pregnancy, lactation and the amount of work undertaken); (2) environmental temperature; (3) the ratio of protein to energy in the products absorbed from the feed.

In practice, however, addition of the VFAs as free acids to rations has rendered them unpalatable (Essig *et al.* 1959, Essig *et al.* 1962) and the acids when added as salts have not resulted in significant differences in rates of body gain in lambs (Essig *et al.* 1959, Nicholson and Cunningham 1964, van Houtert 1991). In beef cattle the addition of 2% sodium propionate to fattening rations did not improve liveweight gains over controls, although it tended to reduce feed intake and increase feed efficiency slightly. Intra-ruminal infusions of acetic, propionic and butyric acids in non-lactating dairy heifers fed a normal ration resulted in increased nitrogen retention and body weight gain, but differences among acids was not significant (Rook *et al.* 1963).

Elliot *et al.* (1965) found that growing-fattening lambs fed a basal ration of pelleted alfalfa hay showed no response in either rate of gain in body weight or feed conversion efficiency when propionate or acetate was incorporated in the feed. The animals in the VFA supplemented groups had, however, a considerably higher fat content in their carcasses than the control fed animals. On an energetic basis, the VFA supplemented animals converted digestible energy to body gain with considerably greater efficiency than the control fed animals.

Rook and Balch (1961) examined the effects on the yield and composition of the milk of the cow of intraruminal infusions of dilute aqueous solutions of individual VFAs, as supplements to a basal diet. A supplement of acetic acid caused an increase in milk yield and in the yields of fat, lactose and protein and a specific increase in fat percentage. Supplements of propionic or butyric acid had no effect on the yield of milk, but a propionic acid supplement specifically decreased the yield and percentage of fat and increased the yields and percentages of protein and solids not fat, whereas butyric acid supplement specifically increased the yield and percentage of fat.

Rook *et al.* (1963) stated that the technique of continuously infusing dilute aqueous solutions of the VFAs into the rumen to study their metabolism is open to the criticism that abnormal physiological conditions might be produced within the rumen and the digestion of the basal diet, and consequently the absorption of the end products of digestion, modified. In their limited observations, there were no marked differences in the efficiency with which acetic and propionic acids promoted liveweight gain. They found that the infusion of acetic acid into the rumen depressed the *ad libitum* intake of hay. All three acids resulted in an increase in N retention. Nicholson and Cunningham (1964) reported that pelleting an all-roughage ration resulted in a decrease in the proportion of acetic acid and an increase in the longer chain VFAs in rumen fluid. Pelleting also increased feed intake and rate of gain.

Eskeland *et al.* (1974) infused glucose, acetate, propionate and butyrate into the jugular vein of lambs receiving either high-concentrate or high-roughage diets. Their results indicated that glucose and propionate were superior to acetate and butyrate as energy sources for protein formation. However infusion of metabolites into the jugular vein bypasses the rumen epithelium where the major conversion of butyrate into ketone bodies may occur. It also bypasses the portal system which would generally result in conversion of propionate into glucose and the formation of additional ketone bodies. Thus their results with propionate and butyrate may differ from results obtained by others with intra ruminal infusion of the energy sources.

Ruminants fed low quality forages absorb very little glucose and the potential for gluconeogenesis from propionate and amino acids is low. Glucose is therefore a potentially limiting nutrient. In addition, as dietary LCFA supply is low, the need for glucose to supply glycerol and NADPH to enable fat synthesis in adipose tissue and for essential functions is increased (Nolan *et al.* 1986). In order to obtain glucose, the animal may have to utilise amino acids to maintain essential functions and then dispose of acetate surplus to requirements into fat. This may reduce the potential for protein

deposition, decrease N retention and may also increase the circulating levels of ketogenic amino acids (Nolan *et al.* 1986). The high acetate level produced by the fermentation of low quality forages and the animals' reduced ability to synthesise glucose may result in reduced appetite and feed intake by the animal. Futile heat-producing cycles may be invoked to reduce the load (Blaxter 1962), and the resulting heat production could further inhibit feed intake of animals in a hot environment. Imbalances in the circulating levels of amino acids may also inhibit feed intake (Harper 1964). Factors that act to reduce feed intake are probably additive (Nolan *et al.* 1986).

2.6 Effect of heat stress on ruminant productivity

2.6.1 Introduction

Environmental temperature affects feed intake as well as the utilisation of metabolic end products and should be considered when formulating ruminant rations (Moose *et al.* 1969). The effects of heat stress on ruminant productivity have been reviewed by numerous authors, for example, Bianca (1965), McDowell (1972), Thompson (1973), Finch (1984) and Johnson (1987a,b).

Ruminants possess only a fraction of the ability of humans to dissipate heat by evaporative cooling and are prone to heat stress, particularly as they have to dissipate heat generated in fermentative digestion. Additionally, ruminants vary in their ability to dissipate heat between species, breeds and individuals: sheep and goats are not able to sweat to nearly the same extent as cattle and are reliant on panting. The Temperature Humidity Index (THI):

$$THI = T(\text{dry bulb}) + 0.36T(\text{dew point}) + 41.2^{o}C$$

has been used to characterise the level of heat stress in ruminants. It combines temperature and humidity into a single figure that can be used to compare temperature and humidity data and animal responses at different locations (Johnson 1987a). At a

THI of 75, fifty percent of the human population are uncomfortable and yet in many areas of the world ruminants are kept at considerably higher THI (see Figure 2.3).

