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Digestive Physiology and Nutrient Metabolism

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KEY TERMS

Fermentation—microbial conversion of substrates into acids and gases under anaerobic (oxygen-free) conditions.

Rumination—the process of regurgitation, re-mastication, re-insalivation, and re-swallowing of feeds, specific to and characteristic of ruminants.

Digestion—mechanical, chemical, and enzymatic breakdown of food nutrients within the gastrointestinal (GI) tract.

Absorption—passage of nutrients from intestinal lumen into the intestinal wall (epithelium) usually followed by passage into the blood.

Required nutrients—nutrients needed to sustain life.

Digestive disorders—diseases resulting from dysfunction of the GI tract.

Prehension—capacity to grasp food for consumption.

Mastication—chewing food to reduce particle size.

Salivation—production of saliva that lubricates ingested foods for swallowing and assists in food digestion.

Ionophores—polyether antibiotics that modify microbial fermentation in the rumen.

OBJECTIVES

By completing this chapter, the reader will acquire knowledge on:

- Animal classification based on feed choice
- Work of digestion by goats
- The role of microorganisms in ruminant digestion
- Digestion by preruminant (young) kids
- Ruminal dysfunction
- Nutrients required within a goat's diet

INTRODUCTION

The gastrointestinal (GI) tract of domestic animals differs, and this difference is related to their preference for and use of dietary components. Animals are classified into three groups based on their diet type. Herbivores are animals that have a digestive system adapted to eat and digest fibrous plant materials; carnivores are animals with a digestive system adapted to digest meat and meat components; and omnivores are those with a digestive system adapted to consume a mixture of plant and animal matter.

As a ruminant, the adult goat can consume and digest fibrous plant materials and therefore is classified as an herbivore. Other ruminants include cattle, sheep, deer, elk, and many other wild ruminant species. These all are even-toed ungulates from the suborder *Ruminantia* of the mammal order *Artiodactyla* (meaning an even number of toes). Among the ungulates, ruminants are the most numerous, widespread, and diverse grass-eating mammals. Of about 250 known genera, 68 still exist, of which 4 (cattle, sheep, goat, and bison) are widely domesticated agricultural species (Leek, 1993b). The ecological success of this group can be attributed to predigestive fermentation. This microbial fermentation process results in catabolism of fibrous plant cell walls (including cellulose) into energy-rich fermentation acids, release of nutrients enclosed within plant cells, and synthesis of microbial protein from nutrients recycled to the rumen such as nonprotein nitrogen (urea) and phosphorus. In addition, the fermentation process yields vitamin K and B complex vitamins provided there are adequate precursors (cobalt for B_{12}; sulfur for thiamin and biotin) for synthesis.

The term "ruminant" reflects the capacity of an animal to ruminate (chew their cud). Anatomically, ruminants possess a unique multicompartment (typically subdivided histologically into three or four sections) fermentation vat generally called the rumen (or the reticulo-rumen) anterior to their gastric stomach. This nonsecretory forestomach and associated organs are designed to support microbial fermentation. Following fermentation, the digesta flows to the ruminant's secretory stomach and intestines for digestion. Subsequent to the rumen, digestion generally parallels that of nonruminant animals. The capacity for this microbially assisted digestion within the rumen permits herbivores like goats to consume diets very rich in fibrous cell walls. Generally, over half of the dry matter consumed will be fermented to microbial products within the rumen reducing the quantity of material that passes to the gastric stomach (abomasum) for postruminal digestion. Anatomical and physiological adaptations of ruminants are geared to providing a favorable ruminal environment for maintaining a high degree of symbiosis between ruminal microorganisms and the host ruminant. These alterations of their GI tract permit ruminants to consume and digest feed resources of much wider variety than nonruminants (Hofmann, 1988).

DIVERSITY OF RUMINANTS IN FEED TYPE

Ruminant species can be subdivided into classes based on their ecological spectrum and feeding type (Hofmann, 1989). At one end of the spectrum are the very selective feeders or concentrate selectors (CS) such as antelopes and giraffes. This class consumes frequent meals that consist of highly digestible nutrients, they ruminate frequently but for short periods of time, and relative to other ruminants, they have a small forestomach compartment. At the other end of the spectrum are the coarse grazers or grass/roughage eaters (GR) that include cattle and sheep. This class can consume very large quantities of food because of their large forestomach capacity that allows slow but efficient fermentation of high fiber feeds. They eat intensively but only a few times of the day, and they ruminate less frequently but for longer periods than CS. Most agriculturally important pasture species are readily consumed by the GR group. Between these two classes are the intermediate group/type eaters (IM) including goats. Within the IM class, the goat is most similar to the CS class having a relative small forestomach when compared to cattle, with less capacity for fermentation of roughage. However, they are extremely adaptable to different environments. When given a choice, goats select and consume the less fibrous portions of plants as well as shrubs and browse. But when fed fibrous feeds and pasture, the volume of the forestomach of goats will increase.

PREHENSION, MASTICATION, SALIVATION

Prehension

Grazing ruminants use both visual cues and taste when selecting a diet. Ruminants will exhibit preferences for certain plant parts and specific forage when grazing and also may select and sort feed components when fed dried forage (hay), but preferences can differ with feeding conditions. Smell and taste appear responsible for selectivity or "palatability" of a diet. Palatability is measured by allowing animals to choose among various diets. Palatability should not be confused with total feed consumption. When animals are not given a choice among a more and a less preferred feed, total dry matter consumption typically is no greater for a feed that is more preferred in a "palatability" study. Much remains to be learned about physical and chemical factors that are responsible for differences in food preference, diet sorting, and total dry matter intake. Some results from preference trials are noted below. Cattle and goats appear to recognize and have preference for a sweet taste. Given a choice, cattle dislike a salty taste, but goats prefer it mildly with pygmy goats having a higher preference for salt (Goatcher and Church, 1970). Goats can distinguish between bitter, sweet, salty, and sour tastes, and are more tolerant than sheep and cattle to a bitter taste (Bell, 1959). Goats enjoy a wide variety of plants that are distasteful to other ruminants presumably because of their greater tolerance to a bitter taste. Grazing goats prefer grasses to legumes and clover over alfalfa (De Rosa et al., 1997, 2002). Goats also show a preference for forage with higher available carbohydrate content (Burns et al., 2001). Why goats prefer some feeds and avoid others is not known, but they appear to have a preprogrammed capacity to recognize nutrients and toxins (Euphagia) and to consume certain plants because of their pleasant smell and taste (Hedyphagia). In most cases, body morphology and size may be determinant factors for food preference. Goats have a smaller size, and thus prefer more digestible and nutritious feeds. When grazing a tall-standing forage, ruminants do not graze to ground level. Presumably, this allows the grazer to keep their eyes above the grazing horizon to be on the outlook for predators. Consequently, grazing animals with a longer snout or with eyes atop their head would have a selective advantage.

Mastication

The mouth is designed to harvest food, mechanically reduce particle size, and mix it with saliva. Saliva is essential as a lubricant to facilitate swallowing. Goats have a pointed tongue and jaws, mobile thin lips, and a deep mouth. Grazed forage is gathered between the labial surface of the lower incisor teeth and the upper dental pad (ruminants lack upper incisors), and forward movement of the muzzle cuts through the forage. Chewing of food is irregular with variable amplitude. In contrast, during rumination, the cud is chewed more slowly and regularly. Premolars and molar teeth aid in mastication. The upper jaw is wider than the lower jaw, so lateral (circular) jaw movement and the shape and spacing of the molar teeth result in shredding of tough plant fibers.

Mastication results in particle size reduction to increase in ports of entry for fermenting microorganisms. In addition, movements of teeth excite mechanoreceptors in the mouth that provide stimuli for production of saliva by salivary glands. Mouth movement also increases the rate and amplitude of primary and secondary cycle contractions of the reticulo-rumen. Feedstuffs that fail to promote chewing (low particle size) result in reduced rumination, saliva secretion, and forestomach motility.

Salivation

Although salivary production is relatively continuous, volumes are greater when ruminants are eating and ruminating. Daily saliva production averages 6–16 liters by sheep and may be greater by goats. Saliva produced by ruminants contains no enzymes, but it is particularly rich in buffers (HCO_3 and HPO_4); these account for its alkalinity (pH = 8.1). Being swallowed, saliva aids in preventing ruminal pH from becoming too low for microbial growth. In the rumen, pH is maintained within a range (5.5–7.0) ideal for microbial growth. The HPO_3 in saliva allows phosphate to be recycled for rumen microorganisms to synthesize nucleoproteins, phospholipids, and nucleotides. Recycled urea, being up to 77% of total salivary nitrogen, also provides ammonia for formation of microbial protein. Urea, recycled in saliva, together with efficient kidney renal tubular urea resorption, appears critical for survival of ruminants consuming forage or feeds with very low protein content (NRC, 2007; Leek, 1993a). In addition, recycling of urea reduces water excretion; combined with very efficient resorption of water by the large intestine, which helps ruminants survive when the quantity or quality of water is limited.

As browsing ruminants, goats have relatively large salivary glands and higher rates of secretion than sheep. The primary functions of saliva are to provide a copious and continuous supply of alkaline buffers to counterbalance the volatile fatty acids (VFA; primarily acetate, propionate, and butyrate) produced during fermentation and to provide an aqueous suspension for rumen solids. Secondary functions of saliva include urea recycling as a source of non-protein nitrogen (NPN) for microbial protein synthesis and phosphate for synthesis of microbial nucleic acid and membrane phospholipids. Saliva also acts as a wetting agent for ingesta, provides an antifoaming agent to prevent frothy bloat, and supplies proline-rich proteins that bind and deactivate dietary tannins.

Saliva provides a medium for short-term adaptation to changes in diet composition, namely, the presence of plant secondary metabolites such as tannins. Salivary proteins influence taste and digestive function. Proline-rich proteins in saliva that bind tannins are present in saliva of browsers but not grazers. Lamy et al. (2008) showed that protein profiles of saliva in the 25–35 kiloDalton (kDa) range differ between goat and sheep saliva (25–35 kDa range). Austin et al. (1989) reported that tannin-binding proteins were present in the saliva of deer but not of sheep and cattle. Hofmann et al. (2008) indicated that in ruminants, the mass of salivary glands is correlated positively with body mass but negatively correlated with the ratio of grass to browse in the diet, perhaps reflecting the need for complex salivary compounds, such as tannin-binding proteins, by browsing ruminants. Silanikove (2000) confirmed that the ratio of salivary gland mass to body size was high for goats indicating their capacity to consume browse plants.

FUNCTIONS OF RUMEN AND RETICULUM

The major physiological activities related to rumen and reticulum will be addressed here. Readers are referred to

Chapter 6 for more detailed descriptions of the functional anatomy of these organs.

The reticulo-rumen is the primary site for fermentation by diverse but specialized microbes. Rumen motility originates in the reticulo-rumen for the processes of rumination and eructation. Environmental features unique for the reticulo-rumen that prove useful for action of ruminal microbes include (1) a reasonably isothermal environment regulated by the homeothermic metabolism of the animal, (2) constant influx of water and feeds, (3) a relatively constant pH achieved through absorption of fermentation acids and salivary buffers, and (4) removal of fermentation end-products by absorption or passage.

