Chapter 2

Range Animal Nutrition

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Introduction

Forage production, defined in Chapter 1 as the integrated end-product of conversion of solar energy into plant biomass, is the foundation of range animal production systems. Because plant biomass is of limited caloric value to man as a primary consumer, the value of this renewable resource is in the production of secondary and tertiary products through grazing animals. Temporal distribution of forage production sets boundaries on the opportunities for directly or indirectly utilizing rangeland resources.

Our purpose in this chapter is to depict the role of grazing animals in converting chemicals fixed in plants into animal products (food and fiber). To do so, we trace physiological processes and interactions within the herbivore and describe how these relate to the diets that are consumed. We conclude with a discussion of the implications of these interactions in the nutritional management of range herbivores, primarily domestic livestock.

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Character of Forage

Forage includes browse and herbage which can be consumed by or harvested and fed to animals (Soc. Range Manage. 1989). The structural characteristics of forage are described in various ways and with nomenclature appropriate to the context in which it is considered. Botanists and agronomists approach plant cellular structure from the standpoint of biosynthesis. At what sites or in what organelles do certain chemical reactions occur that result in processes such as photosynthesis, protein synthesis and nutrient translocation? By contrast, animal nutritionists emphasize attributes of cells and tissues that enhance bio-degradation (Van Soest 1982) and liberation of nutrients. The nutritionist asks what cellular configuration affects the digestibility of protein in the plant leaf. Differences and commonalities in the nomenclature of cell/tissue anatomy and biochemistry employed by botanists and animal nutritionists are illustrated in Figure 2.1.

Strictly for illustrative purposes, consider a teleological comparison of the plant and animal perspectives relating to the plant cell. Cells of young, plant tissue are biochemically active, capturing and storing energy, synthesizing proteins and fats, etc. (a). These are cytoplasmic activities. Cells of older tissue are comparatively low in biochemical activity. Much of the photosynthate and other synthesized compounds have been translocated to the seeds and roots or deposited in other forms in the cell wall. This leaves the cytoplasm comparatively inactive. Similarly, leaves are biochemically more active compared with stems that contribute structure and resilience in the overall plant function (b). Cool-season (C_3) plants have relatively greater cytoplasm compared with warm-season (C_4) plants that are higher in cell wall (c).

Figure 2.1

The animal measures plant chemicals in terms of availability and nutritional worth, irrespective of their phytochemical functions. Which are easily accessible? Which are difficultly accessible or inaccessible? The two perspectives relate, in that cell structure and function in plant metabolism closely align with nutrient availability and worth to the consuming animal.

Forage contains fixed energy largely in the form of complex carbohydrates, waxes, terpenes (essential oils, saponins, etc.) and phenylpropanoids (lignins, tannins, etc.). Plant biomass is a virtually infinite number of combinations of these biochemicals determined by plant species and phenological stages. The structure and form of these biochemicals, to a large extent, determine a plant species' capacity to survive (resilience) which is related to the general inverse relationship between nutritional value to grazing animals and plant resilience. The complex carbohydrates, etc. are generally impervious to mammalian gastric and intestinal digestive enzymes. Readily digested proteins and soluble carbohydrates, including simple sugars and starches on the other hand, usually exist either in lesser proportions (< 40% of dry matter) or are complexed (rendered insoluble and poorly available) with insoluble compounds such as lignins and tannins. Cellulose, the most widely distributed organic compound in nature, is a glucose polymer, differing from starch, in the isomeric arrangement of the bonds between the glucose monomers (Fig. 2.2). Intestinal hydrolytic enzymes can cleave alpha linkages in starch, whereas the beta linkages of cellulose are resistant to these enzymes. Cellulose is of nutritive value only to herbivores that have incorporated anaerobic microbial fermentation in the digestive process (Hungate 1966). In the presence of cellulolytic microorganisms, exposed cellulose is broken down with relative ease. However, in many plant species, especially the warm-season perennial grasses, the cellulose is complexed or "encapsulated" by lignin as plants mature (lignification). Therefore, diet selection, to be discussed in Chapter 3, is nutritionally the important element of grazing animal behavior. This is true for plant species as well as plant structural part (leaf, stem, mast) and physiologic age of the plant tissue (new or old growth) consumed.