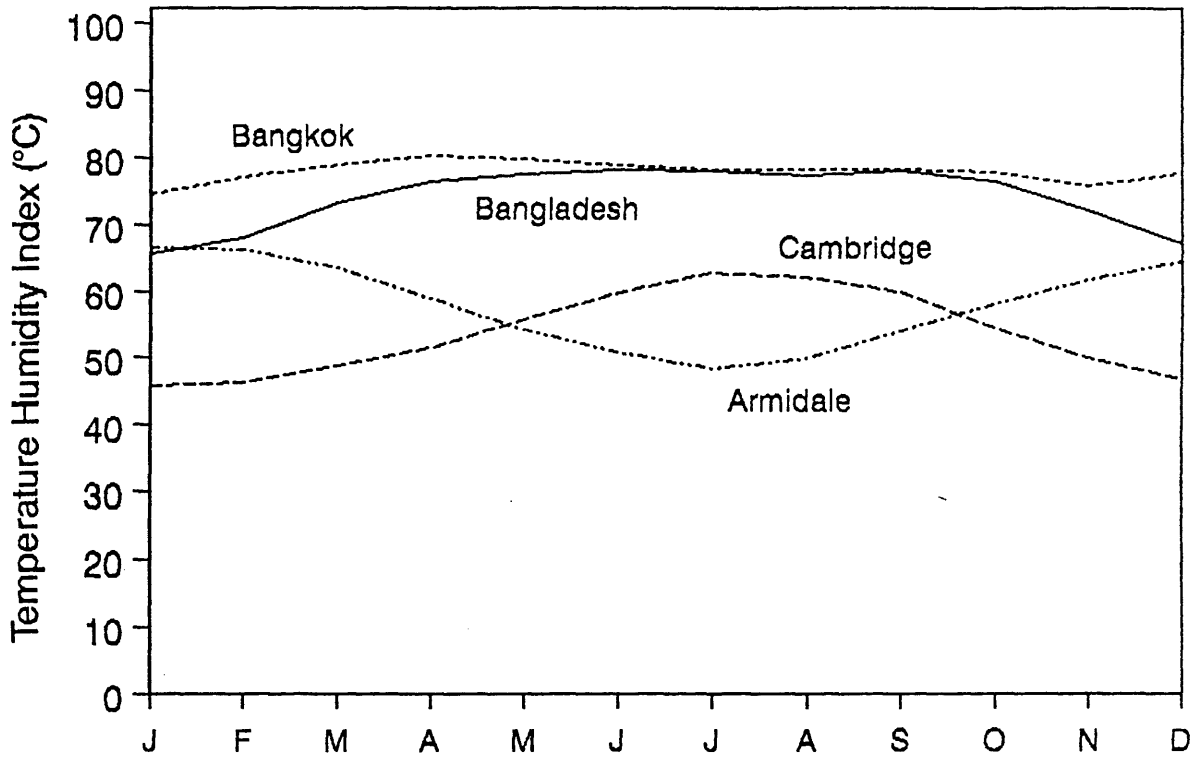


Figure 2.3 *THI of climates in temperate countries as exemplified by Cambridge (UK) and Armidale (Australia) as compared with tropical countries as exemplified by Bangkok (Thailand) and Mymensingh (Bangladesh) (Source: Leng 1990b)*

The thermoneutral zone (TNZ) is the range of ambient temperatures within which normal metabolism provides sufficient byproduct heat to maintain an essentially constant body temperature. The lower and upper limits of the TNZ are dependent on acclimatisation, age, sex, breed, species, body conformation, insulation, feed, behaviour and even the time of day (WMO 1989).

Humidity plays an important role in heat stress (Davis and Merilan 1960). Davis and Merilan (1960) found with lactating Holstein cows changing the temperature from 18.3°C to 32.2°C and relative humidity (RH) from 20% to 50% had very little effect on feed intake and digestibility. However, at 32.2°C and 50% RH, feed intake was decreased by 20% and digestibility increased by 6.2%. Ragsdale *et al.* (1953) (cited by Bianca 1965) found high humidity to effect feed intake of cows only at air temperatures greater than 24°C.

Ruminants have an optimum environmental zone for growth, lactation and reproductive functions and this varies with species, breed and level of productivity (Johnson 1987a). High levels of production are associated with high metabolic heat production. For example, metabolic heat production may be doubled in the high producing dairy cow, causing lactating cows to be more prone to heat stress than non-lactating cows or a male cattle.

It is difficult to apply results from the measurements of thermoregulatory strain resulting from heat stress in a standard hot room with those obtained from the natural outdoor environment (Finch 1984). For example, it was reported that a temperature of 32°C outdoors was equivalent to 50°C in the hot room, the difference being due to solar radiation (Finch 1984). Effective temperature in the natural environment is caused by a combination of solar radiation, humidity, air movement and is also affected by the cyclical variations over the 24 hour period. Animals can accommodate high environmental temperatures for a short period, provided they are able to recover during a cool night. Another difficulty experienced in experimental work assessing the effects of temperature on livestock is the substantial differences in the response of individuals to heat stress. As an illustration, when eight Hereford cows were subjected to a regime of 12 h at 28°C and 12 h at 36°C, three cows had to be removed as their rectal temperatures exceeded 42°C, although the mean rectal temperature of one cow was similar to that of control cows kept at 16°C (Reynolds *et al.* 1985).