Rumen Motility, Rumination, and Eructation

Powerful contractions by the reticulo-ruminal wall include a primary cycle (a mixing cycle or "A" sequence) as well as a secondary cycle (eructation cycle or "B" sequence). Both are initiated by excitation of vagal nerve fiber receptors distributed throughout the reticulum and rumen regions. The primary cycle consists of a double contraction of the reticulum followed by caudally moving contractions of the dorsal ruminal sac and ventral ruminal sac. This serves to pump ruminal fluids atop the floating raft in the rumen allowing fluid to percolate through the raft removing small particles for removal from the rumen. The secondary cycle usually occurs at the end of alternate primary cycles and consists of contractions of the caudoventral ruminal blind sac, a cranially moving contraction of the caudodorsal ruminal blind sac followed by the middorsal ruminal sac and the ventral sac. At the end of this cycle, the point where the esophagus enters the rumen is cleared of liquid so that the headspace gas can escape. Compared to motility before a meal, rate of motility often is doubled during and after feeding. The motor activity responsible for these contractions originates in the bilaterally paired gastric centers in the medulla oblongata of the hindbrain. Reticulo-ruminal motility is important for mixing of digesta, rumination, particle size reduction through attrition, eructation, and VFA absorption.

Two types of sensory receptor mechanisms are responsible for the vagal nerve input: tension receptors and epithelial/mucosal receptors. Tension receptors are located in the muscle layers of all parts of the GI tract. They monitor the tension present in the muscular wall imposed by passive distension and thus may be responsible for limiting intake of low quality feeds based on bulk or mass. The epithelial receptors are located close to the luminal epithelium of the forestomach whereas mucosal receptors are located close to the luminal mucosa of the abomasum and small intestine. These receptors are excited by both mechanical and certain chemical stimuli and may be responsible for chemostatic regulation of intake.

Ingested feed enters the reticulum through the cardia. Heavy materials (stones, sand) may immediately drop to the bottom of the reticulum and remain there. Less dense and fibrous materials float high in the reticulum and cranial sac of the rumen forming a raft of entangled particles. Reticular and rumen contractions move ingested particles caudally to join the fibrous raft in the rumen. Ruminal contents, particularly the raft, are meshed, kneaded, and slowly rotated with powerful rumen contractions. Soupy material common to the reticulum, cranial sac, and ventral sac is randomly pushed out of the reticulum to the omasum and postruminal tract by reticulo-ruminal contractions when the reticulo-omasal orifice is open.

The process of rumination includes four steps: regurgitation, re-insalivation, re-mastication, and re-swallowing. During regurgitation, a bolus of feed gathered near the cardia area of the rumen is pulled back to the mouth, an extrareticular contraction that precedes the usual biphasic contraction and opening of the cardia with antiperistaltic movement of the esophagus bringing the bolus to the mouth. There, the bolus is re-chewed, mixed with additional saliva, and re-swallowed.

Much of the fermentation in the rumen occurs within the fibrous raft. Rumen contractions persistently attempt to break the raft and release the gases for removal via eructation (belching). During the secondary cycle, aided by contraction of the dorsal sac, gases are moved cranially into the reticulum while the raft and fluids are pushed ventrally. If and when the gas layer clears the cardia of its fluid, eructation is evoked.

Fermentation

The primary sites of microbial fermentation within the digestive tract of goats are the rumen and reticulum. The host animal and the diverse population of microbes in a symbiotic relationship ferment feeds yielding products that are useful nutritionally. Microbes that inhabit the rumen and reticulum, being provided with the unique anaerobic environment by the host ruminant discussed above, perform several functions: (1) fermentation of structural (cellulose and hemicellulose) and nonstructural (sugars and starch) carbohydrates into readily metabolized energy sources such as volatile fatty acids, (2) conversion of nonprotein nitrogen from plants and metabolically recycled urea to a high biological value microbial protein, (3) synthesis of vitamin K and most B complex vitamins, and (4) conversion of metabolically recycled phosphate to microbial nucleic acid and membrane phospholipids.

Effect of Diet on Microbial Fermentation

The amount and composition of feed consumed can alter the microbial population and distribution of types found in the reticulo-rumen. Thus, diet can impact rate of digestion, rate of passage, and retention time of digesta in the rumen. Feeds rich in protein can alter the microbial populations to predispose an animal to fermentation disturbances such as ammonia toxicity or other toxins in the feeds. Diets rich in protein stimulate growth of protein-digesting (proteolytic) microorganisms. High fiber diets will increase the proportion of cellulose digesting (cellulolytic) microorganisms within the rumen, and high starch diets promote growth of starch-digesting (amylolytic) microorganisms. Diets rich in protein and starch (up to 80% concentrate diets) are associated with higher fermentation rates, higher digestibility of dry matter, and possibly improved intake. However, diets that contain less than 15% roughage tend to have a negative impact on fermentation and digestion (Vieira et al., 2008) by goats. High concentrate diets lead to greater production of fermentation acids in the reticulo-rumen and place a greater load on rumen buffering system. Goats like other ruminants have more tolerance to downward than to upward shifts in rumen pH (Silanikove, 2000). Generally, methane-producing (methanogenic) and cellulolytic microorganisms in the rumen are more sensitive to lower rumen pH and have a reduced prevalence under such conditions.

Nitrogen, sulfur, and essential minerals must be supplied for optimum microbial fermentation in the reticulo-rumen both for microbial growth and protein synthesis and for fiber digestion. Saliva provides buffering via bicarbonates of sodium and potassium. Through hydrolysis to ammonia, salivary urea also provides buffering for rumen contents. These components must be at optimum levels for optimum rates of digestion and feed intake.

Passage rate of feed residues from the rumen is associated with the plant cell wall content of the diet, action of microorganisms, and rate of particle size reduction. When passage rate is high, more slowly available substrates such as cellulose will escape ruminal digestion leading to a lower extent of fiber digestion. Grinding or pelleting feeds will increase passage rates of particles and thereby will negatively impact fiber digestion relative to feeding long particle forage. Because performance generally is proportional to intake of digested dry matter, a compensatory increase in feed intake may counterbalance this negative impact on digestibility and lead to improvements in both rate and efficiency of gain.

Types of Microorganisms in the Rumen

Microorganisms in the rumen are either facultative or strict anaerobes. A limited supply of oxygen can be tolerated so long as it is actively removed by facultative anaerobes. Because ruminal microbes are obligate anaerobes, inoculation or cross-inoculation from one animal to another via feed, saliva, or air is limited. Inoculation of protozoa can be prevented by maintaining an animal in isolation, but inoculation by bacteria is impossible to prevent. Fecal contamination appears to be the major source of anaerobic fungi in the reticulo-rumen.

Active fermentation in the reticulo-rumen requires semicontinuous influx of substrates and a specialized group of bacteria. Although the majority of rumen bacteria are obligate anaerobes, some facultative anaerobes exist in the rumen and may play roles in rumen dysfunction. Although bacteria at some 10^{10} to 10^{11} bacteria per ml, can account for about half of the rumen biomass, they are responsible for most of the fermentation within the rumen. Larger organisms (protozoa at 10^4 to 10^6/ml) can account for the other half of the biomass in the rumen, but they play a smaller but yet significant role. In addition, fungi can be found within the rumen (Van Soest, 1994).

Bacteria within the reticulo-rumen are diverse and specialized according to the substrates used, the products formed, or their nutrient requirements. The primary groups of rumen bacteria are those that degrade diet components while a secondary group will use end-products of the primary groups as substrates. Functions within these primary groups overlap considerably. The secondary groups (more than 60% of the total) are very important for adjusting fermentation output, providing growth factors for the primary groups, and maximizing efficiency of fermentation. Major primary bacterial and protozoan species found in the rumen are shown in Figure 8.1.

Fermentation of Fiber

The primary cellulolytic bacteria have the unusual capacity of being able to hydrolyze the β1,4 linkages of plant polysaccharides and convert released cellobiose (2 glucose units with a β1,4 linkage) and glucose into volatile fatty acids (VFA) and a transient intermediate formate. Cellulose and starch are converted to glucose, fructosans to fructose, and hemicellulose and pectin to xylose, as transient intermediates. These intermediates are converted

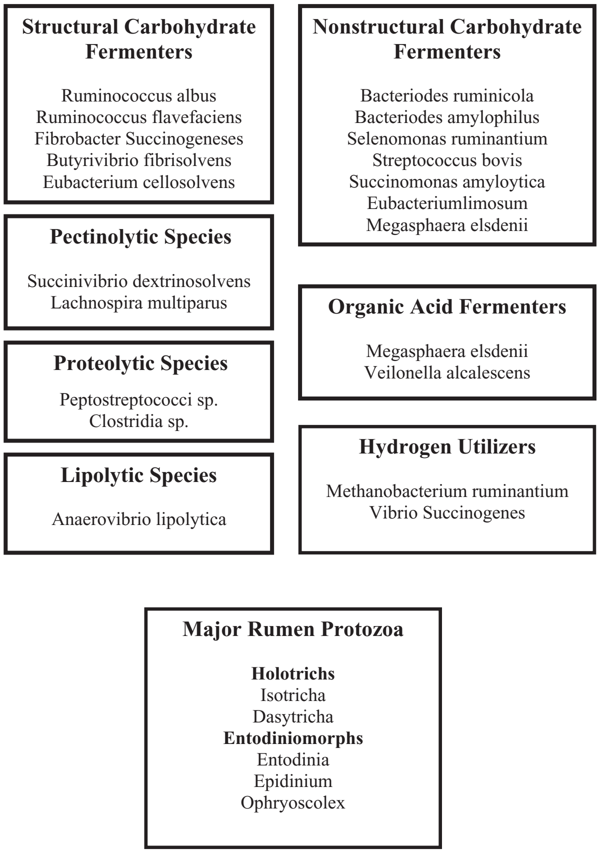

Figure 8.1 Major rumen microorganisms, bacteria and protozoa (adapted from Van Soest, 1994).

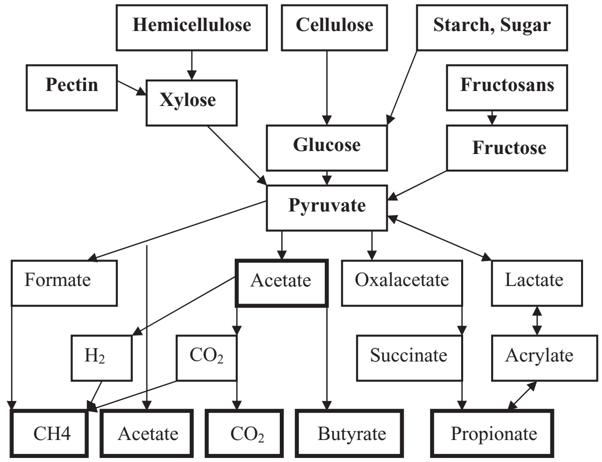

Figure 8.2 Carbohydrate metabolism in the rumen.

further anaerobically to phosphoenolpyruvate (PEP) and pyruvate. Acetate and to a lesser extent butyrate and formate (as a transient intermediate) originate from pyruvate. Via β-OH butyrate, pyruvate yields butyrate. Oxaloacetate and succinate serve as transient intermediates leading to propionate while lactate and acrylate also yield propionate. Propionate production via oxaloacetate to succinate is the most common pathway used by rumen bacteria for producing propionate although production via acrylate is a highly efficient pathway favored when animals consume a high grain diet. *Megasphaera elsdinii*, a secondary fermenter, may be the main organism responsible for this pathway. Methane, generated when acetate and butyrate are formed, and propionate are products of secondary fermenters, and their production is important in optimizing fermentation. Secondary methanogenic bacteria convert formate to methane (Figure 8.2).

