Chapter 1

# INTRODUCTION

The primary objective of research into factors affecting ruminant digestion and metabolism is to improve the efficiency of feed utilization. Improved efficiency may be defined as an increase in production of meat, milk and fibre from a given unit of feed or an increase in the utilization of available resources in any given production system. The former definition usually applies to intensive feeding systems while the latter definition may have more relevance to ruminant production systems in developing countries.

The characteristic feature of all ruminants is an enlargement of the digestive tract stomach which is divided into four compartments (reticulum, rumen, omasum and abomasum). The largest compartment is the rumen, which is a large anaerobic fermentation vat containing a diverse population of microorganisms. These microbes are capable of fermenting carbohydrates, proteins and other organic materials. Products of fermentation (volatile fatty acids and microbial protein) are utilized by the host animal.

Because the reticulo-rumen is the first compartment of the digestive tract, almost all feedstuffs ingested are subjected to some degree of fermentation. An exception is fluids consumed by suckling (milk) which bypass the rumen by means of a tube-like fold of tissue (oesophageal groove) which results in the fluids directly entering the abomasum (gastric stomach).

The main pathways of digestion in the ruminant are shown in Figure 1.1.

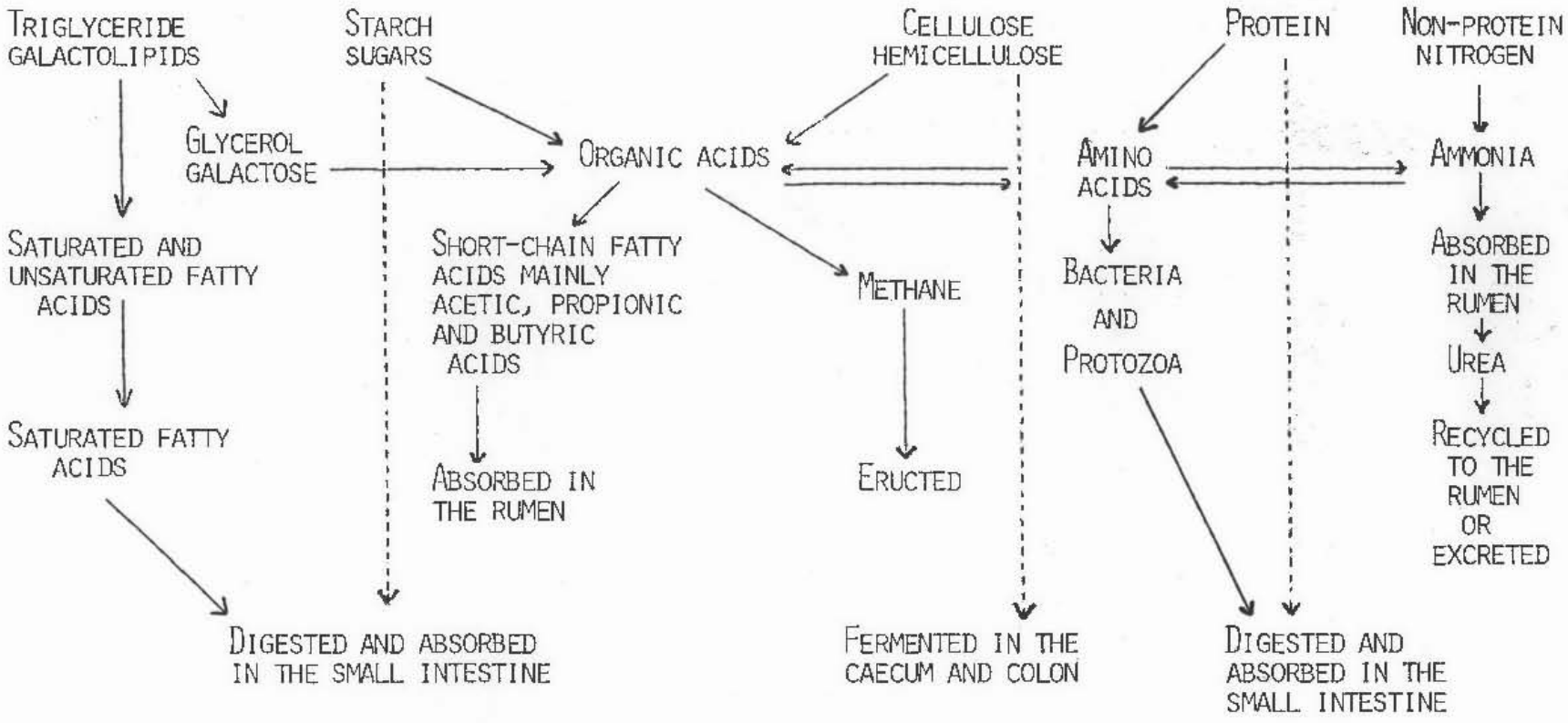


Figure 1.1. A diagram of the main pathways of digestion in the ruminant. Broken lines represent an incomplete fermentation in the rumen (from Thomas, 1975).

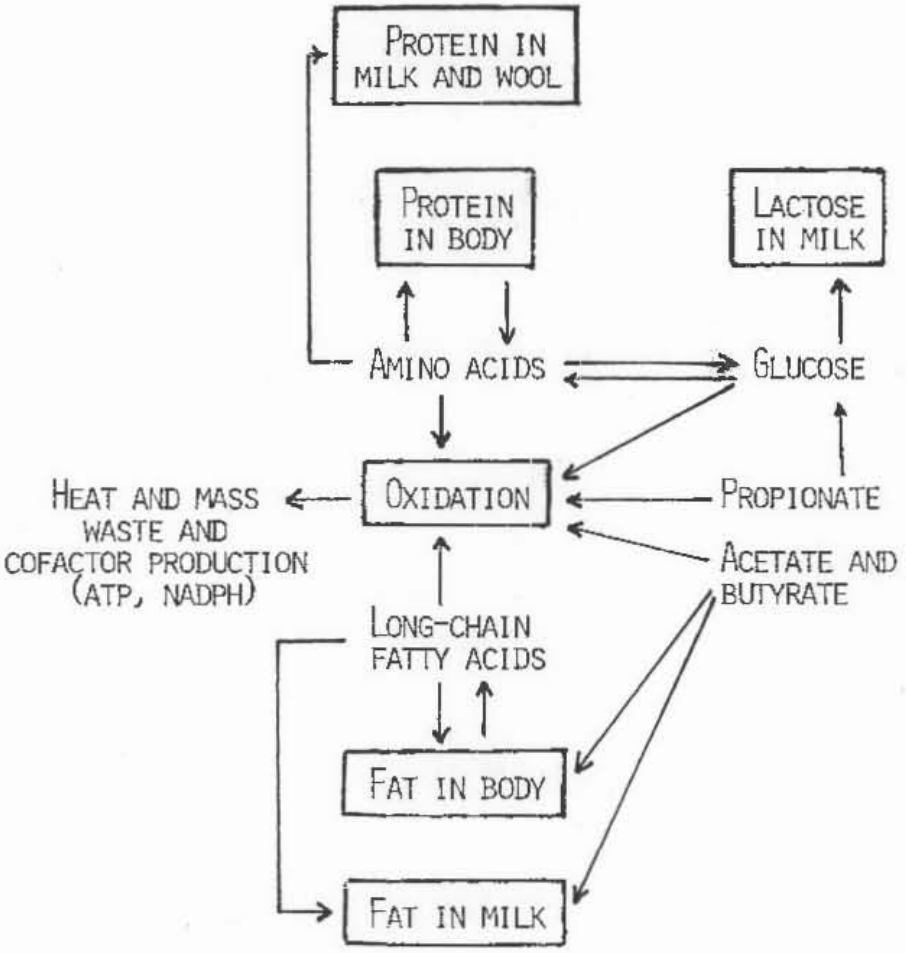


Figure 1.2. A diagram of the origin and possible metabolic fate of major nutrients and metabolites utilized in ruminant production (from Oldham, 1984).

The extent of ruminal digestion of various feedstuffs is determined by the composition and physical characteristics of the feed, the fermentative activity in the rumen and the rate of passage of digesta out of the rumen.

Although rumen fermentation is beneficial because it allows the ruminant to convert cellulose and other feedstuffs that cannot be digested by man into products of substantial nutritional value (meat and milk), many preformed nutrients are degraded to volatile fatty acids, methane and ammonia. Energy in starch is lost as heat of fermentation or methane and the biological value of proteins may be reduced through proteolysis to the point where only ammonia remains. As shown in Figure 1.1, excess ammonia which is not utilized by bacteria for amino acid synthesis is absorbed and converted to urea in the liver. A portion of this urea may be recycled to the rumen but substantial amounts are excreted. Thus, rumen fermentation results in considerable amounts of high quality protein and starch being wasted. By selection of feedstuffs that are resistant to fermentation or by treating feedstuffs by physical or chemical means, nutrients might be able to escape rumen degradation and be digested in the small intestine (note broken lines in Figure 1.1), increasing the efficiency of feed utilization.

Absorbed nutrients may be used in several different ways (see Figure 1.2). The interrelationships between protein and energy yielding nutrients suggest that changes in protein and/or energy supply could markedly affect the pattern and efficiency with which absorbed nutrients are utilized for production. By considering both the pathways of digestion (Figure 1.1) and utilization (Figure 1.2) simultaneously, it appears that predicting the productive response to any ingested feedstuff or combinations of ingested feedstuffs would be extremely complex. However, the large number of variables also suggest that there may be considerable scope for manipulating feedstuffs so as to increase the efficiency of conversion of feed into product.

In this thesis, studies were undertaken to investigate the productive responses to protein and starch (or glucose)

supplements which were able to escape rumen degradation and be digested in the small intestine. From the pathways outlined in Figures 1.1 and 1.2, it appeared that the digestibility and fermentation products (volatile fatty acids and microbial protein) of the basal diet would have a major effect on the responses associated with supplementation. Furthermore, the physiological state of the animals would presumably affect the response to different supplements and the way in which absorbed nutrients were partitioned for various purposes.

By studying the changes in animal production and metabolism associated with postruminal supplements that are fed with various basal diets (in differing physiological states), a better understanding of diet-animal interactions should evolve. This should result in more accurate recommendations for balancing protein and energy inputs to achieve more efficient utilization of feed by productive ruminants.