The most common indicator of heat stress is raised body temperature (Finch 1984). Hyperthermia is deleterious to any form of productivity in domestic animals, regardless of breed (Finch 1984). It appears therefore that the difference between genotypes in susceptibility to heat stress must lie in their temperature regulation mechanisms (Vercoe and Frisch 1970, Turner 1982).

In this section of the review, the effects of high temperature on different aspects of ruminant productivity will be examined. As the literature pertaining to heat stress is voluminous, the most pertinent information to the main subject of the review is discussed with emphasis being placed on the interaction of nutrition with heat stress. The majority of the work on heat stress reported in the literature involved cattle, where-ever possible the literature pertaining to sheep is included.

2.6.2 Physiological changes occurring with heat stress

Metabolic heat production is affected by high environmental temperatures (Bianca 1965). Exposure to a short period of severe heat will increase the metabolic heat production whereas, if the animal is exposed to a mild heat stress for a long period, the metabolic heat production falls. Bianca (1965) attributes the increase in heat production during acute heat stress to the increased cost of panting and considers it a partial breakdown of homeothermy rather than an adaptive change.

2.6.3 Feed intake

Exposure of livestock to thermal stress (either above or below the TNZ) affects voluntary food intake. A general reduction in feed intake has been observed at high temperatures (e.g. Wayman *et al.* 1962, Martz *et al.* 1971, Finch 1984, Schneider *et al.* 1986, McGuire *et al.* 1989) whilst at low temperatures feed intake has been reported to increase (e.g. Moose *et al.* 1969, Weston 1970, Kennedy and Milligan 1978, Young

1987, Young *et al.* 1989). Maintenance requirements have been reported to increase during thermal stress (Graham *et al.* 1959, Blaxter and Wainman 1961).

When an animal is sufficiently heat stressed to increase its core temperature, it will reduce its feed intake in order to reduce the heat generated during ruminal fermentation and body metabolism (Minton 1987, O'Kelly 1987) and thus productivity will be reduced on two accounts. Firstly there is an increased cost of maintenance and secondly, feed intake drops. Leng (1990b) considers that, when a ruminant is heat stressed, any inefficiency of feed utilisation which stimulates metabolic heat production will reduce feed intake and that, by increasing the P/E ratio in the nutrients absorbed to optimise the efficiency of feed utilisation, the metabolic heat load can be decreased which may allow animals to increase voluntary feed intake. As evidence of this climate/nutrition interaction, Leng (1990b) examined the results of recent studies in Australia (Kellaway and Leibholz 1981, Lindsay and Loxton 1981, Lindsay *et al.* 1982, Hennessy 1984, Perdok 1987). In these studies, cattle on low quality forage diets in tropical or subtropical areas were able to increase their forage intakes between 40-90% when supplied with a source of urea and bypass protein. This brought their level of forage intake to approximately the same level of intake as unsupplemented cattle under temperate conditions (see Figure 2.4). The increases in roughage intake due to supplementation with urea and bypass protein of cattle in temperate areas was much less dramatic than in cattle in tropical areas. Leng (1990b) considers that ruminants in hot countries have an advantage in not having to oxidise much acetogenic substrate (or body fat) to keep warm. This energy is therefore available for productive purposes if the diet is correctly balanced. However, if the diet is imbalanced due to low protein (soluble and bypass) intake, acetate, surplus to the animals requirements may have to be channeled into a futile cycle which may add to the animals metabolic heat production.