Cellulolytic bacteria generally have low metabolic rates and higher generation intervals (18 hours). Fermentation is slow and may require B vitamins, minerals, NH_3, CO_2, branch chain fatty acids, and a proper pH (6.2–6.8). This pH requirement matches the pH in the rumen of ruminants fed forage-based diets. Small amounts of iso-acids are required as growth factors for cellulolytic bacteria when grown in culture. These iso-acids are isobutyrate, isovalarate, and 2-methylbutyrate that arise from deamination of branched chain amino acids of valine, leucine, and isoleucine, respectively. However, diet supplementation with iso-acids is seldom needed because these acids are available due to crossfeeding from other bacteria and regularly available from protein catabolism. The typical acetate : propionate : butyrate ratio generated from fermentation of cellulose fermentation is 70 : 15 : 10.

Fermentation of Starch

Primary amylolytic bacteria hydrolyze α1,4 and α1,6 linkages in starch (amylose and amylopectin) to form maltose, isomaltose, and glucose and converting them to VFA, metabolic acids (lactic acid), and formate as a transient intermediate. Although substrates and bacterial species differ, the fermentation pathways generally are similar to those described for fiber fermentation. Amylolytic bacteria have higher metabolic rates and lower generation intervals (15 minutes to 4 hours). Fermentation is rapid and requires NH_3, amino acids, and a proper pH (5.5–6.6). This pH optimum matches the ruminal pH of ruminants fed diets rich in grain. The typical acetate :

propionate : butyrate ratio from starch fermentation is 55 : 25 : 15.

Secondary groups of rumen bacteria convert formate to methane and lactic acid or other acids to propionate. Secondary fermenters have lower metabolic rates, higher generation intervals (16 hours), and a higher optimum pH (6.2–6.8) than amylolytic bacteria. Therefore, when an animal is abruptly transferred to high concentrate diet, rapid fermentation often leads to high acid (lactic acid) production and a rumen pH lower than optimum for amylolytic bacteria but too low for secondary fermenters. Hydrogen disposal is hindered, acids accumulate, and clinical or subclinical rumen acidosis can occur.

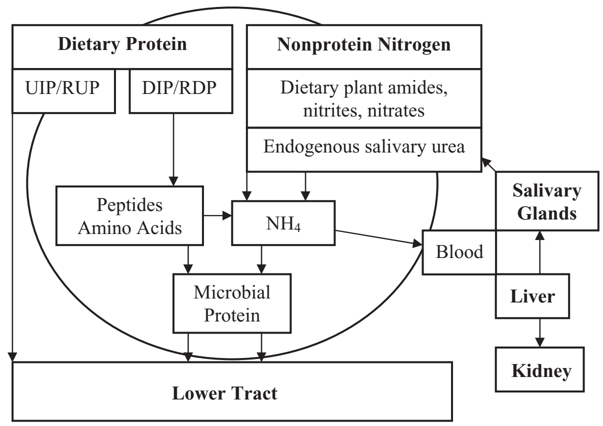

Figure 8.3 Protein and nonprotein nitrogen metabolism in the rumen.
UIP = undegraded intake protein;
RUP = ruminally undegradable protein.
DIP = degradable intake protein;
RDP = ruminally degradable protein.

Fermentation of Proteins

Proteolytic bacteria represent a small portion (12–38%) of total reticulo-rumen bacterial mass and are responsible for ammonia production. Ammonia is required for growth of many cellulolytic and amylolytic bacteria. Peptides, amino acids, and isoacids may be stimulants for their growth and activity. The main dietary substrate for this group of bacteria is dietary protein that can be divided into two classes: ruminally degraded protein (RDP) or degraded intake protein (DIP) and ruminally undegraded protein (RUP) or undegraded intake protein (UIP). The later generally passes to the lower tract undegraded by rumen microorganism. Generally about half of the dietary protein is degraded in the rumen. Extracellular proteases from bacteria degrade dietary protein to yield peptides, amino acids, and ammonia. Amino acids can be used by some ruminal microbes, but most can synthesize their own amino acids from ammonia. When protein supply is high, bacteria readily degrade it yielding ammonia and various metabolic acids. Amino acids are deaminated to keto acids that are fermented to VFA and small amounts of the branched chain VFA—isobutyrate, iso valerate, and 2-methylbutyrate—that arise from valine, leucine, and isoleucine, respectively. Dietary plant amides, nitrites and nitrates, and endogenous salivary urea (nonprotein nitrogen compounds) when fermented also yield ammonia. Bacterial urease activity is high in the reticulo-rumen and readily converts dietary or recycled urea to ammonia. Urea is an important substrate for microbial protein synthesis. The capacity of rumen microbes to use ammonia and convert it to microbial protein depends on the availability of energy, largely from carbohydrate fermentation. The greater the supply of fermented carbohydrate, the greater the ammonia uptake and synthesis of bacterial mass.

Conversion of peptides via amino acids to ammonia is a slow process of oxidative deamination of amino acids. This process requires the transfer of hydrogen via NADH. Ionophores inhibit proteolytic activity in the rumen either through inhibiting transfer of hydrogen needed for deamination of amino acid and ammonia formation, or by alteration of rumen microflora. Because peptides and amino acids are degraded in the rumen, flow of nitrogen to the abomasum and intestines consists largely of undegraded dietary protein and microbial protein (Figure 8.3).

Diet formulators seek to balance the supply of readily available carbohydrates and proteins in the diet to ensure that an adequate supply of ammonia (for protein synthesis) and carbohydrate (for energy) are available for microbial protein synthesis but to avoid excessive protein that will be wasted. Excessive production of ammonia, particularly from nonprotein nitrogen (esp., urea) will increase the risk of ammonia toxicity. Energetically, protein degradation in the rumen is wasteful, and for the animal, energy is required to convert ammonia to urea within the liver and for the kidneys to excrete urea.

Fermentation of Lipids

Ruminants fed forage-based diets typically consume only a small amount (3–7% dry matter [DM]) of structural lipids in the plant leaves. The majority of these lipids are phospholipids and galactolipids with less than 50% being triglycerides that in turn are composed of free fatty acids, mainly palmitic, linoleic, and linolenic. Diets often contain oilseeds that consist primarily (65–80%) of triglycerides that contain the free fatty acids palmitic, oleic, and linoleic. Reticulo-rumen microbes rapidly hydrolyze dietary lipids and synthesize their own body lipids. They hydrolyze triglycerides to form glycerol and respective fatty acids and galactolipids to galactose. Glycerol and galactose are fermented to VFA. The majority of fatty acids is neutralized with calcium and adheres to the surface of bacteria or feed particles (McAllen et al., 1983). Unsaturated fatty acids are saturated, and the positions of the remaining double bonds are distributed along the chains. Hydroxylation of fatty acids and production of keto acids also occurs. Trans fatty acids are more stable, have higher melting points, and are difficult to hydrogenate, resulting in higher concentrations than their counterpart cis acids. Saturated fatty acids are not degraded further but pass to the abomasum as calcium salts. Because unsaturated fatty acids are largely hydrogenated within the rumen, the supply of fatty acids available for absorption from the small intestine (SI), are largely saturated. This contributes to the more saturated nature and higher melting point of tallow (ruminant fat). Biosynthesis of microbial fats in the reticulo-rumen can involve formation of odd and branched chain fatty acids. Fatty acids with 15 carbons and branches are found in microbial lipids.

Metabolism of lipids in the anaerobic environment of the reticulo-rumen is quite limited. Diets with more than 7% of DM as fat may reduce methanogenic and cellulolytic fermentations. Although unsaturated fatty acids do not compete directly with methane production, they serve as a separate sink for excess hydrogen and indirectly reduce methane production. Ionophores added to the diet similarly inhibit hydrogen transport, increase the prevalence of propionate, and may inhibit lipid hydrolysis in the rumen.

Other Fermentation Products

Microbes in the reticulo-rumen synthesize the B-vitamins provided an adequate amount of cobalt for B_{12} synthesis, and an adequate supply of sulfur is available for synthesis of biotin and thiamin. For synthesis of sulfur-containing amino acids (methionine, cystine), sulfur also is required. This can become critical for fiber production because wool and mohair are rich in cystine and cysteine, amino acids that contain sulfur. By complexing with sulfur and reducing its availability, molybdenum and copper can reduce sulfur availability and induce a deficiency. Conversely, excess sulfur complexing with copper can reduce copper availability. A cofactor for tyrosinase, copper is needed for melanin (pigment) formation and the normal crimp in wool, so a deficiency can reduce hair coloration and cause wool to become straight and steely. Rumen microbes are beneficial through partially hydrolyzing oxalates and phytates to increase mineral bioavailability from plants and in addition can detoxify many plant metabolites that are toxic for nonruminants.

Rumen Protozoa and Fungi

Two main groups of ciliate protozoa are found in the rumen. The entodiniomorphid protozoa engulf particles and together with attached or internal bacteria can hydrolyze some structural carbohydrates (cellulose and hemicellulose). Bacteria associated with protozoa may contribute as much as one-third of the total rumen cellulolytic activity. The holotrichs prefer nonstructural carbohydrate such as starches and sugars. Entodiniomorph protozoa also consume and digest bacteria as substrate and use bacterial amino acids for producing protozoal protein. The end-products of protozoal fermentation in the reticulo-rumen include organic acids, CO_2, ammonia, and hydrogen. The extent to which protozoa can digest fiber and synthesize amino acids is unclear because ruminal bacteria always are so closely associated with protozoa so that cultures of ruminal protozoa free of bacteria have never been grown.

Although protozoa are not necessary for rumen fermentation, their role in balancing the fermentation process in the ruminants must not be underestimated. Protozoa engulf starches and sugars to retard rapid fermentation and thereby reduce the prevalence of lactic acidosis. Engulfed starches and sugars can pass to the abomasum and intestines digestion by the host. These are favorable functions of protozoa. Major rumen protozoa are listed in Figure 8.1.

Anaerobic fungi also are present in the rumen, but their contribution to the ruminal microbial mass is quite small, and their turnover rate is slow and similar to that of protozoa. Fungi usually are associated with slowly passed forage particles. Fungi prefer lignified coarse cell walls as a substrate, and contribute to VFA, gases, traces of ethanol, and lactate in the rumen. Their contribution to the rumen digestion is not yet fully understood.