# Chapter 2

## REVIEW OF THE LITERATURE

### 2.1 GENERAL

An understanding of the efficient utilization of feed protein and energy by productive ruminants depends on knowledge of the factors involved in their digestion, absorption and metabolism. The studies undertaken and reported in this thesis focus on the interrelationships between protein and energy for production. In the following review of the literature, certain aspects of ruminant nutrition pertinent to these interrelationships were examined. These aspects included control of feed intake, ruminal and postruminal digestion of protein and carbohydrates, metabolism of glucose, amino acids and free fatty acids and hormonal regulation of these metabolites. A brief discussion has been allocated to existing theories on protein/energy interrelationships and the role of nutrient partitioning in the overall utilization of nutrients.

## 2.2 VOLUNTARY FEED INTAKE

Voluntary feed intake is probably the factor primarily affecting ruminant productivity in nearly all feeding systems. Feed intake in ruminants is largely controlled by two main factors which are the physical and chemical components of the feed. The operation of these factors was described by Conrad et al. (1964) who examined the relationship between digestible energy of feeds and feed intake. By varying the proportions of concentrate to roughage, a series of diets were made which ranged from 50-80% dry matter digestibility. The results showed that lactating cows maintained energy intake by increasing their voluntary intake as digestible energy decreased to 67% digestibility. This indicated that these animals consumed sufficient feed only to meet their energy needs (chemical control). However, when digestibility fell below 67%, energy intake was also reduced, indicating that physical factors were controlling intake.

### 2.2.1 Physical Factors

As shown by Conrad et al. (1964) physical factors control intake of feedstuffs with low digestibilities provided all nutrients except energy are non-limiting. Cell walls of plants compose the major indigestible fraction of forages. Van Soest (1975) explained how plant cell walls influence intake and discussed the concept that cell walls represented the structural volume of forage, which was related to rumen volume. Thus, any process which increases the breakdown of plant cell walls (grinding, alkali treatment, etc) should decrease structural volume and allow more forage to be accommodated in a given rumen volume. Therefore, intake increases when forages are ground (Minson, 1963).

It has usually been accepted that when rumen volume reaches a certain size, distension results in satiety signals being sent to the central nervous system, which inhibits further intake. The overriding satiety signals due to distension originate in the reticulum rather than the rumen (Grovum, 1979). However, the

degree of distension that inhibits intake can vary depending on a variety of factors with physiological changes such as lactation being a notable example (Journet and Remond, 1976; Forbes, 1977).

A major factor affecting distension is the rate of removal of digesta from the rumen. Thornton and Minson (1973) and Poppi et al. (1981a) demonstrated that there was a significant relationship between feed intake and organic matter leaving the rumen. It appeared that forage intake was dependent on the rate at which indigestible plant materials could be broken down to a particle size capable of flowing out of the rumen. Rumination and microbial degradation are important processes in the reduction of particle size. However, Poppi et al. (1981b) observed that there were large numbers of particles in the rumen that were well below the critical size necessary to escape. Therefore, other factors such as rumen motility may influence the rates at which small particles flow out of the rumen.

It is well known that energy intake by cows is less than energy output in milk during early lactation. Bines (1976) suggested that the inability of cows to balance feed intake and milk output was due to physical constraints to rumen expansion caused by abdominal fat occupying potential rumen volume. The results of Lodge et al. (1975) lend support to this explanation, since cows fed at a low level during late pregnancy were able to consume more feed after parturition than cows fed at a high level during late pregnancy. Thus, constraints to rumen expansion may also limit intake.

### 2.2.2 Chemical Factors

If feed intake is not limited by physical factors, then chemical factors must be controlling intake. Chemical factors influencing feed intake include requirements for energy, products of fermentation, circulating metabolites, and circulating peptides reacting with the central nervous system.

As discussed by Blaxter (1962), energy expenditure appears related to intake in non-ruminants and the same relationship generally applies. This relationship suggests that the demand to meet energy needs controls feed intake. However, the relation of feed intake to energy expenditure does not explain why adult animals readily fatten when given unlimited access to feed. In this situation, other factors such as circulating metabolites may be regulating feed intake during fattening.

2.2.2.1 Effects of Nutrients on Feed Intake

Nutrients can also affect feed intake; the role of dietary protein in relation to feed intake has attracted considerable interest. Egan (1965) demonstrated that intake of low protein roughage could be increased by up to 40% when protein was supplied postruminally. Other studies (Weston, 1971; Kempton and Leng, 1979) confirmed an increase in feed intake when a source of postruminally digested protein was added to the diet. These responses tend to support the concept that feed intake is related to amino acid availability. Under these conditions, it appears there was a deficiency of amino acids and energy utilization was limited by amino acids. When protein was made available, productive processes then became limited by energy so the animals responded by increasing their intake.

Dietary protein may also influence intake through its effects on dry matter digestibility in the rumen. In a number of studies with a wide range of protein concentrations and forage sources, increasing protein content in the diet increased dry matter digestibility (see Oldham and Alderman, 1982; Oldham, 1984). Presumably increases in dietary protein stimulate microbial growth by providing peptides or amino acids, which in turn increases microbial degradation of plant materials (see Leedle and Hespell, 1983). The increased digestibility should result in more rumen space available to accommodate a higher intake. In ruminants, protein may be acting at two different levels (nitrogen supply for bacteria or amino acid supply for the animal) to stimulate intake.

In contrast, energy supplements (starches, fats) generally reduce voluntary intake of forages (see Gordon, 1981; Journet and Demarquilly, 1979). Part of this reduction may be due to an increase in energy density of the diet which results in energy requirements being met with a smaller amount of feed. The other reason is that both fats and rumen degradable starches decrease cellulolysis and reduce digestibility of the cell wall fraction of plant materials (see Palmquist and Jenkins, 1980; Van Gylswyk and Schwartz, 1984).

2.2.2.2 Effects of Circulating Metabolites on Feed Intake

The role of fermentative products (volatile fatty acids) in the control of feed intake has been the subject of much research (see Forbes, 1980; Baile and Della-Fera, 1981; De Jong, 1982; Forbes, 1982). Intraruminal infusion of acetate reduces meal size, and intraruminal or intraportal infusion of propionate can reduce feed intake in ruminants. Butyrate produced in the rumen does not seem to affect feed intake.

The role of circulating metabolites (other than volatile fatty acids) in feed intake is unclear. Glucose appears to have only slight effects on feed intake. However, in studies where glucose has been infused postruminally, feed intake generally shows a slight decrease (Clark, et al., 1973; Ørskov, et al., 1977).

2.2.2.3 Effects of Hormones on Feed Intake

It would not be surprising if circulating hormones affected feed intake, but results are contradictory. Baile and Della-Fera (1981) found that short term administration of growth hormone or insulin had no effect on feed intake. However, recent studies reported by McCutcheon and Bauman (1985) indicated that voluntary feed intake was gradually increased when lactating cows received long term treatments with exogenous growth hormone. Deetz and Wargsness (1981) found that both insulin and glucagon depressed food intake. In a series of carefully conducted

experiments, De Jong (1981, 1982) studied the relationships between volatile fatty acids, hormones and voluntary feed intake in goats. The conclusion was that insulin, but not volatile fatty acids, appeared to exert a direct affect on feed intake.

Gastrointestinal hormones have been shown to depress feed intake when administered intravenously in fairly high concentrations (Grovum, 1981). Bassett (1978) suggested the effects of gastrointestinal hormones may be related to their role as mediators of insulin and glucagon secretion, but this area is still unclear.

Overall, circulating peptides that affect the central nervous system may be as important in the initiation and termination of feeding in ruminants as they are in non-ruminants (see Baile, 1975; Baile and Della-Fera, 1981). The factors that influence release of these compounds is not clear and are probably related to the variety of physical and chemical factors previously discussed.

## 2.3 DIGESTION AND ABSORPTION

### 2.3.1 General

The overall digestion of feed in the ruminant is mainly dependent on fermentation in the reticulo rumen. The microbial ecosystem of the rumen degrades feed proteins and carbohydrates to peptides, amino acids, ammonia and simple sugars. These compounds are utilized as carbon and nitrogen sources for maintenance and synthesis of microbial cells. Volatile fatty acids (VFA's) are produced as end products of fermentation, and these are the main energy yielding nutrients utilized by the host. Microbial cells and some unfermented proteins and carbohydrates pass into the abomasum and small intestine, where they may be digested and absorbed, providing amino acids and energy for the host. The advantages of fermentation are that microbes are able to digest plant structural carbohydrates (cellulose and hemicellulose) and release energy which would not be available through simple gastric digestion. Furthermore, bacteria are able to utilize simple nitrogenous compounds for synthesis of

protein and can increase the amounts of protein available to the host compared to the protein existing in the original feed. The disadvantages of fermentation are that starches and proteins that would be available through simple gastric digestion are fermented to VFA's with a loss of energy as methane and heat of fermentation.

Optimizing the utilization of feed by ruminants entails maximizing the potential of microorganisms to convert plant structural carbohydrates and non-protein nitrogen into VFA's and microbial protein. It also means manipulating the system so as to achieve the maximum utilization of preformed proteins and starches by the host animal without reducing microbial growth.

### 2.3.2 Fermentation of Plant Structural Carbohydrates

#### 2.3.2.1 General

The carbohydrates ingested by ruminants can be classified into two general categories; structural and storage carbohydrates. The major plant structural carbohydrates are cellulose and hemicellulose. Mammals do not produce enzymes capable of degrading cellulose. Therefore, utilization of structural carbohydrates is related to the capacity of microbes in the rumen to degrade these components. Van Soest (1975) has reviewed the physico-chemical aspects of fibre digestion and Morris (1984) recently discussed in detail the processes involved in cellulolysis.

In general, resistance of cellulose to microbial degradation increases with plant maturity. This is related to indigestible lignin content which may prevent bacteria from reaching the cellulose. Cellulose and hemicellulose are hydrolysed to simple sugars which are fermented to volatile fatty acids, primarily acetate, butyrate and propionate. High roughage diets promote fermentation patterns with a higher proportion of acetate and methane than grain based diets.

If structural carbohydrates escape rumen degradation, they may be fermented in the caecum and large intestine. Ulyatt *et al.* (1975) suggested that hindgut fermentation may account

for up to 30% of cellulose digestion in ruminants.