Figure 2.2

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The Animal Perspective

Range animals rely on vegetation for the nutrients needed to support bodily processes. The term "quality" is often used to ascribe worth to the components of diet; worth in turn is defined by the chemical composition (e.g., protein content) of the plants selected for consumption. We propose that the proper concept is "nutritional value" because it includes consideration of both the chemical composition of the dietary components and their adequacy for supporting the physiological functions of the consuming animal. For example, a forage species containing 20% protein is considered of higher quality than a similar forage species containing only 10% protein;

yet, both may be equal in nutritional value to an animal having a relatively low protein requirement. Indeed, the lower protein forage may offer greater overall value to the production system if it also possesses a greater tolerance to grazing, higher production of dry matter, or a longer growing season.

Thus, a proper perspective of the plant:animal interface requires a dual focus to balance short and long term production goals. Practices promoting maximum production of animal food and fiber will eventually reduce long term secondary production by decreasing the stability of the forage resource. On the other hand an approach which is overly protective from an ecological point of view is economically and sociologically insupportable (see Chapter 9). Hence, both the animal's needs and consequences that result when these needs are adequately, marginally or inadequately met determine the proper balance between short term and long term productivity.

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Range Herbivores

Foraging animals possessing microbial fermentation capabilities, whether pre-gastric (foregut) or post-gastric (hindgut), are the principal producers of food and fiber from rangelands (McNaughton et al. 1982, Belovsky 1984). Most pre-gastric fermenters belong to the order Ruminantia (Bovidae, Cervidae, etc.) and Tylopoda (Camelidae). Most range livestock and big-game species belong to Ruminantia. Grazing animals relying upon symbiotic pre-gastric fermentation and "ruminants" are considered synonymous in this chapter. In terms of economic importance, these foregut fermenters, including cattle, sheep, goats, cervids and big game animals, are the most common. However, the suborder, Hippomorpha, which includes the horse (Equidae) is important in some range settings.

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Post-gastric vs Pre-gastric Fermentation

Evolution of microbial fermentation in mammals has been the subject of extensive reviews (Hungate et al. 1959, Janis 1976, Hume and Warner 1980). Figure 2.3 illustrates the comparative digestive anatomy of the non-ruminant (minimal post-gastric fermentation) and post- and pre-gastric fermenting herbivores.

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Fiber Digestion

In non-ruminants (a) and post-gastric fermenters (b) in Figure 2.3, foods are exposed to digestion by hydrolytic proteinases (trypsin, pepsin, chymotrypsin, etc.) and carbohydrases (amylase, maltase, lactase, etc.) in the gastric (5) and intestinal regions (6) prior to active fermentation in the large intestine [colon (8) and cecum (7)]. However, because cellulase, the enzyme lysing cellulose, is not present in gastric, pancreatic or intestinal secretions, cellulose passes through the digestive tract essentially unaltered and provides no direct nutrition to the animal. In the colon (8) and/or cecum (7), structural carbohydrates, including cellulose and undigested and endogenous residues that have escaped hydrolytic digestion are exposed to microbial fermentation. Fermentation results in the growth and accumulation of microbial cells (primarily bacteria) high in protein. However, there is limited microbial protein catabolism in and amino acid absorption from the colon/cecum (Janis 1976). Hence, the major by-products of fermentation in these herbivores are short-chain organic acids (volatile fatty acids; VFAs), ammonia, carbon dioxide and methane. A major portion of the VFAs are absorbed and used by the host animal for energy as discussed later.