The Fate of Fermentation End-Products

The main end-products of carbohydrate fermentation are acetic, propionic, and butyric acids. Fermentation of protein also yields these VFA plus valeric acid and branched chain VFA and ammonia. Branched chain VFA deficiencies for microbial protein synthesis would be more likely when dietary crude protein comes largely from nonprotein nitrogen (NPN).

Volatile fatty acids, being weak acids (pK = 4.75 – 4.87), they almost entirely dissociated in the reticulo-rumen at pH 6.6. About one-half of the VFA are absorbed through reticulo-rumen epithelium in their nondissociated form by passive diffusion with absorption rates being correlated positively with length of the VFA and negatively correlated with the rumen pH. The remaining VFA are absorbed as anions by facilitated diffusion in exchange for bicarbonate ions. Epithelial cells of the rumen contain carbonic anhydrase to promote production of carbonic acid from CO_2 and water. Carbonic acid in turn is dissociated into bicarbonate and H ions. These hydrogen ions convert VFA anions into acids for passive diffusion through the rumen epithelium. Transfer of hydrogen from carbonic acid (a weaker acid) to form VFA (stronger acids) lowers the pH and promotes further VFA absorption. Bicarbonate ions released into the rumen during absorption will neutralize more than half of the VFA in the rumen. The remaining VFA are neutralized largely by salivary alkali.

During absorption, some VFA are metabolized. Most of the butyrate is converted to β-hydroxybutyrate (β-OH-BUT) with the remainder being similarly metabolized by the liver. Thus, absorbed butyric acid enters the circulation as β-OH-BUT for metabolism by most ruminant tissues as a source of energy as well as fat, being the four-carbon primer used for synthesis of short and medium chain fatty acids unique to the ruminant's milk fat.

Almost one-third of the propionic acid absorbed is metabolized by the rumen wall to lactic acid. Propionate is completely converted by the liver to oxalacetate and that enters the Kreb's cycle. Lactate is converted to glucose for storage as glycogen by the liver or released as glucose into the circulating portal blood. Propionate and valerate are the only VFA used for gluconeogenesis.

The majority of acetate enters circulating portal blood unchanged except for a small amount that is metabolized to CO_2 by the rumen epithelium. The most abundant VFA in the blood, acetate, is readily used by tissues to form Acetyl-Co-A that yields energy via the Kreb's cycle or forms fatty acids. Mammary tissues use acetate and β-OH-BUT to form the short and medium chain length fatty acids found in milk.

Lactic acid produced by amylolytic bacteria is present as a transient acid in low concentration, and can be used by secondary rumen bacteria to produce propionate. However, the low rumen pH associated with high concentrate diets may inhibit propionate producing bacteria more than amylolytic bacteria; this can result in an accumulation of both isomers of lactic acid (+) and (–) that accentuates the rumen pH decline resulting in ruminal acidosis. Lactic acid absorption rate from the rumen is only one-tenth that of VFA. The liver metabolizes the L (+) lactic acid isomer more rapidly than the D (–) isomer. L lactic acid also is produced by muscle tissue during anaerobic exercise, but D lactic acid is primarily a product of bacterial metabolism found in fermented feeds including silages at up to 10% of dry matter.

Ammonia is produced in the rumen from deamination of dietary proteins, or hydrolysis of dietary NPN or urea from saliva, or diffusing into the rumen from blood. Given an adequate supply of energy from fermented carbohydrates, ammonia is used for synthesis of microbial protein. Excesses of ammonia are absorbed through the rumen wall, readily removed from portal blood, and detoxified by the liver by conversion to urea. Ammonia that escapes liver metabolism (for example, absorbed by the lymphatic system) can prove toxic for ruminants.

Gas production in the reticulo-rumen peaks some 2–4 hours after feeding. The major rumen gases include carbon dioxide (60%), methane (30–40%), and nitrogen, with small amounts of hydrogen sulfide, hydrogen, and oxygen. Carbon dioxide is produced either by decarboxylation during fermentation, or by neutralization by acids of bicarbonate ions that enter the rumen via saliva or exchange across the rumen wall during VFA absorption. Methane is produced from reduction of CO_2 and formate. Loss of methane from the rumen accounts for about 6% of ingested energy. Methane is a contributor to global warming, so reducing methane production by ruminants and by anaerobic bacteria in wetlands, and by release from petroleum are of worldwide concern. Hydrogen sulfide, being toxic to rumen microbes and animals, is produced from ruminal reduction of sulfates in the diet or derived from amino acids that contain sulfur. Hydrogen, present in only small amounts in the rumen, can increase when animals are abruptly switched to a high concentrate diet and fermentation is abnormal. Oxygen enters the rumen together with ingested feed and water and by diffusion into the rumen from blood; it is quickly removed by facultative ruminal bacteria.

Practically no peptides or amino acids are flushed onto the abomasum or small intestine because they are rapidly catabolized by ruminal bacteria. However, the feed and microbial proteins that pass out of the reticulo-rumen undergo lysis by abomasal lysozyme. Microbial proteins, lipids, vitamins, and starch are digested in the intestines and make a substantial contribution to the nutrient supply of the host.

FUNCTION OF OMASUM

The role of omasum in digestive physiology of ruminants is briefly summarized in this section, but further information is presented in Chapter 6. Size of the omasum is considerably larger for cattle than for goats. It is an additional site for fermentation and absorption, but its primary function appears to be regulation of the flow of digesta from the reticulo-rumen to the abomasum. Ingesta from the reticulum flows to the omasum through the reticulo-omasal orifice that is open during the secondary phase of the primary cycle contractions of the reticulum. Prolonged and powerful contractions of the omasal body tend to empty the materials trapped between leaves into the abomasum. Particle size of digesta in the omasum (about 1 mm) is similar to that found in the reticular area adjacent to the orifice, and its physiochemical conditions resemble those of the cranial and ventral regions of the reticulo-rumen. The omasum has a large surface area (leaves) relative to its volume, a factor that gives this organ a large capacity for absorption of VFA, electrolytes, and water. In this organ, chloride (instead of bicarbonate) plays a major role in VFA absorption.

FUNCTION OF ABOMASUM

The abomasum or "true stomach" receives more or less continuous (but at variable rates) input of ingesta containing partially fermented materials, fluids, or particle clumps (of variable composition) from the omasum and, following acidification, passes digesta in a reasonably constant flow to the duodenum. The abomasum plays two important roles in ruminant digestion: (1) transfer of partially digested feed and (2) chemical and enzymatic breakdown of ingesta. The cardiac and fundus regions of the abomasum are responsible for nonacid secretion while the antrum/pyloric region secretes acid.

Distension of the pyloric region, a rise in abomasal pH, and presence of VFA and lactic acid all serve to stimulate gastric secretions and contractions. The presence of acidic conditions and fat in the duodenum inhibit gastric motility and gastric emptying. The G cells in the pyloric gland area release gastrin hormone into the blood that stimulates parietal cells to release hydrochloric acid. Feedback control of acid release comes from a low pH (approaching pH = 2) of gastric contents that stimulates release of somatostatin. A low duodenal pH also can inhibit acid release, likely through inhibiting gastric emptying.

Pepsinogen, an inactive proteolytic enzyme, is released by chief cells of the gastric mucosa. Pepsinogen is autolytically activated and converted to pepsin in the presence of hydrochloric acid. In addition, lysozymes catalyze the hydrolysis of specific glycosidic bonds in mucopolysaccharides that constitute some bacterial cell walls. Ruminant animals secrete large amounts of specially adapted lysozymes into the abomasal lumen. Active at low pH, lysozymes resist pepsin digestion. Acid, pepsin, and lysozymes chemically and enzymatically digest microbial protein and other digesta, preparing the chyme to enter the duodenum for further digestion.

INTESTINAL DIGESTION

Acidic chyme (a mixture of partially digested feeds and digestive juices) enters the duodenum for further enzymatic digestion in and absorption of monomers from the SI. Since the SI is a primary site for both digestion and absorption, luminal flow is regulated so as to provide mixing of luminal contents with digestive juices, time for luminal digestion of nutrients, and exposure of digested nutrients to the intestinal wall for absorption.

Presence of acid in the duodenum provides the stimulus for the intestinal wall to release the hormone secretin in the portal blood that in turn stimulates the pancreas and gallbladder to release bicarbonate-rich fluid into the duodenum to partially neutralize acidic chyme. Cholecystokinin (CCK) from the SI wall is released in the presence of fats or proteins in the duodenum to stimulate the pancreas to release enzyme-rich digestive juices (and some bicarbonate) and the gallbladder to release bicarbonate as well as bile acids and salts. The pancreas secretes all of the enzymes necessary to digest lipids, proteins, and carbohydrates; however, in ruminants most (50–90% of starch) of the readily available carbohydrates and lipids (small amounts of triglycerides and galactolipids in the diet) are cleaved to free fatty acids in the rumen so supply of these nutrients is limited. This may explain why pancreatic juice of ruminants is not rich in lipolytic and amylolytic enzymes.

Pancreatic proteolytic enzymes are secreted in proenzyme form, being exopeptidases such as carboxypeptidase A and B or endopeptidases such as trypsinogen, chymotrypsinogen, and elastase. Trypsinogen is activated by intestinal enterokinase to form trypsin that in turn activates remaining trypsin and other proenzymes. The end-products of pancreatic proteolytic digestion are amino acids and oligopeptides (up to 6–10 amino acid chain). Amino acids and some oligopeptides are actively transported into the epithelial cells where more than 90% of the oligopeptides are hydrolyzed to amino acids and actively transported into the blood. The remaining 10% of dipeptides and tripeptides may diffuse directly into the bloodstream.

Sucrose is not digested in the small intestine, but most will be fermented before reaching the small intestine.

Starch is hydrolyzed by pancreatic amylase to maltose while maltase and isomaltase are hydrolyzed to glucose that is actively absorbed. This process is facilitated by the intestinal enzyme maltase present at the brush border of the epithelial cell.

Digestion of lipids (rumen protected) begins by emulsification of fats as they combine with bile acids/salts and form micelles (hydrophilic outer side). Pancreatic lipase then hydrolyzes emulsified triglycerides to form β-monoglycerides and free fatty acids that can diffuse into epithelial cells. Ruminants may absorb triglycerides without further digestion (Wrenn et al., 1978). In the intestinal epithelial cells, fatty acids and monoglycerides are re-esterified to form triglycerides. Combined with cholesterol, cholesterol esters, phospholipids, and a small amount of proteins (lipoproteins), they form chylomicrons for uptake into portal blood and transport. Under most conditions supply of triglycerides is limited because most lipids have been hydrolyzed to glycerol and fatty acids in the rumen, and unsaturated fatty acids also have been saturated therein.

Soluble vitamins and minerals are primarily absorbed from the SI though some are absorbed from the large intestine. Within the colon of ruminants, fermentation may begin again (postgastric fermentation), but the extent of fermentation is limited because chyme already has been fermented in the rumen and enzymatically digested in the SI. However, water and some electrolytes are absorbed in the small and particularly in the large intestine of animals selected under desert conditions with limited access to water.