### 2.3.2.2 Effect of Starch on Cellulose Digestion

In diets for productive ruminants, an important factor may be the relationship between storage carbohydrates (starches) and cellulose digestion. Addition of 30-40% (sometimes less) starches to roughage diets is known to reduce cellulolysis (Henning, et al., 1980). This may be due to starch fermentation reducing rumen pH to a level unsuitable for cellulolytic organisms, but other evidence suggests that reduced cellulolysis is due to a preference by bacteria for starch rather than cellulose (Van Gylswyk and Schwartz, 1984). However, Cheng et al. (1977) observed that the major portion of bacterial carbohydrate consists of the bacterial slime layer which is formed from monosaccharides and could be derived from starches. The slime layer may be important in attachment of cellulose-secreting bacteria to fibre particles (Morris, 1984). Thus, low levels of rumen degradable carbohydrates might be beneficial to fibre digestion by providing substrate for slime formation.

### 2.3.3 Fermentation and Digestion of Starch

The digestion of starch by ruminants has been reviewed by Waldo (1973) and Ørskov (1973). Most starch is rapidly fermented in the rumen through the same pathways as the sugars released from hydrolysis of cellulose. Increasing concentrations of starch in the diet tend to increase the proportion of propionate and decrease the proportion of acetate in the rumen. Although it has often been assumed that virtually all dietary starch is fermented in the rumen, a number of studies over the last two decades have shown that the starches in some cereal grains are incompletely fermented in the rumen.

### 2.3.3.1. Factors Affecting Ruminal Degradation of Starch

Waldo (1973) reviewed factors affecting ruminal digestion of starch and noted that barley had an average rumen digestibility of 94%, but the mean rumen digestibility of maize starch was only 78%. Sorghum shows

considerable resistance to rumen fermentation (McNeill, et al. 1971) and studies by Elliott et al. (1978) and Rowe et al. (1979) showed that large quantities of rice starch flowed out of the rumen of cattle on molasses or sugar cane based diets. In studies with maize, Waldo (1973) indicated that there was much more variation in the rumen digestibility of maize than barley. A number of factors may contribute to this variation. Particle size appears to be negatively related to rumen digestibility in cattle but not in sheep. Church (1980) attributed this to a higher degree of chewing of grain in sheep. The effect of particle size and presumably surface area on digestion led to a large amount of research on the processing of grains. Flaking of maize increases surface area and reduces the number of coarse particles compared to cracking or grinding. Direct comparisons of ground and flaked maize showed that ruminal digestion of starch was only 83% for ground maize but 95% for flaked maize (Beever, et al., 1970).

Genetic variation in grains may also contribute to differences in rumen degradability. Waldo et al. (1971) found that rumen digestibility averaged 60% and 84% in two different lots of maize. Studies with sorghum varieties indicated that ruminal digestion of carbohydrate could vary from 48-80% depending on the endosperm type (Samford, et al., 1971). Later studies with isolated starches from sorghum and maize varieties indicated only small varietal differences in in vitro digestion by rumen microbes, but larger differences existed in starch digestion by alpha amylase (Hibberd, et al., 1982). The results tend to suggest digestibility differences between grains may not be directly associated with the starch fraction, but may be more related to accessibility of the starch, or other factors such as tannins.

### 2.3.3.2 Factors Affecting Postruminal Digestion of Starch

Since ruminants have evolved on high roughage/low starch diets, it is possible that they do not possess the same capacity to digest starches as non-ruminants. In sheep fed diets

containing barley or maize and fitted with cannulae in the duodenum and terminal ileum, MacRae and Armstrong (1969) found that at least 95% of the starch entering the duodenum was digested before reaching the terminal ileum. Amounts of starch reaching the duodenum varied from 0.8 to 1.9 g/kg metabolic bodyweight. In studies with steers fed maize, Karr et al. (1966) found that 93% of the starch was digested in the small intestine when 4 g starch/kg metabolic body weight reached the duodenum. As more starch escaped the rumen, intestinal starch digestion declined and when 12 g starch/kg metabolic body weight reached the duodenum, only 67% of the starch was digested in the small intestine. These results suggested the capacity for starch digestion was exceeded, which may have been due to inadequate intestinal enzymatic activity or inability to absorb glucose.

Studies by Clary et al. (1967) and Armstrong and Beever (1969) indicated that amylase secretion in sheep increased with increasing levels of starch reaching the small intestine. Thus, adaptation may be important in determining the amount of starch digested postruminally. However, experiments by Mayes and Ørskov (1974) with abomasal infusions of gelled starch suggested that rather than amylase, maltase secretion may be limiting intestinal starch utilization.

Characteristics of the starch itself may affect the digestion of starch. Evidence to support this was found by Ørskov and Mayes (in Ørskov, 1973) when they observed that over twice the amount of gelled starch was digested compared to raw starch. Further evidence of starch characteristics affecting digestion was reported by McAllan and Lewis (1981) when isolated wheat, maize, rice or potato starch was abomasally infused into steers. Wheat and maize starch appeared to be more efficiently utilized than rice or potato starch.

Even if starches are hydrolyzed, there may be limits to the capacity for glucose absorption in ruminants. White et al. (1971) demonstrated that, on a body weight basis, the

capacity to absorb glucose was several fold lower in sheep compared to rats. Ørskov et al. (1971) estimated that the maximum amount of glucose that could be intestinally absorbed by sheep was approximately 300 g/day, and McAllan and Lewis (1981) indicated that up to 1200 g/day of glucose could be absorbed by steers.

From the limited evidence, it appears that hydrolysis of starch in the small intestine of ruminants may be slightly limited by glucose absorption capacity, but more limited by enzyme activity or the characteristics of starches.

Starch that is not absorbed in the small intestine may be fermented in the hindgut. Reviewing several studies, Waldo (1973) found that the mean total tract digestibility of starch was 99%, indicating that little starch escaped digestion. Ørskov and Foot (1969) infused raw starch into the terminal ileum of sheep fed grass and found that the maximum capacity for fermentation in the hindgut was approximately 140 g starch/day. Later studies (Ørskov, et al., 1970) indicated that about 150 g/day of the alpha-glucoside in raw maize starch could be fermented in the caecum and large intestine of mature sheep.

### 2.3.4 Protein Digestion and Absorption

#### 2.3.4.1 General

Much of the dietary protein ingested by ruminants may undergo major transformations in the rumen. Bacteria rapidly hydrolyse proteins to peptides and amino acids, and may further deaminate the amino acids to yield ammonia. Peptides, amino acids and ammonia are utilized by bacteria for protein synthesis. Utilization or deamination of amino acids also must occur quite rapidly, because Annison (1956) detected extremely low concentrations of amino acids in rumen fluid. Although some studies (Krebs and Leng, 1984) have indicated that elevated levels of rumen ammonia (15-25 mg/100 ml) may stimulate microbial degradation of cellulose, only a portion of the total available ammonia may be utilized by bacteria. Excess ammonia is absorbed through the rumen wall and converted to urea in the liver. Urea may be recycled to the rumen through saliva or is excreted in urine.

Besides the obvious inefficiency of degrading protein to ammonia and resynthesizing bacterial protein plus the loss of protein in excreted urea, excess ammonia may have deleterious effects on the animals. Ammonia metabolism has recently been reviewed by Visek (1984). Besides the acute problems of ammonia toxicity, elevated ammonia levels may affect reproduction (Jordan and Swanson, 1979; Folman, et al., 1981) and glucose metabolism (Spires and Clark, 1979). Therefore, the potential benefits of reducing protein degradation in the rumen may exceed the obvious benefits of simply increasing amino acid supply to the animal.

2.3.4.2 Factors Affecting Protein Degradation in the Rumen

It has been estimated that 50-70% of fresh forage proteins are degraded in the rumen (ARC, 1980) and approximately 70% of mixed feed proteins fed to dairy cows are ruminally degraded (Kaufmann, 1982). Protein degradation is related to several factors. Protein solubility in aqueous solution appears to be related to rumen degradability (Chalmers and Synge, 1954), but more recent evidence suggests that soluble proteins can vary in degradability depending on their structural characteristics (Mahadaven, et al., 1980; Nugent, et al., 1983).

Chemical factors are also associated with protein degradability. Natural constituents of plants such as tannins have been shown to decrease protein degradation (Driedger and Hatfield, 1972; Barry and Manley, 1984). Hume and Purser (1974) demonstrated that increasing maturity of subterranean clover was associated with increasing levels of protein escaping the rumen. Since lignin is known to increase with plant maturity, the results suggest that indigestible fractions of plant material may protect proteins from microbial degradation.

Treatment of proteins with formaldehyde can markedly decrease their degradability in the rumen (see Ferguson, 1975). The intermolecular and intramolecular methylene bridges that are formed are stable at rumen pH, but under acidic conditions in

the abomasum the reaction is reversed, with formaldehyde being released and the proteins available for absorption in the small intestine.

Heating can decrease protein degradability and improve nitrogen retention as shown by the early studies of Chalmers et al. (1954). This may explain why processed feedstuffs such as fishmeals (drying required) and some oilseed meals (heating during extraction of oil) can exhibit a large proportion of protein escaping the rumen. The degree of processing may also explain why different sources of protein meals are highly variable in their degradability (Mehrez, et al., 1980).

Rumen turnover and outflow rate will inevitably influence the amount of time that proteins are subjected to bacterial degradation. Therefore, as discussed by Ørskov et al. (1981), the factors which change rumen outflow rates will affect the amount of protein escaping the rumen.

2.3.4.3 Postruminal Digestion of Proteins

Digestion of protein in the small intestine of ruminants is believed to be similar to monogastric protein digestion. Microbial protein has been estimated to be over 80% digestible (see Hagemeister, et al., 1981). The factors that influence the degradability of protein in the rumen can also influence digestibility in the small intestine. Thus, over-treatment with heat or formaldehyde can lead to reduced protein digestibility.

2.3.4.4 Microbial Protein Synthesis

The importance of microbial protein in the nutrition of ruminant animals was demonstrated by Loosli et al. (1949) and Virtanen (1966) when it was shown that ruminants were able to grow and produce milk on purified diets containing only non-protein nitrogen.