Figure 2.3

By comparison the food consumed by ruminants (Fig. 2.3 c) is subjected to microbial fermentation prior (2,3,4) to digestion by hydrolytic enzymes (proteinases and carbohydrases) in the gastric and intestinal segments (5,6). The microbial population is established in the rumen (3) and reticulum (2) (referred to as "rumen", "ruminoreticulum" or "reticulorumen") into which the food enters via the esophagus (1). Consumed material is mixed with existing ruminal microbial populations, portions of previously consumed meals, and both transient and end products of fermentation. After a variable delay period (rumen retention time, RT), particles move into the omasum, and then sequentially to the abomasum (5), small intestine (6), large intestine (7) and rectum (8) from which the remaining residue is excreted as feces (Phillipson and Ash 1965).

Flow dynamics of the ruminal compartment resemble a modified continuous flow system with periodic additions to, and frequent outflow from, the constantly mixed ruminal pool of materials (Fig. 2.4). Rumen retention time of an individual particle may be as short as a few minutes or as long as several days, depending on size of the compartment, levels of dry matter and water intake, particle size and reduction rate, particle density, ruminal motility and chance (Pond et al. 1987). Post-ruminal hydrolytic digestion is similar in the ruminant to that of the non-ruminant (pig) and the post-gastric fermenting animal (horse). The microbial activity in the lower tract (i.e., colon/cecum) of grazing ruminants is quantitatively of less importance than in post-gastric fermenters. However, VFAs and ammonia produced in the cecum may be important to animal status. Krysl et al. (1987a) and Caton et al. (1988b) suggest hindgut VFAs and ammonia production make a significant contribution to the respective pools of these compounds in sheep.

Figure 2.4

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Comparative Protein and Vitamin Nutrition

Proteins are large molecular compounds comprised of approximately 20 individual amino acids bonded together in linear, coiled or branching chain forms. The relative number of each of these amino acids and the sequence in which they are bonded together determine the character of the particular protein in the tissue (muscle, hair, hoof, enzyme, etc.). Protein in the diet must be broken down to the individual amino acids within the gastrointestinal tract and absorbed as such since the large protein molecule cannot be transported through the intestinal wall. These absorbed amino acids are then used to resynthesize proteins that fit the needs of the animal. Some of the amino acids can be formed within the tissue from materials such as other amino acids that are present in excess. On the other hand, some of the amino acids must be absorbed from the gastrointestinal tract preformed and are referred to as **essential amino acids**. If absorbed amounts of essential amino acids meet or exceed the animal's physiological requirements, protein synthesis can proceed at a normal rate. If one or more are not absorbed in sufficient amounts, tissue protein synthesis is restricted and the associated maintenance or production function is impeded.

Vitamins are "cofactors" or catalysts in metabolic reactions, in that they do not appear in the products of reactions, but must be present for reactions to occur. All vitamins or their precursors must be absorbed from the digestive tract as they cannot be synthesized by mammalian tissue. If vitamins are not absorbed in adequate amounts, metabolic activity is restricted.

Protein and vitamin nutrition are both influenced by microbial fermentation and its location within the digestive tract. Pathways of protein synthesis in microorganisms are similar to those of mammalian tissue except that amino acid requirements are much less specific. The microorganisms, as a mixed population, have no absolute amino acid requirements. Ammonia, derived from most nitrogen-containing compounds, including urea, can be used in the synthesis of "microbial protein" (Fig. 2.5). Likewise, most vitamins are synthesized by populations of microorganisms except for vitamin A, D, and E.

Ruminant animals are insulated against essential amino acid and most vitamin deficiencies because these compounds are synthesized by symbiotic microbial populations in the rumen and subsequently presented for hydrolytic digestion in the gastric-intestinal region. Once microbial protein passes from the rumen to the gastric-intestinal region, it is hydrolyzed to the individual amino acids which are absorbed for use at the tissue level. Therefore, ruminants can survive on a protein-free diet as long as the diet contains a form of nitrogen to yield ammonia under anaerobic fermentation (Virtanen 1968). Additional insulation against protein deficiency is conferred by ammonia nitrogen recycling (Weston and Hogan 1967). However, over the longer term, a base supply of amino acids in the form of dietary protein may be necessary for maximal fiber digestion and ruminal protein synthesis (Petersen et al. 1985). Vitamins synthesized by the microorganisms in the rumen are likewise digested in the lower tract.