DIGESTION IN YOUNG RUMINANTS

Newborn Phase

When born, ruminants have a small, nonfunctional forestomach with no microorganisms and no acid or pepsinogen secretion. Colostrum directly enters the abomasum and flows to the duodenum where immunoglobulins (IgM antibodies, γ-globulin) are absorbed intact through phagocytosis by the intestinal mucosa. Colostrum contains an antitrypsin factor that prevents digestion of antibodies within the duodenum. Through this process, the newborn kid develops immunity to most diseases to which the adult doe had been exposed. This absorption proceeds for only some 24–48 hours after birth. Colostrum also provides nutrients including lactose and some microbes (lactobacilli). Limited energy reserves due to limited glycogen storage by the liver and inefficient use of lactose as a source of energy are the main causes of death in newborn kids. Exposure to the dam, to fecal matter, and to the environment readily exposes newborn kids to aerobic and anaerobic microbes, the latter eventually colonizing the rumen.

Preruminant Phase

During this period (up to 3 weeks of age), the newborn is nursing. Most milk bypasses the rumen and flows directly through the reticular groove of the reticulo-rumen to the omasum and abomasum. Sucking stimulates salivary and abomasal secretion more than drinking from a bucket. Saliva of the newborn contains esterase, and the abomasum secretes rennin (chymosin) and hydrochloric acid at this stage of life. Exposed to rennin, milk clots and separates into a hard curd containing butterfat and protein curd (casinogen) that remains in the abomasum for digestion. The remaining whey fraction (albumins, globulins, lactose) leaves the abomasum in bursts. Butterfat is hydrolyzed to glycerol and fatty acids by lipase originating either from milk (mammary glands) or from estrase in saliva. Curd proteins are exposed to further hydrolysis by rennin and acid. In the intestine, the curd, whey proteins, and lactose are completely digested. The intestine of newborns has low maltase activity and therefore cannot fully utilize starch. Intermediary metabolism is driven by glucose, and blood glucose concentrations are sensitive to insulin.

Transitional Phase

In this phase (3–8 weeks of age), young ruminants will ingest progressively larger amounts of roughages and dry food. These stimulate development of salivary glands and the reticulo-rumen. A population of ruminal microbes becomes established due to ingestion of food, water, cud, fecal matter, and other environmental contaminants. Fermentation of feeds produces VFA that stimulate the growth of reticulo-rumen papillae and omasal leaves. To handle the gases produced and larger particles, the muscle wall has the rumen development and rumen motility initiating the processes of eructation and rumination. As this development progresses, intermediary metabolism shifts from a glucose driven- to a VFA-driven system that is less insulin-sensitive.

Pre-weaning and Post-weaning Phase

During this period (8 weeks to adulthood), reliance on milk reduces because milk production by the doe decreases. Reticular groove closure becomes erratic and usually is absent in adults. The forestomach proportions and motility change to attain those of an adult, salivary esterase diminishes and salivary urea is present, and abomasal rennin is replaced by pepsinogen, all of which reflect inborn physiological changes allowing the newborn and preruminant to becomes a functional ruminant.

RUMEN DYSFUNCTION

The major digestive disorders common to ruminants will be discussed briefly. Readers are referred to a more detailed discussion of these problems in textbooks on veterinary physiology (Reece, 2004). Because most dysfunctions reflect specific aberrations in normal rumen function, such discussion helps to reinforce the reader's knowledge about normal rumen function.

Bloat

Bloat is defined as the distension of the reticulo-rumen associated with accumulation of gases produced by fermentation of certain feeds with failure in gas removal by eructation. Bloat is not common in free ranging ruminants consuming grasses but is manifested by mismanagement of the animal and the diet. Van Soest (1994) divided bloat into two types: legume or frothy bloat, and grain bloat that may be either acute or chronic. Legume or frothy bloat usually is associated with animals grazing rapidly growing legume (alfalfa or white clover) pastures grown in temperate climates. Proteins involved with carbon dioxide fixation apparently uncoil and float to the top of the rumen, and this leads to a foam or froth that traps gas in a form that cannot be eructed. Tropical legumes, temperate trefoil, vetch, or sanfoin contain higher amounts of tannins that precipitate proteins. This prevents formation of stable foam. Grain bloat usually is the result of feeding high grain diets (typically wheat and barley) and pelleted feeds. High concentrate diets that have a very small particle size from grinding and pelleting are often implicated. Such feeds are associated with less saliva production per unit of feed and less salivary mucin that helps protect animals from bloat. High amylolytic activity that produces rumen acids (lactic acid) also may reduce rumen motility to promote bloat. Grain bloat is commonly chronic while legume bloat usually is acute. Acute bloat causes death by placing pressure on the heart or blood vessels preventing flow that results in cardiovascular collapse. Oils or detergents that reduce surface tension help to suppress foam formation. In severe cases the rumen can be punctured to release gases as a last resort. Goats, being intermediate food selectors, have relatively larger salivary glands and their habit of browsing helps makes them more resistant to bloat.

Acidosis

Acidosis is defined as an imbalance in rumen fermentation elicited by abrupt introduction of rapidly fermented carbohydrates (starches and sugars) to the diet. When an animal is fed a high concentrate feed without being adapted, rapid fermentation by facultative bacteria produces lactic acid and reduces the rumen pH into a range favorable for amylolytic bacteria. Under normal circumstances, secondary rumen bacteria convert lactic acid or other acids to propionate. But secondary fermenters have lower metabolic rates, higher generation intervals (16 hours), and a higher optimum pH (6.2–6.8) than amylolytic bacteria. Therefore, hydrogen disposal is hindered, acids accumulate, and rumen acids accumulate. Rumen pH may drop as low as 4 and cause rumenitis and rumen parakeratosis, a condition where the rumen epithelium is sloughed from the basal membrane. Lactic acid may be absorbed through the rumen wall into the blood and carried to the liver where the natural L (+) lactate form can be metabolized, but the bacterial form of lactate (the D [–] isomer) may accumulate in the blood causing systemic acidosis and death from a reduced oxygen carrying capacity of hemoglobin. Treatment often involved dosing with bicarbonate buffers while prevention involved feeding more roughage, particularly long hay that induces rumination and saliva production. In severe cases, the rumen may be partially or fully evacuated and replaced with fresh rumen fluid from a healthy animal.

Displaced Abomasum

Ruminants fed finely ground, very high concentrate diets tend to have highly acidic and fluid ruminal digesta with little fibrous material. High acidity and low fiber content of digesta reaching the abomasums is associated with reduced motility and altered gastric function. Impaired motility causes abomasal distension. The abomasum may become engorged with fluids and gas and become displaced laterally. Left displacement is associated with a chronic condition, whereas right displacement is associated with blockage of digesta flow and may prove fatal. The actual cause of this symptom is not clearly understood, but its association with high starch, fine particle diets has been documented.

Urea/Ammonia Toxicity

Urea or ammonia toxicity usually occurs when an excessive amounts of urea is consumed by an animal. Animals grazing lush forage pastures with highly soluble proteins also may be at risk. Bacterial urease rapidly hydrolyzes urea-forming ammonia. In the presence of an adequate supply of readily available carbohydrates such as starch and sugars that are rapidly fermented (amylolytic fermentation), rumen microbes will use available ammonia to produce microbial protein. However, when supply of energy is low, microbial use of ammonia for protein synthesis will be reduced. When ammonia accumulates in the rumen, this increases ruminal pH. An elevated pH increases the amount of ammonia in the un-ionized, absorbable form exacerbating ammonia absorption. The liver can detoxify ammonia by converting it to urea, but some ammonia may bypass the liver through uptake into the lymph system and enter the blood directly. Ammonia toxicity is associated with systemic alkalosis that, probably through altering calcium and magnesium status, intoxicates the central nervous system. Preventive measures include avoiding high urea diets or feeding readily fermented carbohydrates when feeding urea or when animals graze lush, rapidly growing, high protein pastures. Ruminal bacteria adapted to urea form ammonia less rapidly, so adaptation is recommended. Finally, chemical inhibitors of urease or slow release urea complexes can slow the rate of ammonia production and will help avoid toxicity. Treatments include administering VFA (vinegar) to lower rumen pH and reduce the rate of absorption of ammonia. In severe cases, rumen evacuation may be necessary.

Nitrite-Nitrate Toxicity

Nitrite/nitrate toxicity occurs when ruminants consume forage from stressed, often overfertilized grass pastures and crops. Such plants accumulate nitrate as its potassium salt. Accumulation by plants is enhanced by drought and, with cool-season grasses, by low temperature and cloudiness (low light). Nitrate itself is not toxic, but during normal rumen fermentation, nitrate is reduced to nitrite (a toxic intermediate). Nitrite can be converted further into ammonia that in turn can be used to produce microbial protein. If the nitrite intermediate accumulates in the rumen, it is absorbed into the blood and there it unites with hemoglobin and produces methemoglobin. Compared to hemoglobin, methemoglobin has a reduced ability to transport oxygen, and impaired oxygen delivery to tissues will cause death by asphyxiation. Gradually increasing the nitrate concentration of the diet will permit microbes or animals to adapt to nitrate and increase their tolerance to it.

SECONDARY PLANT METABOLITES

Certain compounds found in feeds, forbs, and browse are produced as defenses against invasion by pathogens and, in some cases, against consumption by herbivores. Compared with cattle and sheep, goats have a very high tolerance to such compounds.

Organic Nitro Compounds

Glycoside compounds found in various *Astragalus* species such as crown vetch (Coronilla varia L.) and timber milkvetch (Astragalus miser varia T.) are rapidly hydrolyzed in the rumen producing toxic nitro compounds, that is, 3-nitropropionic acid (NPA) and 3-nitroproponal (NPOH). These compounds can be metabolized in the rumen or absorbed. NPA is toxic while NPOH is converted to NPA by the liver. Rumen microbes may partially metabolize these compounds by reduction of aliphatic nitro groups to their corresponding amines, 3-aminopropanol, and β-alanine, respectively. This explains why ruminants have greater tolerance to these compounds than nonruminants do.

Mimosine Toxicity

Mimosine is an alkaloid, β-3-hydroxy-4 pyridone amino acid, found in genus Leucaena and few other Mimosa species. Leucaena is a legume shrub/tree that provides a high quality feed in certain areas of the tropical and subtropical regions of the world. However, when these feeds comprise more than 30% of the diet, they may cause severe toxicity. Goats may lose hair when fed more than 50% leucaena in the diet. Rumen microbes convert mimosine to 3,4 dihydroxy pyridone (3,4 DHP), a toxic goitrogenic intermediate. However, certain strains of bacteria found in tropical ruminants can degrade mimosine to nontoxic products. Toxicosis has been reported in Australia, Papua New Guinea, Africa, and Florida. Pure colonies of bacteria that can degrade 3,4 DHP were isolated (*Synergestes jonesii*) and have been inoculated successfully into the rumen, increasing tolerance to mimosine (Hammond, 1995).