Approximately 50 to 80% of microbial protein is derived from rumen ammonia (Pilgrim, et al., 1970; Mathison and Milligan, 1971;

Nolan, et al., 1976). Both in vitro and in vivo studies have suggested that the rumen level of ammonia needed for maximum microbial protein synthesis on good quality diets is about 5 mM (Satter and Slyter, 1974; Okorie, et al., 1977). However, Hume et al. (1970) found that maximal flow of protein to the duodenum occurred when rumen ammonia levels reached 9 mM. As discussed by Satter and Roffler (1977), rumen ammonia levels fluctuate widely and will often exceed 5 mM after feeding but decrease below this level within 8 hr. Therefore in animals fed once or twice daily, there is a large amount of time when ammonia is either wasted or not available for maximal microbial protein synthesis.

Since at least 20% and possibly more of microbial nitrogen is derived from sources other than ammonia, the influence of peptides/amino acids on microbial growth has received attention. Salter et al. (1979) found that microbes may prefer nitrogenous sources other than ammonia. A number of researchers have been able to demonstrate considerable increases in in vitro microbial growth when casein replaced urea as the nitrogen source (Maeng, et al., 1976; Cotta and Russell, 1982; Leedle and Hespell, 1983). Buttery (1977), however questioned the value of dietary amino acids for stimulating microbial growth in vivo since there would be a readily available source from lysed bacteria and sloughed rumen epithelial cells. Nolan and Leng (1972) estimated that 30% of microbial nitrogen was continuously being recycled in the rumen. Endogenous non-urea-nitrogen inputs from sloughed cells and salivary proteins have been estimated to contribute 5-10 g nitrogen/day to the rumen in sheep fed roughage diets (MacRae and Reeds, 1980; Kennedy and Milligan, 1980). The microbial population can influence protein available to the ruminant. Protozoa may reduce the amount of microbial protein available to the animal due to predation of microbes and preferential retention in the rumen (Weller and Pilgrim, 1974; Leng, 1982b).

### 2.3.4.5 Efficiency of Microbial Growth

The growth rates of bacteria will affect net microbial protein production. The efficiency of microbial growth in

the rumen has been reviewed by Hespell (1979), Leng (1982a) and Harrison and McAllan (1980). If factors such as ammonia, amino acids, minerals and cofactors are not limiting, efficiency is related to energy supply. Energy, as adenosine-triphosphate (ATP) is required for both maintenance and production. The ratio between these two processes is largely determined by growth rate, which depends on the rate at which ATP is made available. If the concentration of soluble sugars is reduced, bacteria may starve, resulting in large numbers lysing. This would increase the maintenance requirement. The type of substrate is obviously important in supplying continuous and adequate ATP for growth. Studies of Offer et al. (1978) and Hagemeister et al. (1981) indicated that there was a higher efficiency of microbial growth with a combination of starch and cellulose than with either substrate alone. In terms of energy substrates, amino acids are very poor sources. Only 0.9 moles ATP are available per mole of amino acids compared to 3.98 moles ATP/mole of fermented hexose (Baldwin, et al., 1970).

Harrison and McAllan (1980) emphasized in their discussion that as rumen fluid outflow rate increased, efficiency of microbial growth also increased. This component of efficiency could have important implications under conditions where outflow rates are low (high grain/high molasses feedlot diets) but would presumably have little influence in animals where fractional outflow rates are already quite high (lactating dairy cows).

In discussing efficiency of microbial growth, Leng (1982a) emphasized the relationship that exists between the proportion of fermentable organic matter entering microbial cells or VFA's, methane and carbon dioxide. As the efficiency of microbial growth increases, the proportion of substrate directed into microbial cells increases and that entering VFA decreases. This partitioning of energy due to microbial efficiency markedly alters the protein/energy ratio available to the animal.

## 2.4 AMINO ACID METABOLISM

### 2.4.1 Amino Acid Requirements

Amino acids are required for (a) maintenance and synthesis of body tissues (b) synthesis of milk, wool and foetal proteins and (c) synthesis of nitrogen containing compounds such as thyroxine, adrenaline and bile acids.

The amino acid requirements of ruminants are primarily influenced by physiological state and level of production (deposition or secretion of protein). Ørskov (1970) discussed these requirements in regards to protein source (protein synthesized by rumen microorganisms or undegradable dietary protein) and concluded that microbial protein was sufficient to meet requirements for maintenance, slow growth and early pregnancy, but insufficient for rapid growth, late pregnancy or early lactation.

Two approaches are available for estimating amino acid requirements and have been discussed by Oldham (1981). In the dose-response approach, a 'dose' of protein is administered in the feed or infused into the intestine and responses are measured in terms of production, nitrogen retention or changes in metabolic parameters (amino acid oxidation). Most studies using this approach lack measurements of amino acids reaching the small intestine before supplementation, so a true dose-response cannot be estimated. However, the magnitude of response to dose levels may give an indication of the potential response to manipulating protein input.

A second approach to estimating amino acid requirements is by factorial calculations. This method requires knowledge of (a) net deposition or secretion of protein, (b) maintenance requirements, (c) efficiency of absorption of amino acids entering the intestine and (d) net efficiency of utilization of absorbed amino acids. Limiting factors in this method are the large number of assumptions necessary in the calculations. Variables that may influence these calculations are body protein catabolism during late pregnancy or early lactation and metabolism of amino acids in the intestinal mucosa during uptake (Hume, et al., 1972; Tagari and Bergman, 1978).

Overall, ruminant requirements for amino acids are difficult to define. Oldham (1981) concluded that discussion of amino acid requirements for productive ruminants is of limited value until the amino acids that limit production can be defined, what conditions cause these amino acids to be limiting and whether these amino acids can actually be supplied with precision to the site where they are needed. Given these limitations, some predictions have been made of the limiting amino acids in ruminant production. Chalupa (1976) suggested that methionine, lysine, histidine, threonine and arginine are most likely to limit growth and Williams and Smith (1974) suggested that methionine and threonine were the first and second limiting amino acids for growth in calves. Reis (1979) predicted that cyst(e)ine and methionine would be first limiting for wool growth and Tamminga and Oldham (1980) suggested that methionine and lysine may be marginally limiting for milk production.

### 2.4.2 Sources of Amino Acids

The two main sources of amino acid supply for ruminants are derived from dietary protein which escapes ruminal degradation and microbial protein synthesis in the rumen. The factors affecting the rumen degradation of feed protein, and microbial protein synthesis have been discussed previously (see Section 2.3.4).

### 2.4.3 Metabolism of Amino Acids by Tissues

When amino acids are absorbed from the intestine, a portion are subjected to transamination and catabolism by the intestinal mucosa before being released into the portal blood (Tagari and Bergman, 1978). Amino acids are then transported to the liver where they are utilized for gluconeogenesis (see Section 2.5.4) and synthesis of plasma proteins. As discussed by Bergman (1984), the overall transport and metabolism of amino acids within the body appears to be a well integrated system that adapts to various physiological conditions (underfeeding, pregnancy, lactation). The portal viscera, liver, kidney and muscles both add and remove amino acids from the circulation. Alanine, glycine and glutamine-glutamate couplet appear to be the major amino acids involved in inter-organ nitrogen and carbon transport in fed sheep.

### 2.4.3.1 Foetal Metabolism of Amino Acids

During late pregnancy, amino acid metabolism by the foetus will have a major influence on the overall amino acid status of the ewe. Bassett (1980) reviewed amino acid metabolism in the foetus. Concentrations of amino acids are higher in foetal than maternal blood indicating active transport is operating in the placenta. The total quantity of amino acids removed by the foetus exceeds amounts required for foetal protein synthesis, and catabolism of amino acids may account for a substantial portion of foetal oxygen consumption in late pregnancy.

### 2.4.3.2 Muscle Metabolism of Amino Acids

Amino acid metabolism in ruminant muscle has been reviewed by Lindsay and Buttery (1980). Metabolism appears to be similar to non-ruminants except that branched-chain amino acids are catabolized much less in ruminants. Tissue proteins undergo continual synthesis and breakdown. In muscle, this turnover results in losses of creatine which is converted to creatinine and excreted in the urine. The cycle of synthesis, catabolism and resynthesis of protein must result in an energy expense. Baldwin et al. (1980) suggested that protein turnover might account for 10-15% of total energy expenditure in animals.

### 2.4.3.3 Mammary Gland Metabolism of Amino Acids

Amino acid metabolism in the mammary gland has been studied in lactating goats (Mepham and Linzell, 1966), cows (Bickerstaffe, et al., 1974) and sheep (Davis, et al., 1978). Extraction rates of amino acids by the mammary gland were not markedly different between species. Extraction of essential amino acids was higher than non-essential amino acids. Mepham (1982) divided essential amino acids into two groups. The first group (methionine, tyrosine, phenylalanine, histidine and tryptophan) is characterised by virtually complete transfer of these amino acids from blood into milk protein. The second group (threonine, valine, isoleucine, leucine and arginine) is taken up by the mammary gland in excess of the requirement for milk protein synthesis. Out of this group, the branched chain amino acids appear to be extensively metabolised in mammary tissue. This indicates a distinct difference between mammary tissue and muscle tissue in regards to the fate of branched chain amino acids.

Another major difference between amino acid metabolism in the mammary gland and muscle is that once amino acids are deposited in milk protein they are not subject to catabolism like muscle proteins. This increases the efficiency of protein synthesis via milk compared to muscle.

### 2.4.4 Amino Acids as an Energy Source

In discussing amino acid metabolism, it is important to consider the role of amino acids as energy sources. A considerable proportion of non-essential amino acids may be utilized for glucose synthesis (see Section 2.5.4). Besides being a glucose precursor, amino acids may be used directly as an energy source, and most studies indicate that a much larger proportion of amino acid flux rates are converted to carbon dioxide rather than glucose (see Lindsay, 1976). Recent *in vitro* evidence indicates that glutamine may be more important than glucose as an energy source for cellular growth and suggestions were made that glutamine should be given more consideration as an energy source *in vivo* (Zielke, *et al.*, 1984).

### 2.4.5 Hormonal Control of Amino Acid Metabolism

The hormones that are major regulators of amino acid metabolism are insulin, growth hormone, glucagon and glucocorticoids.

#### 2.4.5.1 Effects of Insulin on Amino Acid Metabolism

Insulin stimulates protein synthesis (see Manchester, 1976), but the mechanisms by which insulin affects overall amino acid metabolism are not well understood.