Figure 2.5

The essential amino acids necessary to achieve and sustain maximum production, defined as rapid growth, successful reproduction and heavy lactation in domestic ruminants, cannot be met solely through microbial protein synthesis (Burroughs et al. 1975). Microbial growth is limited by the maximum level of fermentation which can be supported by a given diet (substrate). Obviously, complete fermentation of a substrate in the rumen can yield only a finite amount of microbial protein. Even at maximum fermentation, microbial synthesis is unable to provide sufficient quantities of amino acids to fully satisfy the physiologic requirements for maximum productivity (**genetic potential**) of some particular animals in a highly productive state (e.g., rapidly growing). Maximum productivity can be achieved only by the addition of escape protein (Fig. 2.5), with a favorable amino acid profile, to augment microbial protein production (Anderson et al. 1988).

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Digestion and Flow Dynamics in Ruminants

The chemical components of the diets of ruminants can be separated into two structural fractions of nutritional significance (Van Soest 1967). The first, cell contents (**neutral detergent solubles**; NDS), are those substances found inside plant cells. These organic molecules are soluble and so are readily digestible in the intestine. These substances also tend to be rapidly and extensively fermented before reaching the gastric-intestinal region. The second fraction, cell wall components (**neutral detergent fiber**; NDF) are digested more slowly and less completely. Digestion of the cell wall fraction is performed almost exclusively by microbial hydrolysis and fermentation. Volatile fatty acids produced during fermentation are absorbed through the rumen wall and subsequently metabolized for use at the tissue level as energy. Products of fermentation not absorbed through the rumen wall, including microbial cells, pass to the lower tract together with unfermented dietary residues. These modified (or synthesized) and original dietary and endogenous fractions are exposed to hydrolytic digestion in the gastric-intestinal region.

The total amount and quality of nutrients derived from a grazing animal's diet is determined by the type and amount of forage consumed and the proportioning of the material among five possible fates:

> **Fate 1**. Degraded to products absorbed directly from the compartment (VFAs);
> **Fate 2**. Modified during fermentation in the rumen and subsequently digested in the lower tract (microbial protein);
> **Fate 3**. Escape fermentation in the rumen and undergo hydrolytic digestion in the gastric-intestinal region (bypass or escape protein);
> **Fate 4**. Either modified by or escape fermentation in the rumen and/or hydrolytic digestion in the gastric- intestinal region to be fermented and absorbed in the colon/cecum;
> **Fate 5**. Bypass or escape digestion completely and excreted in the feces.

Some plant components such as cellulose are of greater nutritive value to the animal if they remain in the rumen over an extended period and are either degraded to absorbable end products (e.g., VFAs; Fate 1), or their fermentation contributes to the formation of other substances (e.g., microbial cells) that are subsequently digested (Fate 2). Otherwise such components are destined to either minimal nutrient yield from colon/cecal fermentation (Fate 4) or be excreted (Fate 5). Other components such as non-fiber bound protein and soluble sugars have greater net value if they escape ruminal fermentation and undergo hydrolytic digestion in the abomasum and small intestine (Fate 3) because respiration losses associated with anaerobic microbial fermentation are avoided. Therein lies the reason ruminants can survive, and are indeed productive, on fibrous forage diets, but are comparatively inefficient, compared with the chicken or pig, at converting feeds high in soluble carbohydrates and protein to animal products.