Tannins

Condensed tannins (CT) are polyphenolic compounds present in plants that when eaten may have either positive or negative effects on animals depending on the concentration in the forage and ability of the rumen environment to degrade tannins. Proline rich proteins present in the saliva of certain herbivores including goats bind tannins and reduce their adverse effect on rumen microorganisms. However, the complexes formed are indigestible and are excreted in the feces (Hagerman et al., 1992). Condensed tannins at low levels, 2–5% of dry matter (DM), will bind with ruminally degraded proteins to increase the supply of protein reaching the SI and, when digested, these proteins can improve the amino acid balance of animals. However, higher levels of CT (above 5% of DM) generally have negative effects on ruminal digestion and decrease digestibility. Tannins have shown promise as an anthelmintic for combating nematode infestation of small ruminants in humid and warm environments (see Chapter 11 for more details). This topic deserves further research attention.

METABOLIC DISORDERS

Most prominent disorders are caused by improper feeding management and nutrient imbalances in the feeds offered to goats. Animals selected for rapid growth or high rates of milk production may have a genetic predisposition to these disorders.

Grass Tetany or Hypomagnesemia

Grass tetany is a metabolic disorder associated with hypomagnesemia (low magnesium concentrations of blood). This condition is most prevalent when animals are milking heavily and have a higher requirement for magnesium or early in spring when animals are grazing rapidly growing pastures that are heavily fertilized. Grass tetany occurs when pastures are low in magnesium but rich in nitrogen and potassium that result in a low magnesium : potassium ratio. In addition, plants involved may have high concentrations of tricarbalyllic acid (propane-1,2,3-tricarboxylic acid) that binds magnesium. Clinical signs depend on the severity of the magnesium deficiency and whether animals also are hypocalcemic (low blood calcium concentrations). Affected animals have low feed intake and low milk production. The condition may be chronic and if undetected will predispose an animal to milk fever. Feeding magnesium supplements as magnesium oxide is advised. Magnesium can be mixed with grain for feeding to pregnant and lactating does. Feeding ionophores like monensin to growing animals may increase activity of the sodium-linked magnesium transport system in the rumen and increase efficiency of magnesium absorption.

Milk Fever

Milk fever is a metabolic disorder apparent as hypocalcemia (low blood calcium concentration) of milking does that occurs just after kidding. This disorder usually is related closely to hypophosphatemia (low blood phosphorus concentration) and hypomagnesemia (low blood magnesium concentration). During milk fever, the calcium homeostatic mechanism of goats fails to maintain blood calcium at a normal level. Because calcium is essential for muscle contractions and nerve function, hypocalcemic animals cannot rise or eat. At parturition with the onset of milk production, the drain on blood calcium for milk must be replenished either by additional absorption of dietary calcium or mobilization from bone reserves. Under normal conditions, hypocalcemia triggers parathyroid hormone (PTH) release reducing urinary calcium loss, stimulating calcium resorption, and promoting synthesis of 1,25-dihydroxyvitamin D to enhance intestinal transport of calcium. The lack of a timely response of any of these three mechanisms provokes milk fever. An acid-base imbalance of the body at parturition is a predisposing factor. Metabolic alkalosis impairs the ability of PTH to function normally. Injected calcium gluconate can keep the animal alive until calcium homeostasis is restored. Preventive measures include feeding an acidic (low calcium) diet during late pregnancy to provoke PTH release and prepare the metabolic system to mobilize bone reserves and increase the efficiency of urinary and intestinal calcium transport. Preventive practices include feeding less salt and potassium and improving phosphorous and magnesium intake; adding anions such as ammonium, calcium chloride, and magnesium chloride and sulfate to induce mild metabolic acidosis; and feeding low calcium diets to stimulate PHT release prior to parturition. Oral calcium drenching and vitamin D supplementation at kidding also can help.

Ketosis or Pregnancy Toxemia

Ketosis is a metabolic disorder caused by a negative glucose balance that, combined with an energy drain, provokes fat mobilization. Ketosis usually occurs during late gestation (pregnancy toxemia) or 2–4 weeks after parturition. It commonly is associated with accumulation of triglycerides in the liver combined with depressed glycogen levels. A high amount of glucose is required either for development of multiple fetuses at late gestation or for milk production; this is responsible for the hypoglycemic condition of the animal. As a result of the energy drain, body fat is mobilized leading to an increase in nonesterified fatty acid (NEFA) concentrations in blood that flood the liver with lipid. Esterified fatty acids normally would be exported from the liver or stored. But the mechanism to export triglycerides in ruminants is slow, leading to fat accumulation in the liver. With incomplete oxidation of fat, NEFA are converted to ketone bodies, primarily acetoacetate and β-hydroxybutyrate that are released into blood. Ketone bodies often increase in blood when the amount of energy needed for milk production exceeds energy intake. Feeding management that reduces the severity and length of the negative energy balance can help prevent ketosis. Extra supplemental concentrate fed 1 week before and after kidding reduces the incidence of fatty liver and ketosis. Preventive measures include increasing the feed supply the 2 weeks around kidding; avoiding overconditioning animals during pregnancy;

changing diets gradually; and avoiding environmental stress. Feeding glucogenic compounds like sodium propionate or oral doses of propylene glycol will reduce NEFA formation at kidding and ketone body formation after kidding and may alleviate ketosis. Injection of glucose or glucose-forming compounds will temporarily elevate insulin to suppress fat mobilization and ketone body formation.

REQUIRED NUTRIENTS

Many nutrients are required in the goat's diet for metabolism, both for maintenance of body functions, and for production that includes tissue accretion (growth), reproduction, and production of meat, milk, and fiber. The National Research Council (2007) published an extensive review of nutrient requirements of goats based on current scientific information on goats. Where information about goats was lacking, information from cattle and sheep was used. The nutrient requirements for different classes of goats are presented in Appendix B. For more detailed information on nutrient requirements of goats, the reader should refer to NRC (2007) and Sahlu et al. (2004).

Specific classes of nutrients include carbohydrates and lipids that provide energy; protein or nonprotein nitrogen that provide amino acids and energy; vitamins; minerals; and water. Though often ignored, water is classified as a nutrient that is necessary for digestion, metabolism, and products.

Energy

Energy, as fuel for the body, is defined as the potential to do work. The international unit of energy is the joule (J); however, the calorie (cal) is used most often in the United States. One calorie, equal to 4.184 J, is defined as the amount of energy required to raise the temperature of one gram of water from 15.5–16.5°C at one atmospheric pressure. This is the calorie, sometimes called a small calorie. One calorie or joule is a small amount of energy; therefore, feed or body energy utilization typically is expressed in terms of kilo (1,000; kcal or kJ) or mega (1,000,000; Mcal or MJ) calories or joules. All functions of the body including prehension, digestion, and metabolism require energy. Energy in the body is in constant flux. Amounts of energy required will vary with breed, sex, age, climatic conditions, and activity. Energy is expended for maintenance, growth, reproduction, and formation of products.

Flow of Energy in the Body

Ingested energy (gross energy [GE]) represents input while its destination is expressed as net energy (NE) for body maintenance, growth, and production. Energy loss occurs at each stage of digestion and metabolism. Readers are referred to NRC (1981a) for more detailed information on nutritional energetics. Gross energy is measured as the amount of heat released when 1 gram of feed is oxidized to carbon dioxide and water in bomb calorimeter. The GE value of feeds is proportional to the carbon and hydrogen contents of the feed's organic matter, carbohydrates, proteins, and lipids. Because all GE is not available to animals, GE is not precisely related to usefulness of a feed to an animal.

Digestible energy (DE) is an index of the amount of feed energy value presumably available for meeting an animal's requirement for energy. Within the GI tract, available GE is digested while waste is removed from the system as feces (fecal energy [FE]). Apparent digestible energy is the difference in energy between GE and FE. The term "apparent" reflects the fact that some energy in feces does not come from feed but instead represents inherent loss of enzymes, sloughing tissues, and microbial cells that collectively are called "metabolic fecal matter." Depending on the nature of feeds, DE can be as high as 80% for concentrate diets and as low as 50% for forage diets. Straw may be even lower (45% DE).

Total digestible nutrients (TDN) is another index of available feed energy that accounts for the higher energy content of lipids. TDN is the sum of digestible nitrogen free extract (NFE) (carbohydrates), digestible crude protein (CP), digestible crude fiber (CF), and 2.25 times the digestible ether extract (lipids) for animals fed at an energy intake equal to maintenance. TDN can be approximated from DE, with 1 kg TDN being about 4.4 Mcal DE, or by empirical equations using feed composition data such as CP, neutral detergent fiber (NDF), and acid detergent fiber (ADF) together with their predicted digestibility. The TDN value of a feed may be lower when feed intake is above maintenance due to reduced time for digestion of nutrients by the GI tract. Total digestible nutrient values also appear to overestimate the energy availability from diets rich in fiber relative to high concentrate diets (Moore et al., 1953).

Metabolizable energy (ME) deducts energy lost in urine (UE) and energy lost in rumen gases (GasE) or methane from DE. Compared with DE or TDN, ME more precisely estimates the usable energy available to support tissue accretion, milk, and conceptus. The energy loss in urine (4–5% of GE) and heat of gases loss in fermentation (4–5% of GE) can be considerable. The UE losses are higher for ruminants than nonruminants because microbial nucleic acid by-products as well as urea are excreted in urine. Gaseous energy loss increases as the level of dietary fiber increases, but it is reduced as a percent of GE when energy intake increases. Consequently, methane losses are less when animals have high feed intakes or consume either high-concentrate diets (Johnson and Johnson, 1995) or when browse comprises an important dietary component (Woodward et al., 2001). Components of browse including essential oils or unsaturated fatty acids might inhibit protozoa or methanogenic bacteria to reduce GasE. Loss of energy in UE and GasE are quite predictable and result in a high correlation between DE and ME. The ME for ruminants generally is calculated as ME = DE × 0.82 for forage-based diets; however, this may be an underestimate with diets rich in concentrate or browse that tend to have lower gaseous losses.

Because sufficient data are not available to calculate the net energy (NE) of feeds or the net energy requirements of goats, NE is used less commonly than DE, TDN, and ME for formulating diets. The NE considers an additional loss of energy, heat increment (HiE). Heat increment is subtracted from ME as NE = ME − HiE. Heat increment is defined as the increase in heat production following feed consumption in a thermoneutral environment (NRC, 1981a). It includes both the heat of fermentation in the GI tract and the heat of metabolism (i.e., heat released when nutrients are metabolized). Heat increment is useful to keep animals warm when they are exposed to low environmental temperatures but presents a burden otherwise, and must be dissipated. Heat increment losses account for 25–40% of GE, increasing as fiber content of the diet increases, and as feed intake and tissue gain increase. Net energy relates more closely to animal performance than DE, TDN and ME, each of which overestimate energy value of feeds.

Net Energy Requirements

Net energy required for maintenance is that portion of energy used for basal metabolism, muscular activity, tissue repair, involuntary metabolic processes, and voluntary activities that are necessary to sustain life. Life-sustaining activities account for walking to seek and obtain food, browse, shade, feeders and waterers, or other related activities such as social activities specific to goats like jumping, playing or fighting. Maintaining body temperature under extreme environmental conditions also will impact the maintenance energy requirement. Energy available in excess of maintenance is available for a wide variety of activities such as tissue gain, reproduction, lactation, hair/wool production, or physical work.