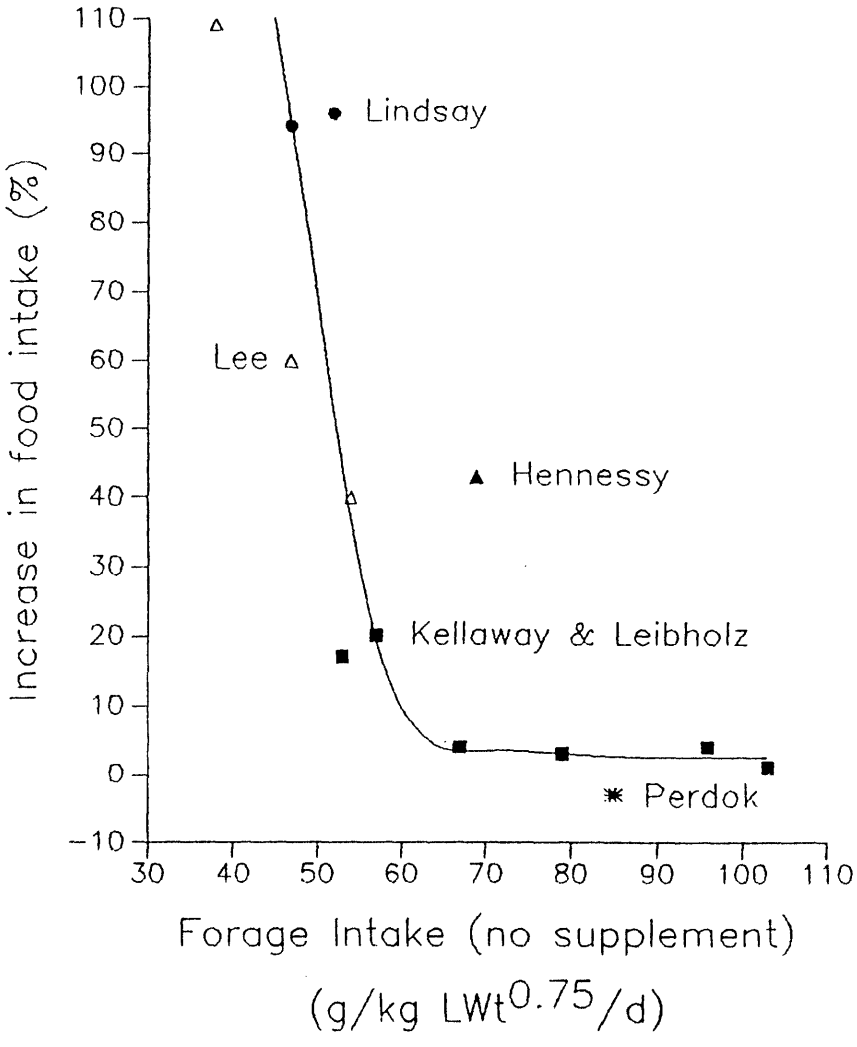


Figure 2.4 *Intake of low-quality forage by cattle in relation to intake of the forage following supplementation with a bypass protein meal or bypass protein meal plus urea in different climatic zones (Source: Leng 1989a) The research of Lindsay and Loxton (1981), Lindsay et al. (1982), Lee et al. (1987) and Hennessy (1984) was done at sites in the tropics or subtropics, whereas the research of Kellaway and Leibholz (1981) and Perdok (1987) was done under more temperate climate conditions.*

This additional heat increment in ruminants in hot environments may force the animals to reduce its feed intake in order to reduce its metabolic heat production.

It is generally accepted that high roughage diets imbalanced in terms of nutrients absorbed in the small intestine increase metabolic heat production (Blaxter 1967, Leng 1990b, Ørskov and McLeod 1990). Thus the substitution of a high fibre ration for a low fibre ration with the same energy and protein content increased milk yield and decreased

body temperature, respiration rate and percentage milk fat in Holstein cows kept under environmental temperatures of between 27°C and 43°C (Stott and Moody 1960). Lambs housed in a cool environment (0°C to 5°C) had greater feed intakes and liveweight gains than those kept in a warm (23°C to 29°C) environment (Moose *et al.* 1969). Feed intake was found to vary in relation to the amount of concentrate fed in lambs housed under differing environmental temperatures (Moose *et al.* 1969). Lambs fed 70% concentrate diets in warm environments usually had greater liveweight gains and carcass weights and grades than lambs fed 30% concentrate + 70% roughage diets. Conversely, those fed 35% concentrates in the cool environment usually had higher liveweight gains than those fed 70% concentrate. In one experiment, it was shown that the lower heat increment of the 70% concentrate ration was insufficient to maintain body temperature in the cold environment and that a greater portion of net energy was required for maintenance. However, the high heat increment of a diet containing 35% concentrate was a burden at 29°C and a large expenditure of net energy for maintenance was required to dispose of excess heat resulting in less net energy for production. From these results, Moose *et al.* (1969) concluded that the magnitude of the differences is sufficient to justify a consideration of environmental temperature in the formulation of ruminant rations.

The work by Wayman *et al.* (1962) demonstrated a greater tolerance by cattle to high temperatures when fed a ration low in fibre and high in readily available energy. They reported that exposing lactating Holstein cows fed a diet high in fibre to 31°C caused a 32% decrease in feed intake compared with a decrease of only 20% when a low fibre diet was fed. The low fibre diet they used consisted of 30% cane molasses, 35% alfalfa hay, 5.5% soybean meal, 27.5% shelled corn and 2% salt and bonemeal. The proportions used in the high fibre diet were 10, 45, 5.5, 37.5 and 2% respectively. By force-feeding the cows both diets through rumen cannulae, these authors were able to report that high ambient temperatures *per se* caused a decrease in production and

suggested that part of this effect could be due to a decreased rate of feed passage through the rumen.

A significant increase in energy requirements per unit of body mass was reported for lactating cows kept at high temperatures and significant amounts of protein were found to be channelled into non-productive sources including protein losses through sweat glands (McDowell *et al.* 1969).

Feed intake of Friesian heifers was reduced when they were subjected to a temperature of 38°C (Colditz and Kellaway 1972). No significant reductions in feed intake were noted in either Brahman or Brahman x Friesian heifers subjected to the same temperature and diet; however the rectal temperatures of the Brahman and Brahman cross cattle increased by only 0.2 to 0.7°C compared with the 1.1°C increase of the Friesians. This indicated that the Friesian heifers experienced greater heat stress than the Brahman or Brahman cross heifers. McGuire *et al.* (1989) reported that a portion of the negative effects of thermal stress on milk production can be explained by a decreased nutrient intake and decreased nutrient uptake by the portal drained viscera of the cow.

2.6.4 Rumen motility

Atteberry and Johnson (1969) observed that the frequency of rumen contractions in cows was markedly reduced after 5 days exposure to a temperature of 38°C. Their data indicated that high environmental temperatures (38°C) depress rumen activity directly rather than indirectly via feed intake. Collier *et al.* (1981) reported a significant decrease in the number of rumen contractions per minute (2.2 vs. 1.4) and a increased rectal temperature from 38.8°C to 39.7°C in unshaded Holstein cows compared with shaded Holstein cows. Rumen retention times of steers fed forage diets increased from 36.6 h to 43.2 h when the environmental temperature increased from 18°C to 32°C with

associated increased digestibility of dry matter and cellulose of the diet (Warren *et al.* 1974).