Thus, inherent species differences in gastrointestinal flow dynamics ultimately influence which species are adapted to particular components of the vegetation on rangeland. Cattle and bison, which have a relatively large capacity rumen compartment in relation to both body size and nutrient requirements (Demment and Van Soest 1985), also have a long rumen retention time (RT) (Fig. 2.6). These anatomical factors permit cattle to extract a large amount of nutritional value from fibrous materials, often in amounts adequate to satisfy all their nutrient requirements. Conversely, small ruminants, e.g., sheep and goats which possess a relatively small rumen compartment in relation to body size and nutrient requirements cannot extract comparable levels of nutrients from the same fibrous forages. Even though nutrient requirements are greater per unit body weight in small ruminants, rumen capacity is significantly less, retention time significantly shorter and flow rate significantly faster than in large ruminants (Table 2.1). Hence for relatively equivalent intake levels, fibrous diets are of less nutritional value to small ruminants.

Figure 2.6

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Foraging Strategies of Ruminants

Smaller ruminants have evolved two strategies to overcome the metabolic dilemma described above. The first strategy is reduced RT (Van Soest 1982) which allows a slight shift in the site of digestion of the highly digestible components out of rumen fermentation (Fate 1 and/or Fate 2) and into the gastric-intestinal region (Fate 3) thereby decreasing respiration losses associated with fermentation. Also, the shorter RT is associated with a greater level of intake and a slightly depressed fiber digestibility. Taken together this results in a greater level of intake, a slightly lower digestibility compared to larger ruminants, but an opportunity to equal or exceed total digested nutrient intake (Huston 1978). This strategy is important in survival but is seldom effective in allowing the small ruminants to match the productivity of large ruminants when both are limited to high fiber diets. The second strategy is to consume a high quality diet which necessitates a greater degree of discrimination in diet selection. Size and prehensile agility of the lips, teeth and tongue ultimately determine an animal's ability to selectively consume plant species, individual plants on offer within a species, and even discrete plant parts, all from a heterogeneous assemblage of plant biomass. Significant differences in the morphological structure of mouth parts exist in pre-gastric fermenters and post-gastric fermenters (Fig. 2.7) which reflect the types of forages consumed. Generally, increased pliability of the lips and manipulative capacity of the tongue denote greater levels of selectivity.

Table 2.1

Range herbivores have been variously classified into as many as six classes based upon the types of foods eaten (Langer 1984). Figure 2.6 is a modified form of the system described by Hofmann and Stewart (1972) applied to ruminants.

Bulk/roughage grazers (cattle, bison, cape buffalo, etc.) graze comparatively indiscriminately on the herbaceous fraction of vegetation by wrapping their tongue around individual clumps of plant growth and, with a short jerking motion of the head, break the clump loose then draw it into their mouths. Once in the mouth, the material is wetted with salivary secretions, chewed slightly, formed into a cylindrical "bolus" with the teeth and tongue, then swallowed (Fig. 2.4). Later, when the animal is at rest, swallowed material is regurgitated, chewed extensively, then reswallowed (rumination).

Concentrate selectors (white-tail deer, mule deer, dik-dik, etc.) characteristically have pliable and often split lips, soft muzzles and agile tongues (Fig. 2.7). Hence, these animals can select plants or plant parts high in cell contents (protein and other soluble fractions; NDS) and low in cell wall (cellulose and fibrous fractions; NDF). Bite sizes are smaller and more discrete, even consisting of single leaves, leaf tips, fruits, seeds or fallen mast.

Figure 2.7

Intermediate feeders are a diverse group characterized by dietary plasticity not found in either bulk/roughage feeders or concentrate selectors. Diet is characterized by variety and frequent compositional changes. The domestic sheep is classified as an intermediate feeder, but its diet often approximates the bulk/roughage group. The goat is a true intermediate feeder, and its diet selections clearly overlap the entire array of forages.

Such a classification of the feeding behavior of grazing animals is useful to better understand species adaptability to specific forage conditions but should not lead the reader to believe these are rigid relationships because "crossover" in feeding habits regularly occurs. Especially within sympatric ruminant populations, all species select diets from an array of available plant materials which vary in space and time (see Chapter 3). Availability is the first and most important determinant of what a grazing animal consumes. When the opportunity is presented for selection among types, species and morphological parts of plants, ruminant populations regularly exhibit "preferences" in the materials selected. This ability to discriminate between available materials is sufficiently pronounced that in vegetatively productive periods the diets of ruminant species grazing in common are almost completely different Conversely, during periods when the amount and diversity of forage are limited, dietary overlap between sympatric species is very high.