Insulin stimulates uptake of amino acids by peripheral tissue. However, uptake appears to be selective, with alanine, leucine and valine exhibiting the largest reductions in plasma concentration following administration of insulin (Brockman, *et al.*, 1975; Prior and Christensen, 1978). Further studies showed that this reduction was maintained only if insulin and glucose were infused together (Prior and Smith, 1982). It is of particular interest to note that leucine has been shown to promote protein synthesis and inhibit protein breakdown (Goldberg, *et al.*, 1980). These observations may have been related to a pharmacological effect rather than a

physiological effect of leucine. Overall, these studies suggest that insulin may promote protein deposition by selectively stimulating uptake of some branched chain amino acids.

Studies with foetal lambs suggest that the effect of insulin on protein deposition may be more related to insulin decreasing protein catabolism rather than increasing protein synthesis (Chrystie, et al., 1977). In vitro studies also suggest that muscle protein catabolism is inhibited by insulin (Jefferson, et al., 1974). Insulin appears to have little effect on hepatic metabolism of amino acids (Brockman, et al., 1975).

#### 2.4.5.2 Effects of Glucagon and Glucocorticoids on Amino Acid Metabolism

In contrast to insulin, glucagon markedly stimulates hepatic removal of glucogenic amino acids. Administration of glucagon reduced the arterial concentration of alanine, glycine, glutamine and serine by approximately 30%, doubled the conversion of labelled alanine to glucose and increased the net hepatic output of glucose (Brockman, et al., 1975; Brockman and Bergman, 1975). It appears that release of both insulin and glucagon are stimulated by amino acids and both hormones decrease the arterial concentration of amino acids. The net result is quite different however, with glucagon increasing glucose synthesis from amino acids while insulin increases peripheral uptake of amino acids.

Glucocorticoids act in a similar manner to glucagon. Catabolism of muscle tissue is increased when glucocorticoids are administered and there is an increased incorporation of amino acid carbon into glucose (Reilly and Ford, 1974; Bassett, 1968). The evidence suggests that glucagon operates during the fed state while glucocorticoids become important during the fasted state.

#### 2.4.5.3 Effects of Growth Hormone on Amino Acid Metabolism

As discussed by Young (1980), growth hormone stimulates transport of amino acids and increases protein synthesis, but unlike insulin, it does not appear to alter rates of protein catabolism in muscle. Growth hormone has been shown to increase nitrogen retention in growing ruminants (Davis, et al., 1970), mature, fibre-producing ruminants

(Wynn, et al., 1979) and lactating dairy cattle (Bines, et al., 1980).

It is interesting to note that in sheep, administration of growth hormone increased nitrogen retention but decreased wool growth, while the opposite effect was observed when administration of growth hormone ceased. The results suggested that under the influence of growth hormone, sulphur amino acids were being directed towards tissue deposition rather than wool growth. However, further studies with continuous intravenous infusion of growth hormone and methionine failed to indicate any response of wool growth to growth hormone (Wynn, et al., 1980).

The complex interrelationships among hormones affecting amino acid metabolism indicate that a single type of response to a single hormone inadequately describes the effects observed in vivo. For example, although exogenous growth hormone stimulates nitrogen retention, correlations between endogenous growth hormone and growth rate have been either zero or negative (Trenkle and Irvine, 1970; Purchas, et al., 1970, 1971). Part of the explanation for this difference may be related to the fact that the same hormones affecting amino acid metabolism also influence (or are influenced by) energy metabolism.

2.4.5.4 Effects of Amino Acids on Hormones

Several studies have indicated that amino acids absorbed from the intestine may affect hormone levels. Bassett et al. (1971) observed a positive correlation between the amount of protein digested in the small intestine and plasma concentrations of insulin. Berzins and Manns (1974) observed that amino acids could stimulate the release of pancreatic glucagon. Several studies have been conducted to determine the response of growth hormone to the addition of protein supplied postruminally. Plasma growth hormone concentrations have been increased in goats (Oldham, et al., 1978), sheep (Barry, 1980) and cows (Oldham, et al., 1982) when casein was infused into the abomasum or protected from ruminal degradation by formaldehyde treatment. In contrast, other studies showed that abomasal casein infusion failed to elicit a response in growth hormone in goats (Gow, et al., 1979) and cows (Peel, et al., 1982 a).

The conflicting results indicate that responses of hormones to

dietary protein are still unclear, but suggest that absorbed amino acids may affect hormones which in turn may influence the metabolic fate of amino acids in the body.

## 2.5 GLUCOSE METABOLISM

### 2.5.1 Glucose Requirements and Uses

Glucose is the major form of carbohydrate circulating in the blood and is a key nutrient utilized for both maintenance and production.

In terms of maintenance, glucose is essential as an energy source for the central nervous system. Lindsay and Setchell (1976) demonstrated that 95% of the carbon dioxide produced by the sheep brain was derived from glucose. Leng and Annison (1962) also presented evidence indicating that glucose was an essential metabolite for sheep red blood cells. The role of glucose as the major fuel for the central nervous system means that glucose homeostasis is of prime importance in ruminants. Bassett (1978) suggested that most changes in ruminant hormonal patterns could be attributed to the need to maintain glucose homeostasis.

Glucose is also an important nutrient in lactation, pregnancy and growth. Milk production places a considerable demand on glucose supply, primarily for the synthesis of lactose. Annison and Linzell (1964) demonstrated that glucose was essential for milk production and that up to 80% of the glucose available to the animal may be used for milk synthesis. During pregnancy there is also an increased demand for glucose. Setchell *et al.* (1972) showed that glucose was the principal metabolic fuel for the foetus and that 60-70% of the glucose produced by ewes in late pregnancy was utilized by the foetus. During growth, glucose may be used both as an energy source and for synthesis of ribose in the formation of deoxyribonucleic acid (DNA). Recent research into cellular growth suggests that the absolute requirement for glucose in growth may be more related to its role as a substrate in anabolic reactions rather than its use as an energy source (Zielke, *et al.*, 1984).

Glucose may also have an important indirect role in fat synthesis in ruminants. Compared to non ruminants, ruminants utilize very little glucose as a carbon source for fatty acid synthesis, due to the low activity of key enzymes (ATP-citrate lyase and NADP-malate dehydrogenase) in ruminant tissues (see Bauman and Davis, 1975). However, substantial quantities of glucose may be used to provide reducing equivalents (NADPH) via the pentose phosphate pathway, which are used for the stepwise elongation of fatty acids from acetate. Bickerstaffe et al. (1974) showed that 30-40% of the carbon dioxide produced during oxidative metabolism in the lactating mammary gland was derived from glucose, suggesting that a significant amount of glucose may have been utilized for the formation of milk fatty acids from acetate. Glucose is also used in fat synthesis as a precursor of glycerol for triglyceride formation.

Although its relative importance is not clear, glucose may also be used as the carbon skeleton for amino acid synthesis. Early studies (Black, et al., 1955) indicated that when labelled glucose was injected into dairy cows, appreciable amounts of the label appeared in tissue protein.

### 2.5.2 Glucose Entry Rates

If animals are in a steady state in which plasma glucose concentrations are kept constant, the rate of utilization of glucose will equal the rate of production, which has been termed glucose entry rate. Use of isotopically labelled glucose has allowed estimates to be made of glucose entry rates under a variety of conditions (see Leng, 1970) of which diet and physiological state have the largest impact.

Glucose entry rates appear to be affected most by energy intake and precursor availability (Judson and Leng, 1968; Herbein, et al., 1978). Physiological state can also have a marked effect on glucose entry rates with large increases reported during late pregnancy in sheep (Wilson, et al., 1983) and early lactation in cows (Bennick, et al., 1972) compared

to the non-pregnant or non-lactating state. The observed effects of physiological state on glucose entry rates indicate that glucose entry rates are often not related to plasma glucose concentration. For example compared to the non-lactating state, glucose entry rates during early lactation may increase by 50% while plasma glucose concentrations only increase by 20% (Bergman, 1983).

### 2.5.3 Sources of Glucose

Generally, ruminal fermentation of dietary starches prevents little glucose from being directly absorbed from the gastrointestinal tract. Therefore, in ruminants, most glucose must be synthesized from glucogenic precursors. The liver is the major site of gluconeogenesis in ruminants. Approximately 85% of the total glucose entry rate in fed sheep is produced by the liver, with the remaining portion produced by the kidneys (Bergman, et al., 1974).

However, under certain conditions a proportion of dietary starch may escape fermentation and be absorbed as glucose in the small intestine (see Section 2.3.3). In non-pregnant, non-lactating sheep, glucose entry rates have been estimated at 100-110 g/day (Leng, 1970). If 100 g of starch/day escaped fermentation and was absorbed, virtually all the glucose used in maintenance could be met by bypass starch.

### 2.5.4 Glucose Precursors

There are four major groups of precursors that can be utilized in gluconeogenesis: (a) propionate, (b) glucogenic amino acids, (c) glycerol and (d) lactate. The total contribution that each precursor makes to glucose flux is difficult to determine. Two approaches have been used in ruminants, as discussed by Bergman (1983). By measuring the transfer of labelled precursor to glucose, a minimum value is obtained due to crossover of the label within the TCA cycle. Alternatively measurement of precursor uptake by the liver and kidney through determination of arterio-venous concentration differences and blood flow will give a maximum value since the precursor may

be metabolised to compounds other than glucose.

### 2.5.4.1 Propionate

Propionate, which is produced during rumen fermentation, is the only volatile fatty acid which is a major source of glucose. Over 90% of the propionate absorbed from the rumen is removed from the portal blood as it passes through the liver (Bergman and Wolff, 1971). In sheep fed 800 g lucerne/day approximately 0.9 moles of propionate were produced (Judson and Leng, 1973a). If all this propionate were converted to glucose, approximately 80 g/day of glucose would be available to the sheep, which would supply a major proportion of glucose needs for maintenance. However, studies have indicated that there is an extremely large amount of variation in the proportion of glucose (30-70%) synthesized from propionate (Bergman, et al., 1966; Wiltrout and Satter, 1972; Judson and Leng, 1973a). These differences may be due to availability of propionate (Steel and Leng, 1973), availability of absorbed glucose or other glucose precursors (Judson and Leng, 1973a,b) or physiological state. Wilson et al. (1983) estimated that only 37% of propionate production was utilized for glucose production in non-pregnant ewes, but this figure rose to 60% in lactation.