2.6.5 Rumen fermentation

When Hereford heifers were exposed to a rise in temperature from 25.6°C to 32.2°C, there was a slight drop in total VFA production in the rumen due mostly to a decrease in acetic acid concentrations (Weldy *et al.* 1964). Weldy *et al.* (1964) suggested that the decrease in acetate:propionate ratio found may be associated with the fine grinding of the diet. In contrast, Kelley *et al.* (1967) found that high temperatures increased the acetic:propionic ratio and that total VFA level decreased when feed intake was controlled at a constant level. Olbrich *et al.* (1972) reported that, when Zebu and Scottish Highland heifers were fed a diet consisting of 48% cracked corn, 15% alfalfa meal, 7% soybean meal, 12% molasses and 18% cottonseed hulls and subjected to temperatures of either 10°C or 31°C, a significant reduction in total VFA in rumen fluid was observed at the higher temperature. Though the concentration of acetic and propionic acids was significantly decreased at the higher temperature, the molar percentage of acetic acid increased from 62% to 64% and molar percentage of propionic acid decreased from 22% to 18%. On high roughage diets, the increase in the acetate to propionate ratio that occurs during heat stress may further heat stress the animal by stimulation of futile cycling to get rid of acetate excess to its requirements (see Section 2.5.2). In addition, the diet was low in potentially bypass protein and so the animals rely on the products of fermentation for their protein and energy supply.

2.6.6 Lipid metabolism

Plasma concentrations of cholesterol and phospholipid were found to be significantly higher in Zebu than in British breed calves, but hyperthermia depressed the

concentration of these components similarly in both breeds (O'Kelly 1973). Increased rectal temperatures in calves were associated with a large increase in the excretion of faecal fatty acids which may have been due to reduced alimentary absorption. Once control of normal body temperature was lost, increased rectal temperatures led to similar metabolic changes in animals of both breeds (O'Kelly 1973).

Dietary supplementation with linoleic acid was associated with an increased ability of newborn lambs to withstand an imposed thermal stress of 30 ^{o}C dry bulb 17 ^{o}C wet bulb (Noble *et al.* 1981). O'Kelly (1968) reported that the increased tolerance to heat shown by Zebu cattle is correlated with increased levels of linoleic acid in body tissue indicating a role of linoleic acid in enabling animals to tolerate heat.

2.6.7 Nitrogen metabolism

Increased nitrogen excretion is a well established effect of heat stress (O'Kelly 1973). O'Kelly (1973) reported an increased urinary total nitrogen excretion in British and Zebu calves at raised rectal temperatures with a resultant decrease in nitrogen balance. Measurement of faecal fat in these calves showed that it was significantly higher in the British calves and that the amount of fat excreted during hyperthermia approximately doubled in all calves. This could be a mechanism for ruminants in a hot environment to get rid of dietary fat when a poorly balanced diet is fed and may be similar to the high fat content in milk produced by buffalo (Preston and Leng 1987).

Vercoe and Frisch (1970) examined N metabolism in British and Brahman cross steers offered a low N roughage diet. They found that exposing British and Brahman cross steers, offered a low nitrogen roughage diet, to high temperatures increased the urinary total nitrogen and urea nitrogen after 6 days at the high temperatures. Creatinine excretion increased in response to increased rectal temperatures suggesting an increase in

skeletal muscle protein metabolism. The diet they used was a low quality (1.2% N) chaffed tropical pasture hay which would produce high acetate to propionate levels in the rumen (Leng 1990a). Hence, in addition to being heat stressed, the animals would have to cope with an imbalanced supply of nutrients which probably led to the catabolism of glycogenic amino acids to provide precursors to utilise the excess acetate. This would lead to increased excretion of urea nitrogen and also to increased heat production due to futile cycles to reduce the acetate load.

2.6.8 Mineral metabolism

Large amounts of potassium are reported to be lost in sweat of cattle at high environmental temperatures (Schneider *et al.* 1986). Little is known of the mineral metabolism of sheep at high temperatures.

2.6.9 Hormonal response

Administration of growth hormone (16.66 mg/day) to lactating Holstein cows under moderate heat stress (28.9^{o}C) increased milk and milk fat yields (Mohammed and Johnson 1985). Plasma growth hormone was higher in cows cooled with spray and fan under shade than for cows in shade alone (Igono *et al.* 1987). The cows in the latter group had maximal rectal temperatures greater than 39^{o}C whilst cows in the shade plus spray and fan groups had rectal temperatures below 39^{o}C. Johnson and Ragsdale (1960) reported that, as temperature increased from 2 to 27^{o}C, there was a gradual decrease in thyroid activity and that above 27^{o}C the rate of decrease in thyroid activity accelerated. O'Kelly (1973) also reported a decreased thyroid activity in calves exposed to heat stress.

2.6.10 Reproduction

Extensive work has been done in this area, particularly with sheep, and it is outside the scope of this review to do more than highlight some of the main effects of heat stress on the reproductive ability of ruminants.