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Summary of Comparative Nutritional Physiology of Herbivores

The distinction of ruminants relative to their adaptability to forage-based animal production systems, stems from three characteristics unique to this group of animals. First, by virtue of the evolution of a pre-gastric fermentation chamber, ruminants can more effectively utilize structural carbohydrates (NDF) than either non-ruminants or post-gastric fermenters of comparable size. Increased retention time under conditions of anaerobic fermentation leads to more complete digestion and utilization of forage. It must again be noted that ruminant species vary widely both in RT and the extent of fermentive degradation of forage components.

Secondly, whereas non-ruminants depend on preformed amino acids and vitamins in their diets, ruminants are comparatively free of these requirements. Simple forms of dietary or endogenous nitrogen (ammonia releasing compounds i.e., urea, proteins, amino acids, etc.) can be used by ruminants in the microbial synthesis of protein which subsequently is digested in the gastric-intestinal region. This adaptation is further enhanced by the ability to recycle urea via salivary and ruminal mucosal secretions. Microbial protein generally fulfills the minimal amino acid requirements of ruminants for maintenance and moderate levels of production. Genetically possible levels of production in animals in stages of high productivity cannot be achieved without the addition of escape protein to increase the supply of essential amino acids.

Lastly, dietary overlap of sympatric animal species can be very high or low depending upon forage diversity and availability, environmental conditions and management. The net effect of these three physiological and behavioral characteristics is that ruminants, as a group, are well adapted to production systems on rangeland.

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Nutritional Requirements of Grazing Animals

The nutrients required by animals are energy, protein, vitamins and minerals. The **concept of requirements** is generally seen as the amounts necessary to support "normal" metabolic activity. That is, the animal's requirements are thought to be met when it gives evidence of normal health and vigor, normal rate of growth, normal reproduction and/or normal lactation levels. Obviously, "normal" is not identical in all members of the same species at all times so these requirements should be seen as a set of ranges.

Nutrients as limiting factors, while an important concept, should not be thought of as a rigid one-to-one relationship. Generally, nutrients are utilized in the hierarchical order of maintenance, reproduction, lactation and storage (Fig. 2.8). However, across a population of animals, reproduction and lactation can occur when the diet does not provide the "required" levels for these functions. Within that same population, a certain proportion of animals can even reproduce or lactate at nutrient levels well below maintenance "requirements." Despite the absence of rigor, the concepts of nutrient requirements and priority of use are fundamental to an understanding of animal nutrition and management.

The overview of nutrient requirements which follows is a general outline. The National Research Council Series on nutrient requirements (NRC 1981b, 1984, 1985a) should be referred to for greater detail.

Figure 2.8

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Energy Requirements

Energy is required primarily in making (anabolism), but sometimes in breaking (catabolism) chemical bonds during animal metabolism. Metabolic processes requiring energy include muscle contraction, nerve impulses and tissue synthesis.

An example of energy being expended to synthesize protein from amino acids (AA) to form tissue is shown in Equation 1.

$$(1)\quad AA_1 + AA_2 \xrightarrow[\text{ATP} \;\rightarrow\; \text{ADP} + \text{P}]{} AA_1 - AA_2$$

Amino acids are bonded together in peptide sequences during protein synthesis. The energy necessary for this bonding comes from a **coupled reaction** during which a high energy phosphate bond in adenosine triphosphate (ATP) is cleaved yielding adenosine diphosphate

(ADP) and a free phosphate radical. Formation of these high energy bonds occurs as a result of **respiration** (Equation 2).