One of the major areas likely to affect the estimate of glucose derived from propionate is the crossover of the radioactive label into intermediates in the citric acid cycle, resulting in transfer of labelled carbon into carbon dioxide rather than glucose (Krebs, et al., 1966). Studies by Cridland (1984) have indicated that crossover can be considerable and may be a major reason for the low estimates of glucose derived from propionate.

### 2.5.4.2 Glucogenic Amino Acids

Amino acids are another major source of glucose precursors. Krebs (1965) estimated that 55 g glucose could be synthesized from 100 g of protein absorbed from the intestine. Studies with

($^{14}C$) labelled amino acids have indicated that between 10-30% of the glucose in sheep and lactating cows may be derived from amino acids (Egan, et al., 1970; see Lindsay, 1976). Alanine, aspartate, glutamine, serine and glycine are the major amino acids utilized for glucose synthesis. Heitmann and Bergman (1980) observed that alanine, glutamine and glycine were also the major amino acids released from skeletal muscle of sheep. It appears that amino acids form a second pool of glucose precursors that might be drawn upon to maintain glucose status if energy intake and propionate production were reduced. The role of amino acids as glucose precursors appears to be limited to non-essential amino acids, since only very small amounts of essential amino acids are converted to glucose (Egan and MacRae, 1979).

2.5.4.3 Glycerol

Glycerol exists in combination with fatty acids and is stored as triglycerides. During periods of undernutrition, fat stores are mobilized and glycerol is released during lipolysis. Bergman et al. (1968) estimated that approximately one-third of the glycerol removed from blood is converted to glucose. Because blood levels are normally quite low, glycerol contributes only about 5% of total carbon for glucose. However, during starvation, 20-30% of the glucose may be derived from glycerol.

2.5.4.4 Lactate

Lactate can be produced from anaerobic metabolism of glucose intracellularly, and in rumen fermentation. Small amounts of lactate may also arise from the metabolism of propionate in the rumen epithelium (Wiegand, et al., 1972; Weekes and Webster, 1975). Annison et al. (1963) estimated that approximately 15% of the glucose formed in fed sheep was derived from blood lactate. However a portion of glucose and lactate is converted back and forth in the Cori cycle which would not lead to a net synthesis of glucose.

### 2.5.5 Hormonal Control of Glucose Metabolism

The critical importance of glucose as an energy source for the tissue of the central nervous system necessitates that homeostatic mechanisms must be operating in the control of glucose metabolism. The major hormones involved in glucose metabolism in ruminants appear to be insulin and glucagon.

#### 2.5.5.1 Insulin

Although insulin plays a major role in glucose metabolism in non-ruminants, several studies have suggested that ruminants are less sensitive to insulin than non-ruminants (Ballard, et al., 1969; Weekes, et al., 1983). However, studies by Reid et al. (1963) showed that the lack of insulin produced effects in ruminants just as severe as in non-ruminants.

Bassett et al. (1971) found that although insulin concentration was not related to plasma glucose concentration, it was closely correlated with rates of glucose turnover in sheep fed a range of intakes.

It has often been assumed that insulin has an inhibiting effect on gluconeogenesis but this conclusion is debatable. West and Passey (1967) reported that insulin infusion or glucose infusion (which presumably would stimulate insulin secretion) decreased hepatic glucose output. In studies with cows in different physiological states, Lomax et al. (1979) found that glucose infusions in lactating cows evoked a moderate increase in insulin secretion and a marked reduction in hepatic glucose output. However, glucose infusions in non-lactating cows did not alter hepatic glucose output, although insulin levels were markedly increased. Thus, physiological state appears to influence the effect of insulin on gluconeogenesis.

A further inconsistency with the inhibitory effect of insulin on gluconeogenesis is the fact that insulin levels increase rapidly after feeding (Bassett, 1975) but hepatic glucose output also markedly increases at the same time (Thompson, et al., 1978).

2.5.5.2 Glucagon

The previously discussed results (Section 2.5.5.1) suggest that insulin cannot be viewed alone in regards to gluconeogenesis, but must be considered in relation to the other major hormone involved in glucose metabolism, which is glucagon. Glucagon stimulates hepatic uptake of all glucose precursors (lactate, propionate, amino acids) and their conversion to glucose (Brockman, et al., 1975; Brockman, 1978). Bassett (1975) therefore suggested that the insulin/glucagon ratio is of greater significance in ruminant glucose metabolism than the absolute level of either hormone alone.

Overall, it appears that the effect of insulin is directed at glucose utilization in peripheral tissues and the effect of glucagon is on the production of glucose via gluconeogenesis.

2.5.5.3 Growth Hormone

Growth hormone may have an indirect role in glucose metabolism. Bassett et al. (1971) demonstrated an inverse relationship between growth hormone and insulin and that growth hormone concentration was negatively correlated with the amount of organic matter digested. Since glucose entry rate is positively correlated with digestible energy intake, this suggests that growth hormone might decrease as glucose entry or turnover rate increased. However, during lactation, injection of growth hormone has resulted in either increased lactose secretion or increased glucose turnover rates (Peel, et al., 1982a,b; McDowell, et al., 1983). Oldham (1984) suggested that growth hormone may increase the oxidation of free fatty acids and decrease the oxidation of glucose, thereby sparing glucose for lactose formation.

## 2.6 LIPID METABOLISM

There are two main differences that distinguish lipid metabolism in ruminants from non ruminants. First, acetate is the major precursor for fatty acid synthesis in ruminants while glucose is the major precursor in non ruminants (Bauman

and Davis, 1975). Second, virtually all fatty acid synthesis occurs in adipose tissue in ruminants while the liver is often the major site of lipogenesis in non ruminants. Both of these differences appear to be related to glucose metabolism. Since gluconeogenesis in the liver contributes the vast majority of glucose to the ruminant animal, having lipogenesis occurring in peripheral tissues allows the liver to function primarily as a gluconeogenic organ. Since ruminants do not absorb large quantities of glucose, the utilization of acetate as the primary lipogenic precursor may be a mechanism for the conservation of glucose.

### 2.6.1 Requirements for Lipids

As in non ruminants, ruminants have a requirement for essential fatty acids (linoleic and linolenic) to maintain integrity of nervous tissue. In the productive state, there is a high requirement for synthesis of milk fat and adipose tissue. It is not uncommon for fat secretion in milk to exceed 1 kg/day (30 kg milk x 3.5% fat), and the carcass of steers and lambs commonly contain over 80% of the carcass energy in fat.

### 2.6.2 Sources of Lipids and Lipid Precursors

#### 2.6.2.1 Dietary Lipids

Ruminant diets are generally characterised by a low level of lipid. Forages and concentrates usually contain between 3-8% ether extract (MAFF, 1975; NRC, 1969). This lipid fraction is usually in the form of diglycerides and triglycerides. Dietary lipids are rapidly hydrolysed by rumen bacteria to yield free fatty acids, and unsaturated fatty acids are hydrogenated. Bickerstaffe *et al*. (1972) estimated that 80-90% of the unsaturated fatty acids are converted to stearic acid in the rumen. Due to the relatively low rates of fatty acid synthesis in non-lactating ruminants, dietary lipids may be a major source of adipose tissue fatty acid.

2.6.2.2 Acetate

Acetate is an important precursor for long chain fatty acid synthesis in ruminants. This is in marked contrast to non ruminants where glucose is the major precursor of fat (Bauman and Davis, 1975).

Acetate is produced during rumen fermentation and is absorbed into the portal blood. Early studies (Annison and White, 1962) suggested that a substantial proportion of acetate turnover must be derived from endogenous sources other than rumen fermentation. Bergman and Wolff (1971) demonstrated that the liver was an important site of endogenous acetate production.

In mature ruminants, approximately 30-35% of adipose tissue triglycerides are synthesized de novo, with acetate being the major precursor (Vernon, 1981). The principal fatty acids synthesized are palmitic, stearic and oleic acids. Acetate is utilized for the synthesis of fatty acids in the mammary gland, and fatty acids up to 16-carbon length can be synthesized from acetate; however, 18 carbon fatty acids are not synthesized from acetate (Popjak, et al., 1951a,b; Annison, et al., 1967b). Approximately 20-40% of the fatty acids in milk fat are synthesized from acetate in the mammary gland. The remaining fatty acids (60-80%) in milk are derived from plasma triglycerides of dietary origin or synthesized in adipose tissue.

2.6.2.3 Beta-Hydroxybutyrate

In the fed ruminant, butyrate is produced during fermentation. Extensive metabolism of butyrate in the rumen epithelium results in large amounts of beta-hydroxybutyrate being formed (see Annison, 1984). Butyrate that is not metabolized in the rumen epithelium is transported to the liver and converted to beta-hydroxybutyrate. Oxidation of free fatty acids in the liver also give rise to beta-hydroxybutyrate. In fed sheep, butyrate accounts for approximately 80% of the beta-hydroxybutyrate,

with 20% arising from free fatty acids (Leng and West, 1969).

Significant amounts of beta-hydroxybutyrate are taken up by the mammary gland and are incorporated into milk fat as initial 4 carbon units (Linzell, et al., 1967).

2.6.2.4 Lactate and Pyruvate

Lactate, glucose, propionate and pyruvate are interrelated in lipid metabolism. It has usually been presumed that these precursors are of minor importance in fatty acid synthesis, especially glucose, which is in direct contrast to fatty acid synthesis in non ruminants. Lactate however, has been shown to be incorporated into subcutaneous adipose tissue at a rate that was 38% of the value for acetate incorporation (Prior, 1978). However, this accounted for less than 3% of lactate turnover, indicating the low overall rates of fatty acid synthesis in non-lactating ruminants rather than the importance of lactate as a lipid precursor. Pyruvate is incorporated into fatty acids at a lower rate than lactate, but still at much greater rates than incorporation of glucose (Vernon, 1981).

2.6.2.5 Glucose and Propionate

Glucose is only used to a small extent as a carbon source for fatty acid synthesis. This appears to be due to very low levels of the enzyme, ATP-citrate lyase in ruminants. However Ballard et al. (1972) demonstrated that intravenous infusion of glucose for extended periods increased the activity of ATP-citrate lyase and increased the rate of fatty acid synthesis from glucose.

Different fat depots appear to utilize precursors at different rates. Recent evidence (Smith and Crouse, 1984) suggested that glucose provided a large proportion of acetyl units for lipogenesis in intramuscular but not in subcutaneous adipose tissue. The importance of this is questionable though, since overall fatty acid synthesis rates were quite low in intramuscular compared to subcutaneous adipose tissue.