Fertilisation rate decreased and percentage of abnormal ova increased in ewes that were exposed to high ambient temperatures (32^{o}C) before mating (Dutt *et al.* 1959). Collier *et al.* (1982) subjected Holstein cows in the last trimester of pregnancy to either shade (29.8^{o}C) or no shade (37.5^{o}C) treatments. Rectal temperature, respiration rate and heart rate were higher in cows given no shade. Calf birth weights were lower in the no shade group and milk yield, which was linearly correlated with calf birth weight, was lower in the no shade group. Chronic heat stress during mid-gestation reduced foetal weight by 18% resulting, at least in part, from decreased uterine and umbilical blood flows, which led to a reduction in uterine, utero-placental and foetal nutrient uptake and secretion rates in mature Hereford cows (Reynolds *et al.* 1985). Crossbred ewes subjected to heat stress during the last third of gestation produced smaller lambs than ewes not heat stressed (Brown *et al.* 1977). One group of ewes restricted in feed intake to that of the heat stressed ewes produced heavier lambs than the heat stressed ewes. Thus the reduced birth weight of lambs from heat stressed ewes occurred independently of the level of feed consumed.

2.6.11 Methods to reduce heat stress in ruminants

The scope for manipulating either the environment or the diet of grazing ruminants to reduce the effects of heat stress is small compared with that for intensively housed animals. However, the following three sections discuss the means used to control heat stress in ruminants.

2.6.11.1 Environmental manipulation

Methods to manipulate the environments of intensively housed ruminants include fans, shades, misting, force ventilation, sprinkling, zone cooling, evaporative cooling, air conditioning and chilled drinking water (Baker *et al.* 1988).

Morrison *et al.* (1973) reported that sprinkling British beef cattle under shades for 1 min every 30 min when the temperature was above 27°C resulted in significantly higher feed intakes and liveweight gain compared with cattle under shades and not sprinkled. However, this means of alleviating heat stress would not be suitable for woolly sheep and is aimed at the high producing dairy cow.

Because of the high heat capacity and high latent heat of evaporation of water, several research groups have investigated the use of chilled drinking water as a means of improving the ability of cattle to withstand heat stress. Lofgreen *et al.* (1975) observed that British beef cattle in pipe and cable corrals in a hot (32°C) environment consumed more feed, gained more weight, and in 3 out of 4 years improved energy utilisation when given access to water cooled to 18.3°C compared to 32.2°C. The level of roughage in the ration did not effect the response to cold water. It is interesting to note that Brahman x British crossbred cattle under the same conditions performed similarly on cold or warm water. The warm water did not depress feed intake or energy utilisation in the Brahman cattle as it did with the British cattle because they were more heat tolerant.

Consumption of chilled (10°C) water at the hottest period of the day reduced heat stress in lactating Holstein cows though the effect was only temporary (Stermer *et al.* 1986). Lanham *et al.* (1986) reported that giving lactating Holstein cows chilled (10°C) water for 10 minutes at 1400 h after a being without water from 0800 to 1400 h reduced body temperature by 0.75°C and respiration rate by 15.8/min for approximately 137 min. In another study Milam *et al.* 1986, observed that lactating Holstein cows drinking water

chilled to 10°C increased dry matter intake and milk yield and that this could lead to production gains that were economic for dairy stock in areas of high ambient temperature and high humidity. However in a later experiment, Baker *et al.* (1988) did not demonstrate any economic advantage in supplying chilled water (10°C) during the hottest part of the day to lactating Holstein cows. They suggested that further studies were needed in which chilled water was made available continually.

Collier *et al.* (1981) examined the effect of shade or no shade on lactating dairy cows and found that shade decreased rectal temperatures by 0.9°C and respiration rates by 36.3/min. They observed a delayed response of milk yield to black globe temperature and suggested that it may be related to altered feed intake or delayed response in change of metabolic or endocrine state of the animal.

In Israel, forced ventilation of the resting areas in which multiparous dairy cows spend most of the daylight hours resulted in a significant increase in 122 d milk yield and in conception rate (Folman *et al.* 1979) Primiparous cows were less effected by heat stress than multiparous cows. Berman *et al.* (1985) reported that forced ventilation was effective in reducing the rise in body temperature of lactating Holstein cows exposed to temperatures above 25°C.

Cooling dairy cattle that were in a hot (28.6°C) environment 5 times per day for 30 min by a combination of wetting and forced ventilation significantly decreased rectal temperature (Flamenbaum *et al.* 1986). It was noted that the main disadvantage of sprinkling is that it creates an environment saturated with humidity which markedly reduces the capability of animals to dissipate heat by evaporation. Cows cooled with spray and fan under shade had improved thermal balance, lessened physiological changes and increased milk yields compared with cows under shade (Igono *et al.* 1987).

2.6.11.2 Dietary manipulation

A high energy (low fibre) ration designed to meet the protein requirements of lactating dairy cows was compared with a similar ration which supplied 50% in excess of the calculated protein requirements (Leighton and Rupel 1960). Leighton and Rupel (1960) observed trends in body temperature, respiration rate and milk production which favoured the high protein diet but the differences were not significant. These authors did not report the form of protein nor its potential as bypass protein. If it was a readily digestible protein, it may not have contributed significantly to the animals protein requirements or change the P/E ratio and hence would not be expected to have any significant effect (see Section 2.4.2).