In most animal systems, glucose is broken down (oxidized) during respiration to carbon dioxide and water. During this chemical change, energy is captured in the formation of a high energy phosphate bond, which is then available for tissue protein synthesis (Equation 1) or another energy-requiring metabolic process. In ruminants, energy is captured primarily during respiration of VFA's that are produced during fermentation in the rumen (Fig. 2.4) then absorbed into the bloodstream in the rumen wall. These VFAs are metabolized through a network of pathways (simplified in Fig. 2.9) and ultimately yield carbon dioxide (CO_2), water (H_2O) and captured energy in the form of high-energy bonds (ATP). Although ruminant tissue can metabolize glucose (1) and protein (2), most captured energy arises from either acetate (3), propionate (4) or butyrate (5), the main VFAs produced during rumen microbial fermentation.

Figure 2.9

Grazing ruminants derive energy primarily from plant carbohydrates, lipids and proteins, but not all consumed energy is captured in a form usable to the animal. **Total dietary energy** includes all combustible energy of the diet measured in calories (cal), kilocalories (kcal; 1000 cal) or megacalories (Mcal; 1000 kcal), but not all dietary energy is captured in a form utilizable by the animal. That is, if a cow consumes 20 pounds of hay which if burned would give off 50,000 kcal of heat, then the cow would have eaten 50 Mcal total energy. This total or gross energy (GE) is partitioned (Fig. 2.10) into digestible energy which is DE = GE - fecal energy; metabolizable energy which is ME = DE - Urinary and methane energy; and finally net energy which is NE = ME - heat increment. Net energy is the amount of energy available for **maintenance** (energy required to maintain normal health and vigor) and **production** (energy required for growth, reproduction, lactation, etc.). The metabolizability of digestible energy, ME/DE, is rather constant at approximately 82% (NRC 1984). However, the digestibility of gross energy, DE/GE, and the net availability of metabolizable energy, NE/ME, vary with the chemical composition of the diet and the metabolic function for which the net energy is used.

Expressions of the energy value of feeds and forages are defined in Table 2.2. Components of the diets of grazing animals can have dry matter digestibility (DMD) values from 14-85% depending on the amount of cell contents (NDS) and cell wall constituents (NDF) in the dry matter. The net availability of metabolizable energy (NE/ME) in a forage varies from about 90% when used for maintenance down to less than 20% for an incremental increase in intake high on the productivity curve (Fig. 2.11; Van Soest 1982, Fox et al. 1988). Therefore, the energy value of a quantity of forage varies as a function of its digestibility and its ability to meet the energy required to support a desired metabolic process or productivity level.

Figure 2.10

[Table 2.2](#)

[Figure 2.11](#)

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Protein Requirements

Ruminant animals require protein in the diet to supply nitrogen (ammonia) and amino acids for intraruminal microbial activity and amino acids for cellular-level tissue metabolism. Protein expressions are defined in Table 2.2. Suboptimal protein supply to the microbial population in the rumen results in a lowered fermentation rate, decreased digestibility of food consumed and decreased voluntary intake (Kempton and Leng 1979). Protein requirements in ruminants include protein and/or nitrogen requirements of the ruminal microbial population. Generally, microbial requirements are met at 6-8% crude protein in the diet. Animal requirements range from 7-20% in the diet depending upon species, sex and physiologic state. Normally animal protein requirements are satisfied by a combination of microbial and dietary escape protein (Fig. 2.5). As animal protein requirements increase, the animal becomes more dependent on dietary escape protein.

Priority of protein use can be expressed in the same fashion as priority of energy use (Fig. 2.8). Maintenance requirements are met first and include repair and replacement of body tissue. After maintenance requirements are met, absorbed amino acids are used for productive functions until one of three limitations are encountered:

1. The supply of amino acids in the correct proportion is depleted. That is, the synthesizing system literally runs out of one or more of the necessary amino acids to build the protein;

2. One or more of the other necessary nutrients required in coupled reactions become limiting. This is easily understood for limited energy by reviewing the coupled equation, Equation 1. Alternatively, other nutrients, particularly vitamins or minerals, are not present in the proper proportion and limit protein synthesis;

3. The animal's genetic capability for performing a particular function has been reached. Genetic potential should be viewed as a variable range in a manner similar to nutrient requirements, but generally as a point on the production curve beyond which additional nutrients produce no practical response. Thus a beef cow's requirements for protein or energy are met at a lower level of protein or energy intake than that required by a dairy cow.