Rather than being used as a carbon source for fatty acid synthesis, the importance of glucose in lipid synthesis is more related to its utilization in (a) the synthesis of glycerol which is used to form triglycerides, and (b) its use as a means of making available reducing equivalents (NADPH) via the pentose-phosphate cycle, which are necessary for the elongation of fatty acid chains. However, Bauman and Davis (1975) calculated that glucose could not provide sufficient reducing equivalents to account for all the fatty acids synthesized and discussed the role of the isocitrate cycle in providing reducing equivalents for fatty acid synthesis in ruminant tissue.

Propionate contributes very little to fatty acid synthesis except under conditions where excessive amounts of propionate are produced such as high grain diets. Garton et al. (1972) showed that high propionate levels could result in production of propionyl-CoA and methylmalonyl-CoA which give rise to odd chain and branched-chain fatty acids. These fatty acids may comprise up to 20% of the fatty acids in subcutaneous adipose tissue, resulting in a condition known as soft back fat syndrome.

### 2.6.3 Turnover, Uptake and Oxidation of Lipids and Lipid Precursors

#### 2.6.3.1 Acetate and Beta-Hydroxybutyrate

Acetate is an important energy substrate for ruminants in the fed state. Studies by Annison and Linzell (1964) and Annison et al. (1967a) indicated that acetate oxidation accounted for approximately 30% of total carbon dioxide production in lactating goats and non-pregnant sheep respectively.

Further studies by Pethick et al. (1981) showed that 80% of the whole body turnover of acetate was utilized for energy. Muscle, gut and liver utilization accounted for 43, 25 and 17% respectively, of total acetate entry rate. Most of the acetate taken up by the gut and muscles was

oxidized but a significant proportion of acetate taken up by the liver was not directly oxidized, suggesting incorporation of acetate into other compounds such as fatty acids and cholesterol.

In fed lactating goats and cows, uptake of acetate by the mammary gland accounted for 10-40% of total acetate entry rate and approximately 30% of the acetate was oxidized (Annison and Linzell, 1964; Bickerstaffe, et al., 1974).

The contribution of beta-hydroxybutyrate to overall energy metabolism is relatively low in fed sheep. Annison et al. (1967a) estimated that beta-hydroxybutyrate accounted for approximately 10% of the total carbon dioxide output in fed sheep. Beta-hydroxybutyrate appears to be of more importance as an energy source during fasting (Pethick and Lindsay, 1982).

2.6.3.2 Free Fatty Acids

Plasma free fatty acids (or non-esterified fatty acids) constitute a small proportion of the plasma lipids but have a high turnover rate. Free fatty acids are bound to albumin and represent the main transport form of adipose tissue fatty acids. They roughly reflect rates of lipolysis and during periods of high energy demand (late pregnancy and early lactation), turnover rates of free fatty acids increase (see Ciesecke, 1983).

Palmitate, stearate and oleate account for approximately 70-90% of the free fatty acids in ruminant plasma (West and Annison, 1964; Pethick, et al., 1983). Although turnover rates have been shown to be linearly related to plasma free fatty acid concentration (Pethick, et al., 1983) other studies have indicated that as the concentration of palmitate increased in plasma, the relative increase in palmitate turnover was much more than turnover rates of stearate or oleate (Leat and Ford, 1966; Annison, et al., 1967a). Therefore turnover rates of one particular fatty acid may not be representative of the entire pool.

Assuming entry rates were similar, Pethick et al. (1983) determined that oxidation of free fatty acids accounted for 34% of the total carbon dioxide production in fed, pregnant sheep which represented nearly 50% of the fatty acid entry rate. In the same study, it was demonstrated that simultaneous uptake and release of free fatty acids occurred in muscle. Gross extraction of free fatty acids was less than 10%, but accounted for 50% of the carbon dioxide produced by muscle. Approximately 20% of the free fatty acids were converted to ketone bodies before being oxidized.

In the lactating state, free fatty acid entry rates can be quite high and provide an important energy source for the animal. Although direct evidence is lacking, Oldham (1984) has suggested that the relative oxidation rate of fatty acids probably increases in early lactation, thereby sparing glucose and amino acids from being oxidized. Plasma non-esterified fatty acids are both taken up and released by the mammary gland, but their net contribution to milk triglycerides and energy metabolism in the mammary gland appears small (Linzell, et al., 1967).

### 2.6.4 Regulation of Lipid Metabolism

The regulation of lipid metabolism involves the deposition of energy in fat stores during excess energy intake and the release of fat during times of energy deficit. The major hormones involved in regulation of lipogenesis and lipolysis are growth hormone and insulin, with glucagon and glucocorticoids exhibiting minor effects.

#### 2.6.4.1 Insulin

It is generally assumed that insulin is the major hormone involved in lipogenesis. Insulin stimulates fatty acid synthesis from acetate in ovine and bovine adipose cells (Yang and Baldwin, 1973; Vernon, 1982). Vernon et al. (1981), studying the pregnancy/lactation cycle, showed that plasma insulin levels were high during periods of lipogenesis and lower during periods of lipid

mobilization. However, Prior and Smith (1982) questioned the importance of insulin in fatty acid synthesis and suggested that the main effect of insulin on lipogenesis may be its ability to increase uptake of glucose, increase the formation of glyceride-glycerol and increase the activity of lipoprotein lipase, resulting in increased triglyceride deposition. In contrast to adipose tissue, uptake of glucose by the mammary gland appears to be insensitive to insulin (Hove, 1978a, 1978b) and mammary synthesis of fatty acids from acetate is also unresponsive to insulin (Baldwin and Louis, 1975). Low insulin secretion during early lactation would then appear to allow more lipid and glucose to be utilized by the mammary gland with less of these nutrients utilized by adipose tissue.

2.6.4.2 Growth Hormone

Growth hormone appears to have the opposite effect of insulin on lipid metabolism, and tends to cause a flow of carbon away from adipose tissue. Growth hormone concentrations are negatively correlated with carcass fat content (Trenkle and Topel, 1978) and increasing levels of growth hormone are associated with decreasing rates of fatty acid synthesis in adipose tissue (Vernon, et al., 1981). Administration of growth hormone to lactating cows has been shown to increase the plasma concentration and entry rate of free fatty acids (Peel, et al., 1982b).

It is still unclear whether the lipolytic responses associated with growth hormone are due to direct or indirect effects of the hormone. Lipolytic responses to growth hormone have often been reported, but Bauman (1984) suggested impure preparations of growth hormone may have caused this effect. Trenkle (1981) proposed that growth hormone may be interfering with insulin receptors which would inhibit lipogenesis. Vernon (1982) observed that the lipogenic properties of insulin were inhibited by physiological concentrations of growth hormone.

2.6.4.3 Glucagon

Glucagon may have lipogenic or lipolytic qualities depending on the interaction with other hormones. In fed sheep, Bassett (1971) showed that glucagon depressed free fatty acids in a manner similar to insulin. In diabetic sheep, Brockman (1978) was able to demonstrate that glucagon was lipolytic. Under conditions of positive energy balance, insulin levels should be elevated and glucagon may act as a lipogenic agent. Under conditions of negative energy balance (early lactation, fasting), glucagon may contribute to lipolysis.

2.6.4.4 Albumin

Although hormones appear to be the major regulators of lipid metabolism, albumin levels may also be important in regulating free fatty acid release. Metz et al. (1973) showed that as the ratio between free fatty acids:albumin increased from 0.1 to 6.5, there was a gradual inhibition of free fatty acid release. At a level near saturation (7 moles of free fatty acid/mole of albumin) they noted a 90% inhibition in free fatty acid release. If postruminal casein increased plasma albumin levels, this mechanism may help in explaining why lactating cows in negative energy balance have proceeded to milk more and lose more weight when casein was administered via the abomasum (Ørskov, et al., 1977; Ørskov, et al., 1981,b).

## 2.7 PRTOEIN-ENERGY INTERRELATIONSHIPS

### 2.7.1 General

From the previous review, it is evident that digestion and metabolism of protein and energy are closely interrelated. At the level of intake and digestion, increasing the protein content of the diet may increase digestibility and/or voluntary feed intake. Therefore, as emphasized by Oldham (1984), many of the production responses related to changing protein levels may be attributed to changes in energy intake. At the

level of metabolism, amino acids may be utilized as a precursor of tissue proteins or glucose, and conversely, glucose may supply the carbon skeletons for amino acid synthesis. These metabolic interrelationships between protein and energy appear to be coordinated by hormones such as insulin and growth hormone which have major effects on both nutrients.

### 2.7.2 Protein/Energy Ratios

A useful way of studying protein-energy relationships is to evaluate rations in terms of protein/energy ratios. Because of the major alterations of protein and energy during rumen fermentation, it is more accurate to discuss protein/energy ratios in ruminants as the ratio between intestinally absorbed amino acids and energy yielding nutrients absorbed from the gut.

#### 2.7.2.1 Effects of Protein/Energy Ratios in Lactation

The protein/energy ratio can have marked effects on the utilization of nutrients during lactation. At a low protein/energy ratio the supply of amino acids would be less than demand for milk synthesis. In this situation, excess energy-yielding nutrients would either be stored as fat or oxidized. If stored as fat, the reduced energy secretion in milk would be counterbalanced and efficiency of energy utilization should remain fairly constant. If the excess nutrients were oxidized, then the efficiency of feed utilization would be reduced. Cowan et al. (1980) observed trends in lactating ewes indicating that the efficiency of energy utilization declined as the protein/energy ratio declined. At high levels of intake (3.7 x maintenance) Tyrrell et al. (1981) observed that as the dietary protein content decreased in both percentage and insolubility, both digestible and metabolizable energy decreased. These results suggest that lowered efficiencies of energy utilization in lactation do occur as protein/energy ratio decreases, but the effects may be due to changes in both digestibility and metabolizability.

When the protein/energy ratio is increased, there is no longer a need to dispose of excess substrate through oxidation or storage. The additional nutrients should increase milk

protein output and milk yield in general. Many studies have shown this type of response to postruminal infusions of casein (Clark, et al., 1973; Vik-Mo, et al., 1974). Further increases in the protein/energy ratio may stimulate milk production so that additional energy is drawn from body reserves to balance the amino acid supply. Ørskov et al. (1977) observed this situation when lactating cows were fed restricted amounts of energy and postruminally infused with increasing amounts of casein.