Ilian *et al.* (1988) supplemented 0, 5 or 10% animal fat in the diets of sheep reared in hot (38.1^{o}C, 22.5% RH) or cool (26.4^{o}C, 32.8% RH) environments. Significant decreases in feed intake was observed when fat was added to the diets and feed efficiency was improved. Addition of fat to the diet improved average daily weight gain in both environments and this effect was more pronounced in the hot environment. O'Kelly (1987) studied the metabolic responses to hyperthermia of *Bos taurus* and B. *indicus* x B. *taurus* cattle on two maintenance diets, 2.5% fat and 9.2% fat, which were isonitrogenous and isocaloric. Exposure to heat increased rectal temperatures, evaporative water loss and urinary N excretion in all animals but, within breeds, the 9.2% fat group maintained a lower rectal temperature and urinary N excretion and higher evaporative water loss than the 2.5% fat group. The amount of urinary N excreted was lower in Brahman cross than in British animals on both diets and temperatures. The mode of action of fat in increasing resistance to heat stress is not known but the low heat increment due to fat could contribute to a lowered endogenous heat production and in

addition, the fat may act as a defaunation agent in the rumen (Bird and Dicko 1987) and thereby increase the P/E ratio available to the animal.

Stott and Moody (1960) investigated feeding of low fibre, highly digestible rations on tolerance of lactating dairy cows to high temperatures. One group of cows was fed 2.5% of their bodyweight as alfalfa hay whilst the second group was given only 1% of their bodyweight as alfalfa hay. Concentrates were fed at a rate to balance the rations in terms of energy and protein required for production and maintenance. The low fibre ration resulted in a lowering of body temperature by 0.28 ^{o}C and respiratory rate by 14/min and a raising of the yield of fat corrected milk by 0.54 kg/d (Stott and Moody 1960).

The intake and utilisation of nutrients in sheep fed different levels of roughage under heat stress was investigated by Bhattacharya and Hussain (1974). Three rations that they used consisted of barley hay and a concentrate mixture in the ratios of 25:75, 50:50 and 75:25. Ration 4 consisted of 75% hay and was supplemented with tallow to make it isocaloric to ration (1) All rations were isonitrogenous. Their results indicated that the effect of high environmental temperature on the depression of intake and utilisation of energy was more pronounced in sheep fed high roughage diets than in those fed low roughage diets. In response to high temperature, feed intake was reduced by 50% in the 75% ration as compared with a 14% reduction in the 25% ration. Addition of fat in the 75% roughage ration reduced the feed intake depression to 33%. Respiration rate, heart rate and rectal temperature increased significantly with high temperatures and the effects were greatest in the 75% roughage fed group. Nitrogen utilisation was not affected by ration composition or ambient temperature. When the concentrate portion was examined, it was found that the protein source was soybean meal which is known to be very soluble in rumen fluid. Thus the animals would probably have a low P/E ratio in

the nutrients absorbed which would decrease their ability to utilise the high acetate levels produced with roughage feeding.

Addition of sodium bicarbonate, sodium chloride or potassium increased milk yields in lactating cows fed a basal diet of 38% corn silage and 62% concentrate and subjected to heat stress (Schneider *et al.* 1986). The addition of 1.8% potassium to the diet increased feed intake. Addition of salts to the diet of sheep would probably not produce much benefit as sheep do not sweat significantly.

Holstein cows receiving energy in a more concentrated form (i.e. as fat) showed no significantly different response to heat stress than cows on control rations (McDowell *et al.* 1969). Altering protein levels during thermal stress has been suggested as a means of improving protein efficiency ratio (PER) (Ames and Brink 1977). On the basis of experiments with both lambs and cattle fed during both cold and heat stress, Ames *et al.* (1980) have recommended reducing crude protein levels in rations fed to livestock during periods of thermal stress (hot or cold). They found that reduced growth rates during periods of thermal stress combined with constant protein intakes lowered PER and that by decreasing protein intake average daily gain could be maintained and PER increased. In this series of experiments, Ames and his colleagues followed National Research Council guidelines for protein requirements and in addition, the protein source they used was very soluble. Thus the P/E ratio available to the animal was not likely to be influenced to any great extent by small changes in the soluble protein content of the basal diet. In addition, Ames and his colleagues accepted the depression in growth rate due to thermal stress as inevitable and therefore decreased the protein intake to match the decrease in feed intake. Addition of a bypass protein to these high concentrate diets may have resulted in an increase in feed intake and subsequent increases in growth rate.

2.6.11.3 Genetic manipulation

From studies of the responses of temperate and tropical breeds of cattle it is apparent that animals within a breed differ in their general tolerance to heat (Weldy *et al.* 1964, McDowell *et al.* 1969, Reynolds *et al.* 1985). This large genetic diversity offers ample scope for selection within as well as between breeds of animals for effective thermoregulation (O'Kelly 1988). Differences in the efficiency of mechanisms for heat loss appear to be an important difference between breeds in their ability to withstand thermal stress (Holmes *et al.* 1978b, Finch 1984).

Holmes *et al.* (1978b) found an average increase in heat production of 5% when rectal temperature increased by 1.5^{o}C-2.0^{o}C. They found no differences in heat production caused by increased rectal temperature between Friesian or Brahman x Friesian calves and concluded that differences in heat tolerance must be due to differences in efficiency of the mechanisms of heat loss.

Hopkins *et al.* (1978) considered that the prospects of making long term alterations to the environment to lessen the impact of existing conditions does not appear to be favorable economically and that the alternative possibility of selecting animals more suited to the environment offers a more practical solution. They examined the rectal temperatures of tropical Merino sheep taken in the sun during summer and showed that these could be divided into high and low rectal temperature groups. Animals of low temperature status (e.g. 39.4^{o}C) also exhibited a low respiration rate (e.g. 110/min) in comparison with their counterparts (40.0^{o}C and 190/min). The comparatively high rectal temperatures of the latter group of sheep was associated with a very poor production history.