Composition of tissue gain varies depending on the age of the animal. Younger animals tend to gain more water and protein, but as animals age, more water and fat are deposited. Gender of the animal also can influence the pattern that animals deposit protein or lipid. Deposited water plus protein (lean) requires less energy (1.2 Mcal/kg) than deposited fat plus water (8 Mcal/kg). Other factors such as genotype, rate of gain, or energy density of diet may affect energy requirements for gain.

Energy required for reproduction depends on the stage of pregnancy, number of fetuses carried, and development of mammary tissues. The additional energy required for pregnancy typically is so small that they can be ignored until about 100 days in gestation. Most of the fetal and mammary growth occur during the last 50–60 days of gestation for goats. Data are insufficient to determine requirements for pregnancy of goats accurately. Estimating or measuring the energy requirements for and efficiency of lactation also are complicated because animals mobilize body energy reserves to produce milk while, later in lactation, body energy reserves are replenished simultaneous with lactation. Efficiency of converting energy from feed to energy in milk for ruminants averages 0.62; however, efficiency can be higher (0.84; ARC, 1980) when mobilized energy is used for milk production.

Energy requirements for fiber growth in Angora or other fiber-producing goats depend on rate of fiber growth, the amount of energy in the fiber, and energetic efficiency of fiber growth. Energy also is expended for exercise or work. According to the NRC (1981b), additional energy needs for low, medium, and high activities are 25, 50, and 75% of maintenance energy requirements, respectively.

Energy Sources

Energy is released during oxidation of nutrients in the body, being produced with oxidation of carbohydrates, fats, proteins, and other organic compounds by the body. Any organic compound capable of being fermented and converted to VFA, or of being digested and absorbed as a monosaccharide or fat from the digestive tract can enter the Kreb's cycle and be converted to energy. One gram of carbohydrate or protein upon oxidation will produce 4–5 calories of energy while a gram of fat, with a higher energy density, can produce 9 calories. With most practical diets, carbohydrates provide the majority of energy for ruminants with only a small portion coming from fats. Proteins generally are the most expensive part of the diet and are fed to meet protein (amino acid) requirements, but excesses will be oxidized yielding energy.

Carbohydrates

Carbohydrates, also called polysaccharides, usually comprising 60–70% of ruminant diets, are the main source of energy for ruminants. They include diverse compounds classified as monosaccharides (single sugar unit), such as glucose, fructose, or polymers of monosaccharides, that is, oligosaccharides (2–10 sugar units), such as maltose and lactose, and polysaccharides, such as cellulose, hemicellulose, and starch. Carbohydrates also are divided into two main groups based on their availability for fermentation or digestion: (1) nonstructural carbohydrates (NSC) being found inside the cells of plants that are readily available and fermented such as sugars and starch, and (2) structural carbohydrates (SC) being present as plant cell walls that resist digestion but are partially fermented in the rumen and in the cecum/colon.

Nonstructural carbohydrates include sugars, starches, organic acids, and other reserve carbohydrates such as fructans. Starches generally comprise 50–100% of NSC in most plants. NSCs are well digested and provide the main source of energy for both ruminal microbes and the host ruminant. Nonstructural carbohydrates typically are measured by enzymatic methods and differ slightly from nonfibrous carbohydrates (NFC) that are calculated by subtraction as NFC = 100 − (%NDF + % CP + % Fat + % Ash). The difference between NSC and NFC includes pectin and organic acids. Pectin is not included in NSC. The levels of NSC in the diets of dairy cattle should not exceed 30–40% of the ration dry matter while the maximum level for NFC can be slightly (2–3%) greater. The optimal concentration of NSC or NFC in the diet of dairy goats has not been determined.

Structural carbohydrates separated from cell contents by solubilizing away materials solvent in acid and base yield crude fiber (CF), or in a pH neutral detergent solution yield neutral detergent fiber (NDF), or an acid detergent solution yielding acid detergent fiber (ADF). Neutral detergent fiber represents much of the fiber in the plant cell walls and includes cellulose, hemicellulose, and lignin. Acid detergent fiber is equal to NDF minus hemicellulose. Generally, ADF is less digestible than NDF, and ADF concentration in a feed is negatively related to energy digestibility of that feed. However, digestibility of NDF is affected by its source (from forage or grain), and the proportions of its components: cellulose, hemicellulose, and lignin. NDF from nonforage and present in small particles is less effective for maintaining rumen pH than NDF from coarser forage particles. The recommended dietary requirements for dairy cattle for NDF to support optimum milk production with no depression of milk fat is set at 25% of diet dry matter with not less than 19% of NDF from forage (NRC, 2001). There is no recommendation stated for dairy goats.

Lipids

Lipids are organic compounds defined by being soluble in a nonpolar solvent like ether or chloroform. Lipids will include long chain fatty acids (FA), triglycerides, phospholipids, and other substances such as sterols and cholesterol. Lipids are generally classified as (1) simple lipids, mainly neural fats and waxes; (2) compound lipids, including phospholipids, such as lecithin, cephalins, and nonphosphorylated lipids, such as glycolipids and lipoproteins; and (3) derived lipids, such as fatty acids and sterols. Fats are lipids, but not all lipids are fats. For example, petroleum products are lipids but are not fats. Fat generally refers to stored, energy-rich compounds that have high concentrations of long-chain fatty acids including triglycerides, phospholipids, nonesterified fatty acids, and salts of long-chain fatty acids. Fats are dense sources of energy providing more than twice the energy per unit of weight of carbohydrates and proteins with more than 85–90% of this additional energy being available for metabolism. Fats also provide fat-soluble vitamins such as A, D, and E that rumen microbes are unable to synthesize in the rumen, and the essential fatty acids such as linoleic acid and linolenic acid. Fat is present in grains and forage at levels of 2–5% of dry weight. In addition, fats often are added to diets of ruminants in the form of oilseeds, animal or animal-vegetable blends (with a saturated : unsaturated FA ratio of 1 : 1), dry granular fat, or rumen-protected fat. Feeding more than 6–7% of diet DM in the form of fat will decrease intake and has been associated with depression in cellulose digestion in the rumen.

Proteins

Proteins are large molecular weight nitrogenous compounds composed of amino acids. Proteins are vital to living cells and play important roles (1) as enzymes, hormones, and structural components of the cells, (2) for immunity and heredity, and (3) for oxygen transport, muscle contraction, acid-base balance, osmotic pressure, and blood clotting. Proteins generally are classified as either (1) simple proteins that upon hydrolysis yield mainly amino acids and their derivatives, (2) conjugated proteins, or (3) derived proteins. Simple proteins are classified based on their solubility as globular proteins (albumin, globulin, glutelins, and prolamines) or fibrous, less soluble proteins (collagen, elastin, and keratin). Conjugated proteins are simple proteins with an additional nonprotein prosthetic group, such as nucleoproteins, glycoproteins, metaloproteins, etc. Derived proteins include peptones and metalloproteins. Globular proteins are present in all feeds, whereas fibrous proteins are more abundant in feeds of animal origin. Seed proteins are rich in glutelins and prolamines, whereas leaf protein is primarily albumin. Feedstuffs also contain NPN compounds, peptides, free amino acids, nucleic acids, amides, amines, and ammonia. Grasses and legumes have the highest and most variable content of NPN (nonprotein nitrogen, typically being any protein that is not precipitated by a protein precipitant like tungstic or trichloroacetic acid). The NPN content of fresh forage is mainly short peptides, free AA, and nitrates, whereas fermented forage is rich in free AA, ammonia, and amines but lower in peptides and amines.

Metabolizable Protein

Metabolizable protein is used for maintaining and repairing body tissues, tissue gain, conceptus gain, and milk or wool production. The goal of feeding protein to ruminants is to provide amino acids to complement the microbial protein and supply dietary protein that escapes destruction within the rumen and to reach the small intestine to be digested therein and provide AA for absorption. The crude protein and digestible protein systems commonly were used in the past as indices of ruminants' protein needs. These have been displaced through the metabolizable protein (MP) concept that should define requirements more accurately. True MP supply is the total of microbial protein synthesized in the rumen plus the amount of dietary protein that escapes fermentation (UIP) that in turn is supplied by the diet and by recycled nitrogen. Microbial protein synthesis in the rumen requires both a nitrogen source and available energy. Most cellulolytic bacteria require ammonia for growth while amylolytic bacteria may require amino acids. Protozoa meet their nitrogen need from digestion of bacteria, feed, or fungal protein. Outflow of microbial protein from the rumen is associated with both liquids and solids. Faster rates of rumen outflow will increase microbial yield by reducing the time that microbes spend in the rumen and thereby the amount of energy bacteria used for maintenance. Protozoa have a slower generation rate and limited outflow from the rumen and thereby have a very low efficiency for production of microbial protein. Passage rate also can affect how much of the intake protein is degraded in the rumen. Although dietary protein is divided into two fractions, degradable intake protein (DIP) and undegradable intake protein (UIP), extent of degradation of DIP will vary with time available for degradation that in turn is altered by level of feed intake. This in turn influences the amount of MP available. In the small intestine, amino acid absorption rate appears more variable for UIP than that for microbial protein. Small intestinal protein digestion is assumed to be 80–85% and MP is estimated to be between 60–64% of CP.

Nitrogen Recycling

The liver synthesizes urea from ammonia in blood. Ammonia in turn is absorbed through the rumen or intestinal wall or is produced during nitrogen metabolism by tissues. In goats, some 18–85% of blood urea is recycled to the rumen either via saliva or directly via diffusion through the rumen wall (NRC, 2007). The intakes of ruminally degradable intake protein and available fermentable carbohydrates regulate the degree to which intake or recycled urea is used whereas salivary flow and rumen pH influence the extent to which urea is recycled and to which ammonia is retained within the rumen. Recycled nitrogen (urea) contributes to rumen microbial protein, fecal nitrogen, and urine nitrogen. The metabolizable protein represents the proportion of protein that is digested (DP) and absorbed and not eliminated by the kidneys. Nitrogen recycling by ruminants is a significant survival tool that helps conserve protein when quality of feed is marginal. However, urea recycling may be simply a fortunate side benefit of adaptation to a desert environment. Through recycling N, excretion of urine is reduced and this in turn reduces the need for water, a factor important for survival under desert conditions.

Minerals

Minerals are essential components of a diet and play multiple major roles in the body. Collectively they are assayed as and thereby called "ash" and comprise the inorganic portion of the diet. Minerals do not yield energy or produce protein for the animal, but their presence is crucial for nutrient metabolism. Minerals also provide structure with bone and teeth formation; play significant roles as electrolytes in acid-base balance and body fluid volume regulation; maintain osmotic pressure, membrane permeability, and nervous transmission; regulate cell replication and differentiation; and act as coenzymes or cofactors in metabolic activities and body immune function. Fourteen different mineral elements have been identified as required in the diet of goats.