Increasing the protein/energy ratio can also increase the efficiency with which body reserves are used for milk production in sheep (Cowan, et al., 1981).

There is a point at which increasing the protein/energy ratio may stimulate excessive mobilization of body reserves resulting in acetonemia. Ørskov et al. (1981b) observed this problem when high levels of fishmeal were added to low energy diets of cows in early lactation.

An excessive protein/energy ratio would occur when the capacity to secrete or deposit amino acids in milk or tissue protein respectively, had been exceeded. Some of the amino acids could be utilized for glucose synthesis, but non-glucogenic amino acids would be deaminated and oxidized. In dairy cows fed protein in excess of requirements, the energy cost involved in synthesizing and excreting the amino group as urea has been estimated at 50 kJ/g N in excess of requirements (Tyrrell, et al., 1970).

2.7.2.2 Protein/Energy Ratios in Growth

In theory, it would be expected that responses in growth to changes in protein/energy ratios would be similar to responses observed in lactation. A low protein/energy ratio would stimulate fat deposition, while increasing protein/energy ratios should favour protein deposition.

On diets of grass and legume forages which varied in maturity and hence protein/energy ratios (higher ratio with early

maturity), absolute amounts of energy deposited as protein increased with increasing protein/energy ratios (Waldo, et al., 1982). However, the relative percentage of energy deposited as protein decreased as protein/energy ratios increased. This was attributed to an increase in total energy intake on the higher protein diets. In contrast, comparisons of growth on formaldehyde treated and untreated grass silage showed that both total energy deposited and percentage of energy deposited as protein increased with formaldehyde treatment (Waldo and Tyrrell, 1980). These results suggest that increasing amino acid supply by formaldehyde treatment of grass silage definitely affected the partitioning of energy between fat and protein deposition in cattle. Similar results were observed by Andrews and Ørskov (1970) in growing lambs fed diets with increasing levels of bypass protein.

The changing rates of deposition of protein and lipid as growing animals reach maturity means that the optimal protein/energy ratio will also change. An adequate protein/energy ratio during early growth would be an excess protein/energy ratio during the fattening stage.

2.7.2.3 Effect of Protein/Energy Ratios on Wool Growth

Wool differs from milk and tissue (excluding suint in 'greasy wool') because it is a product essentially composed of only protein. Therefore, it would be unlikely that energy would have any direct effect on wool growth. However, it is well known that wool growth increases with digestible organic matter intake (DOMI). Ferguson (1972) separated DOMI into protein and non-protein fractions. The effect of the non-protein fraction on wool growth was relatively constant and would reflect energy utilized for microbial protein synthesis. The protein fraction had variable effects on wool growth which would reflect the variation in rumen degradability of different proteins.

Although energy may not have a direct effect on wool growth, variations in the protein/energy ratio have been shown to affect wool growth in milk fed lambs (Walker and Norton, 1971) and mature wethers abomasally infused with amino acids and glucose (Black, et al., 1973).

In the lambs, there appeared to be an optimum ratio for wool growth of 12.2 g digestible protein/MJ of metabolizable energy (ME). At a lower protein/energy ratio, wool growth was depressed and energy diverted to body weight gain. Above this ratio, wool growth also declined, suggesting the capacity to utilize amino acids had been exceeded. In the mature sheep a different pattern emerged. At low levels of digestible protein intake, (20 g/day) decreasing the protein/energy ratio decreased wool growth. However at high levels of protein intake (110 g/day), wool growth actually increased as the protein/energy ratio decreased from 34 to 11 g digestible protein/MJ ME. The results suggested that additional glucose may have been sparing amino acids from being oxidized or utilized for gluconeogenesis. It appears that the optimal protein/energy ratio for wool growth may be affected by physiological state (early growth, pregnancy, lactation) and by the interrelationship between glucose and amino acids.

### 2.7.3 Effect of Energy Precursors on the Protein/Energy Relationship

Depending on the composition of the basal diet, different fermentation patterns and products may be produced. Because the metabolic fate of volatile fatty acids may differ (propionate being glucogenic, acetate being lipogenic and butyrate being ketogenic), the response to protein may differ depending on the relative contribution these products make to the metabolizable energy pool.

Changes in fermentation pattern are often reflected in changes in the partitioning of energy between milk and tissue. When approximately isoenergetic amounts of acetate or propionate were infused into the rumen of lactating cows, total ME increased slightly with propionate, but the proportion of energy secreted in milk was 25% lower on the propionate infusion compared to the acetate infusion (Ørskov, et al., 1969). Similar changes were observed when maize and beet pulp were compared as energy supplements. Tyrrell et al. (1973) found that maize (high propionate) markedly reduced the proportion of energy secreted in milk compared to beet pulp (high acetate).

These results suggested that increasing production of

propionate caused energy to be directed towards fat deposition in tissue than secretion in milk. They also suggest that the type of energy precursor may affect the response to protein.

In experiments where increased dietary protein caused increased milk fat secretion and reductions in body weight, the basal diet was characteristically high in roughage (high acetate) and fed at low levels (Krohn and Anderson, 1980; Ørskov, et al., 1981b).

Less et al. (1982, cited in Oldham, 1984) investigated protein responses on diets which would result in high proportions of propionate or acetate. Between diets, protein had similar effects on protein and lactose secretion, but milk fat was elevated to a much larger degree on the high acetate (beet pulp) diet compared to the high propionate diet (flaked maize). The importance of these findings was that protein could not alleviate the low milk fat syndrome associated with high propionate. Similar results were obtained when lactating dairy goats received abomasal infusions of casein or saline and ruminal infusions of either propionate or acetate (Lough, et al., 1983). Milk fat could not be increased with casein/propionate infusions compared to propionate alone. However, the results suggested a synergistic effect between acetate and postruminal casein for increasing milk fat secretion.

In growing and fattening animals, protein may act in a similar manner to possibly enhance fat deposition on high roughage (high acetate) diets. MacRae and Lobley (1982) suggested that the variations in efficiency of energy utilization for fattening observed on forage diets may be related to the availability of reducing equivalents (NADPH). Higher levels of protein might provide more reducing equivalents and thus result in more acetate being used for fatty acid synthesis rather than being oxidized.

## 2.8 NUTRIENT PARTITIONING

The fact that nutrients are partitioned to different tissues at different rates is well known but not well understood. Hammond (1952, cited in Bauman and Elliot , 1983) first emphasized the

changing priorities for nutrient use during bone and muscle growth, pregnancy and lactation.

Perhaps most interesting is the partitioning of nutrients between tissues that have simultaneous demands for nutrients. Corbett (1979) reviewed the physiological factors affecting wool growth, and from a number of studies concluded that wool growth was depressed during pregnancy and lactation. Although it was unclear which physiological state reduced wool growth more, these findings indicate that pregnancy and lactation have priority over wool growth for available protein.

There does not seem to be a clear partitioning effect between wool growth and liveweight gain in growing sheep. Thus, both of these functions may be equally effective in competing for available nutrients. However, evidence in mature sheep (Williams, 1966; Wodzicka-Tomaszewska, et al., 1968) suggests that during compensatory growth, efficiency of wool production was reduced, indicating that liveweight gain had priority for nutrients compared to wool growth.

When dairy cattle have not reached mature weight, nutrients are required for both liveweight gain and milk production. In a recent study with diets varying in protein and energy density fed to first lactation cows, the results led the authors to suggest that there was a higher priority for growth than for lactation when nutrients were not limiting (MacLeod, et al., 1984). Similar effects were noted when high protein diets stimulated milk yield in mature cows but not in heifers (Roffler, et al., 1978).

In mature cows, milk production has a much higher priority for nutrients than other tissues, as evidenced by the considerable loss in liveweight during early lactation.

However, during late lactation, the increase in liveweight gain is energetically more efficient than weight gain in a

non-lactating animal (see Moe, 1981). This indicates that the physiological effects of lactation can positively influence the partitioning of energy for restoring body reserves.

The coordinated partitioning of nutrients between tissues for different functions is most likely regulated by the endocrine system. The regulation of nutrient partitioning has recently attracted much attention. Bauman and Currie (1980) proposed that two types of controls regulated partitioning: homeostatic controls and homeorhetic controls. Homeostasis is involved with short term changes that can occur during the absorptive and post absorptive periods after food intake. Through effects such as the insulin/glucagon ratio, nutrients may be stored when blood levels are raised and released as blood levels diminish. Thus nutrient supply remains relatively constant to the body tissues. In contrast, homeorhetic controls chronically change the partitioning of nutrients so that more nutrients are directed to a particular tissue for a particular function. In the short term, homeostatic controls would presumably override homeorhetic controls so that nutrient supply to vital organs would always be maintained.

As a homeorhetic regulator, growth hormone has received the most attention. In lactation, growth hormone has been shown to redirect the flow of carbon away from peripheral tissues and towards the mammary gland (Peel, et al., 1981).

The effects of growth hormone and other potential homeorhetic regulators (prolactin, œstrogenic and androgenic hormones) have recently been discussed by Bauman and Elliott (1983) and Bauman (1984).

## 2.9 SUMMARY

Maximizing production in ruminants depends on the total amounts and relative proportions of protein and energy made available to the animal. Due to rumen fermentation and subsequent synthesis of microbial protein, the protein/energy ratio in feedstuffs can be markedly altered and may be very different from the protein/

energy ratio absorbed by the animal. Dietary characteristics (rumen degradability of proteins and starches) can potentially alter the protein and energy available for production. Fermentation patterns can alter the proportions of energy precursors which may change the products formed from available nutrients. Interrelationships between metabolism of absorbed amino acids and energy indicate that there are multiple uses for these nutrients. The particular fate of any absorbed nutrient will depend on the physiological state of the animal and the relative supply and demand of these nutrients for a particular product (muscle, fat, fibre, or milk).

The endocrine system plays an important role in influencing protein/energy interrelationships from the control of feed intake to the partitioning of nutrients for various functions.

The studies described in the following chapters were investigations aimed at understanding the protein-energy interrelationships involved in liveweight gain, fibre growth and milk production. Besides measurements of production, detailed studies were also made on fermentation, digesta flow, hormonal patterns and entry rates of metabolites so that the underlying mechanisms involved in production responses might be better understood.