The effect of coat colours on thermal balance, behavior and weight gain in Brahman, Shorthorn or Brahman x Hereford-Shorthorn crossbred cattle was examined by Finch *et al.* (1984). These authors found that coat colour had significant effects on growth and that this effect was greatest in the Shorthorns where white steers gained 0.13 kg more per day than steers with a dark red coat colour. In addition to colour, steers with deep or woolly-type coats had poorer growth rates, spent less time in the sun and had shorter grazing times. They concluded that coat colour is a trait which, interacting with coat type, exerts an influence on performance of cattle under heat stress.

A high negative genetic correlation between daily gain and the increase in rectal temperature after heat treatment was found by Gomes da Silva (1973) who suggested that heat tolerance should be taken into account in every beef cattle selection program for the tropics.

Turner (1982) found that fertility in beef cattle was affected by rectal temperature. For cows in the same environment, rectal temperatures were 0.5^{o}C higher in British breed than in Zebu cross cows and 0.3^{o}C higher in lactating than in dry British cows (no effect in Zebu cross cows).

The ambient temperature at which rectal temperatures were increased by 1.3^{o}C was shown to be about 31^{o}C for *Bos taurus* steers and 45^{o}C for Brahman cross steers given a diet of chaffed lucerne hay (Vercoe 1969). In addition Vercoe observed that increased rectal temperature of both breeds increased the urinary N excretion but had no effect on the apparent N digestibility. If this resulted in a reduced urea-N recycling to the rumen it could lead to an N deficiency in the rumen which in itself might have an influence on heat stress through reduction in the P/E ratio in the nutrients absorbed in these animals (see Leng 1990b)

Olbrich *et al.* (1972) also reported that Scottish Highland heifers at 31°C had higher rectal temperatures than Zebu heifers (39.7°C vs. 38.5°C). Additionally at 31°C, the Scottish Highland heifers had respiration rates three times that of the Zebus. O'Kelly (1987) reported that, to achieve hyperthermia in Brahman cross animals, a constant environmental temperature of 38°C dry bulb (DB), 29°C wet bulb (WB) was used as compared with 32.2°C DB, 25.5°C WB for British steers. The diet used in this experiment was either lucerne hay or a mixture of lucerne hay and whole cotton seed. In Australia, sweating rates of *Bos indicus* cattle were shown to increase exponentially in response to increases in body temperature. In comparison, *Bos taurus* sweating rates tended to plateau after an initial increase (Finch *et al.* 1982). In this study, there was a negative correlation between heat dissipation and metabolic heat production which indicated lack of adaptation in the productive traits such as high food intake and metabolic heat production with ability to dissipate heat stress. *Bos indicus* cattle demonstrated an ability to lower resistance to internal heat transfer to a far greater extent than *Bos taurus* breeds and maintained their low resistance at high levels of heat stress (Finch 1985). The diet used in these studies was *ad libitum* lucerne chaff, which by itself, would generate a fairly large metabolic heat load.

In a further study Finch (1985) showed that Brahman and Brahman/Shorthorn crosses were able to remove a significant portion of metabolic heat non-evaporatively from the skin at lower air temperatures than Shorthorn cattle. The Shorthorn cattle stored heat and their body temperature increased. The woolly coats of *B. taurus* may act to trap water vapour and impede vaporisation thereby decreasing efficiency of evaporative heat loss.

2.7 Conclusions

Ruminants fed low quality roughages require supplementation to achieve reasonable rates of growth and reproduction. Data are accumulating which show that supplementation with critical nutrients will increase the efficiency of growth of ruminants fed low quality straw to that ruminants fed on high quality concentrate rations.

Research is needed to clarify the role of these critical nutrients in the metabolism of ruminants. There is still considerable controversy as to the origin of the increased metabolic heat production found when roughage diets are fed. A theory proposed by Preston and Leng (1987) is that the increase in metabolic heat production is due to an imbalance of nutrients and that when critical nutrients are supplied then metabolic heat production will fall. It is theorised that ruminants in tropical areas will be more affected by the high metabolic heat production associated with roughage feeding. If critical nutrients reduce the heat increment caused by intake of roughage then growth rates of these animals could be equal to or greater than that achieved by animals fed on similar rations in more temperate areas.

The contradicting theory (see Section 2.5.2) is that the increase in metabolic heat when roughage diets are fed is due to the energetic cost associated with intake and digestion of roughage feed, and, that roughage diets require increased rumination and fermentation activities which lead to greater production of heat than a concentrate diet of the same ME content.

Whilst it was beyond the scope of the research reported in this thesis to measure heat production from the gut when roughage diets are fed, it was practical to investigate the effect of high temperature. Under conditions of heat stress, ruminants that are metabolically imbalanced and fed roughage diets will be disadvantaged.

From the review of the literature on the effects of heat stress on ruminants, it is apparent that there is little information available on the interaction of heat stress and diet, although certain areas of ruminant production under conditions of high temperature have been thoroughly investigated.

Means of supplying the nutritional needs of the rumen microorganisms are generally known (see Section 2.4.1). The roles of nutrients supplying either aminogenic or glucogenic precursors need to be clarified as there is still considerable controversy as to whether glucose is a limiting nutrient for ruminants on low quality roughages (see Section of 2.5), and the exact function of bypass protein is not known.

The experiments reported in this thesis were aimed at increasing knowledge on the possible interactions between high temperature and supplementation and the mode of action of critical nutrients in ruminant feeding.