Minerals generally classified based on the quantities required as either (1) macrominerals or major minerals that are needed in "gram per day" quantities and include calcium, phosphorous, sodium, chloride, potassium, magnesium, and sulfur or (2) microminerals or trace minerals that are needed in very small amounts as "mg per kg" and include cobalt, copper, iodine, iron, manganese, selenium, and zinc. Additional trace elements that may be needed under certain conditions include aluminum, arsenic, boron, chromium, fluorine, silicon, tin, and vanadium (Underwood and Suttle, 1999). Most minerals in excess can prove to be toxic. Minerals whose excesses are less tolerated by animals include fluorine, molybdenum, lead, arsenic, aluminum, cadmium, and mercury.

The main source of minerals is various feeds and occasionally water and air. Soil also can provide minerals directly through consumption during grazing and feeding. Plants generally have a mineral composition characteristic of the soil though soil pH can alter the availability of soil minerals for plants. Acid soils lead to decreased availability of most macrominerals but will increase the availability of many trace minerals. Alkaline soils may increase molybdenum or selenium availability but will decrease the availability of most trace minerals.

Most forage is a rich source of potassium and iron but often is deficient in sodium, copper, selenium, and possibly iodine. Cereal grains are deficient in most minerals. High protein feeds generally are richer in mineral content than forage and cereal grains. Legume forage usually is richer in minerals than grasses, and leaves are richer than stems. As forage matures, protein content decreases while phytates and oxalates will increase; these changes reduce mineral content and mineral bioavailability.

Nutrient balance among minerals will alter mineral absorption. Specific imbalances, induced by man through mismanagement or natural conditions, can result in mineral interactions and reduced mineral absorption. For example, acid soils promote molybdenum absorption by plants, and high molybdenum intakes may reduce copper uptake and induce copper deficiencies in animals. Goats given the opportunity for browsing tend to balance their mineral needs; however, in confinement, deficiencies or toxicities can occur.

One general symptom of mineral deficiency is "pica." Goats exhibit pica as a peculiar craving that results in eating or chewing on wood or digging or licking soil. Assessment of mineral status of animals can help to identify mineral excesses or deficiencies and diagnose the source of a pica problem. This assessment includes collective knowledge of mineral content of the feeds, water, soil, animal fluids and tissues, as well as clinical signs and symptoms. Diagnosis is confirmed when the problem is corrected and the animal recovers.

Physiological stages of production may impact mineral requirements and if not corrected, induce deficiencies. Minerals are needed for body metabolism and for all phases of growth and production, particularly for skeletal growth of young animals, conceptus growth of pregnant does, and milk and fiber production. Mineral requirements of goats are not fully understood or investigated, and established requirements are extrapolated largely from information from cattle and sheep. Recent research findings on mineral requirements of goats confirm major differences between species and have been documented for copper (Solaiman et al., 2001).

Vitamins

Vitamins are complex organic compounds that are needed only in small amounts, that perform multiple physiological functions, and that are involved in many metabolic processes. Vitamins are generally classified by their solubility as either (1) water soluble vitamins, that include the B complex vitamins and vitamin C, and (2) fat soluble vitamins, A, D, E, and K. Although fat-soluble vitamins only have oxygen, hydrogen, and carbon in their structure, water-soluble vitamins are more variable in composition with some containing nitrogen, sulfur, and cobalt. Water-soluble vitamins are synthesized in the rumen by fermentation in the presence of adequate cobalt for vitamin B_{12} and sulfur for thiamin and biotin synthesis. Although ruminants may be self-sufficient for synthesizing their own B vitamins, supply of certain B vitamins may limit production under some conditions. Ruminants can synthesize vitamin C (ascorbic acid) because they have the enzyme L-gulanolactone oxidase to convert gulanic acid to gulanolactone during ascorbic acid synthesis. Fat-soluble vitamin A is present in forage as its precursor β-carotene, but vitamin E often is added to diets. Vitamin D can be obtained through exposure of skin to sunlight but must be supplied when animals are indoors or have limited exposure to ultraviolet arrays. Vitamin K can be produced by rumen fermentation when the rumen is free from antivitamin K activities (coumarin) produced by molds that grow on white clover and produce the antivitamin dicoumarol. Although some fat-soluble vitamins are required in the goat's diet, research data to establish requirements are lacking; therefore, requirements have been extrapolated from data for cattle and some from data from sheep.

Water

Water is the largest single component of the animal's body making up between 50 and 81% of total weight at various stages of development. Water has unique properties and functions in metabolism and physically. Water facilitates cellular reactions with its high dielectric constant and hydrogen-binding property that promotes ionization of electrolytes and allows oppositely charged ions to move independently. Water helps in the transportation of metabolites, nutrients, and hormones throughout the body. In the gastrointestinal tract, water provides moisture for rumen fermentation and aides in excretion of waste. Certain characteristics of water, including its high specific heat, high thermal conductivity, and latent heat of vaporization, assist in body temperature regulation. Water requires heat to raise its temperature, has a high heat transfer capability, and requires heat to change from liquid phase to vapor or to solid phase. Vaporization of water is the main route by which the body will lose heat. Other functions include lubrication of joints and conduction of sound through the body.

Body water is gradually displaced by body fat as animals grow and mature. Milk production increases the water requirement and body water content. Males tend to have more body water than females. Turnover rate of water in the body under normal conditions ranges from 2–8 days but may increase with potassium and salt intake, temperature, and humidity.

An animal obtains its water from drinking, from water in feeds (called bound water or preformed water), and from metabolic water. Metabolic water is the water released during oxidation of the carbohydrates, fats, and proteins. Metabolic water of nutrients relates to their oxidation state. Fats are the least oxidized compounds and have a high ratio of carbon and hydrogen to oxygen. One hundred grams of fat when metabolized will release 109 grams of water, carbohydrates yield only 60 grams, and proteins yield only 42 grams. Disposal of end-products of protein metabolism (urea) requires additional water. Preformed and metabolic water can meet the water needs of many grazing animals.

The body loses water through four main channels: (1) kidneys, (2) skin, (3) lungs, and (4) intestines. Kidney water excretion through urine is under hormonal adrenocorticotropic hormone (ACTH) control. Water loss through skin is either insensible (radiation) or sensible (perspiration) and is affected directly by solar radiation input, temperature, humidity, and wind velocity. Lungs lose water through vaporization; this loss is affected directly by temperature and animals' activity. Water loss through the lungs and skin, accounts for one-third of total water loss. Intestinal water loss through feces is affected by animal species, being lower for sheep and goats than cattle. Water lost by any channel except lungs will also include loss of electrolytes.

Water requirements are not fixed. Under normal conditions, voluntary water intake is proportional to feed intake. However, high ambient temperature will increase water consumption. An animal may drink only 3 liters of water per kg of feed at 5–6°C versus about 15 liters at 40°C. Season of the year also can change the water requirement. Daily water intake generally is estimated at 5–6% of body weight but may be 10% of body weight in extreme cases. Dietary factors as well as environmental factors can influence water intake. Dietary factors that increase water intake include intake of dry matter, protein, fat, and salt. Feeds with higher water content such as pastures and fresh cuts may displace intake of imbibed water. However, water intake often increases with intake of ensiled feeds because of their higher osmolarity. The primary environmental factors that affect water intake are high temperature and high humidity; both increase water intake. Design, accessibility, and cleanness of water also may alter water consumption by goats.

Water Distribution

Total body water (TBW) is distributed into two major compartments: (1) extracellular fluid (ECF) that comprises some 31–38% of TBW, and (2) intracellular fluid (ICF) that comprises the remaining 62–69% of TBW. The ECF includes blood plasma (25%) and intestinal fluids (75%) with volume being regulated by maintaining a constant Na concentration. The ICF includes water plus other regulatory electrolytes, potassium, other inorganic ions, and different proteins within cells. The volume of ICF is closely regulated by volume sensors, hormones, and water transport mechanism supported by the liver, heart, and kidneys. Fluid exchange between the two pools is important for the survival of animals under desert conditions and the Mediterranean environment. Water content of the forestomach will comprise from 10–30% of TBW and is a major temporary water reservoir whose volume will change over time with meals and drinking bouts. Withholding food and water for 20–24 hours is a routine procedure that will minimize the variation in body weight measurement or "shrunk weight." Alternatively, body weight measured without food and water restriction is called "unshrunk weight."

Water Requirements

Requirements for water are not determined directly but instead the requirement typically is calculated as voluntary intake of water for animals given free choice access to water. Water intake usually is calculated from dry matter intake according to the following equation (NRC, 1985):

$$\text{Total Water Intake (liter/day)} = 3.86 \times \text{Dry Matter Intake} - 0.99$$

Adjustments are needed to consider effects of season, environmental temperature, breed of animal, and physiological stages of growth. Water intake usually is higher in summer and with hot temperatures. Breeds of animals adapted through natural selection to a shortage of water may consume less water and lose less water with feces. Gestation may increase water intake an average of 126%, being even greater for animals bearing twins and triplets. Water needed for lactation is estimated at 3.5 liter of water/kg of milk production. The water content of milk is usually sufficient for growing the newborn up to 2–3 weeks of age; however, providing free access to extra water is recommended. The water need for nursing offspring is set at 8–13 mL/g body weight gain for growth plus another 120–140 mL/kg of metabolic body weight ($BW^{0.75}$) for maintenance. Water needs for weaned animals for growth is set at 7–8 mL/g of body weight gain with another 143 mL/kg $BW^{0.75}$ required for maintenance (NRC, 2007).

SUMMARY

Goats are one of four existing true ruminant domesticated agricultural species among ungulates that continue to be very successful forage-consuming mammals. Goats benefit from a predigestive fermentation GI tract that allows for the breakdown of fiber to yield energy-rich fermentation products and the synthesis of microbial protein from nonprotein nitrogen sources or recycled metabolic nitrogen. The other benefits include production of vitamin B complex. Goats use visual cues and taste to select for diets based on the concentrate part of the plants and for shrubs and browse. They have larger salivary glands that secrete tannin-binding protein in the saliva to detoxify tannin associated with browse species. The newborn kid and up to 3 weeks of age is preruminant, its intermediary metabolism is glucose driven, and blood glucose is insulin sensitive. By 8 weeks as a young ruminant, the intermediary metabolism shifts to VFA driven and is less insulin sensitive.

Rumen dysfunction is not common in free-ranging ruminants, and it appears to be manifested by mismanagement of normal balances between animal and the diet. They may include bloat, rumen acidosis, displaced abomasums, urea toxicity, and nitrate toxicity. Goats require nutrients for maintenance, growth, gestation, and production of milk, meat, and fiber. Carbohydrates and lipids provide required energy; proteins are provided through true protein or nonprotein nitrogen; vitamins and minerals are provided through feeds or supplements; and water is provided free choice. Knowledge of work of digestion and nutrient metabolism in goats will help in proper management and decision making when raising goats. Some of the information presented in this chapter has been extrapolated from sheep and cattle data. Information regarding digestive physiology and nutrient requirements for goats is very limited and needs further investigation.

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