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Vitamin Requirements

Vitamins are organic compounds that must be present at the cellular level to act as catalysts in metabolic processes. As noted earlier, many of the vitamins are synthesized by the ruminal bacteria and subsequently absorbed from the intestinal tract. With few exceptions, vitamin A is the only vitamin that is likely to limit the productivity of grazing ruminants. Vitamin A does not occur in plant tissue, but is synthesized by the animal from chemical precursors in plants, mainly beta carotene, but other plant pigments as well. Vitamin A deficiency is most likely to develop during an extended period of low temperature and/or drought when green plants are unavailable to the animal. The second most likely deficient vitamin in grazing ruminants is vitamin E. This condition can become especially severe when combined with low selenium in the diet.

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Mineral Requirements

Minerals required by animals are classified as either macro-minerals or micro-minerals according to the amounts required. Those required in relatively large amounts, the **macro-** or **major elements**, are sodium, chlorine, calcium, phosphorus, magnesium, potassium and sulfur. In each case these elements are either a constituent of animal tissue or are required in large amounts to carry on metabolic functions. Mineral elements required in small amounts, **micro-** or **trace elements**, include iodine, iron, copper, zinc, manganese, cobalt, molybdenum and selenium. These generally have special functions as either low level components of certain tissues, or as cofactors for certain metabolic reactions.

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Macro-minerals

All of the major elements are potentially problematic in the range setting. Those most likely deficient in range forages are sodium, chlorine and phosphorus. Deficiencies of salt (sodium chloride) and/or phosphorus can result in perverted animal behavior such as indiscriminate eating of rocks, sticks, bones, etc. and reduced forage intake and productivity. Deficiencies of the remaining four are unlikely under normal range conditions, but where deficiencies occur, the effects can be as devastating as in the cases of the more common deficiencies. A magnesium deficiency, for example, is associated with grass tetany that occurs during lush plant growth periods that appear to provide the opportunity for high production. Reduced potassium can also depress animal productivity, by reducing the appetite and so the food intake. Particular attention should be given to the macro-mineral status of animals grazing on drought or winter dormant forages for extended periods of time.

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Micro-minerals

The trace elements, although needed in only minute amounts, are crucial to normal animal metabolism. Iodine is a component of the hormone thyroxine, iron equips blood cells to carry oxygen, and cobalt is required by microorganisms to synthesize vitamin B_{12}. Many of the minor elements are cofactors in the enzyme systems involved in energy and protein metabolism. Therefore, "minor" or "trace" should not be interpreted as meaning of less qualitative importance. Animals cannot function normally without an adequate supply of any of the required elements, major or minor.

It is not possible at this writing to make definitive predictions about micro-mineral deficiencies and toxicities due to the wide disparities in the amounts required as compared to the macro-minerals. Trace element deficiencies are less widespread, less predictable, more difficult to recognize and probably quantitatively less important than major element deficiencies. Exceptions to this general statement include those regions deficient in selenium, iodine or cobalt. It should be noted that rangelands deficient in these micro-elements are extensive throughout the world.

Toxicities resulting from consuming excessive amounts of micro-elements also occur in natural settings. An example is peat scours, a high molybdenum induced copper deficiency, on high organic matter soils. Yet, the importance and extent of trace element imbalances on rangelands remains largely undetermined.

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Nutritive Value of Forages

Nutritive value is an inclusive expression used to encompass all nutritional attributes of a forage in relation to its overall value to the consuming animal. However, the term is often used in the more restrictive sense of **forage quality**, including protein content, digestibility or simply palatability. The reader is encouraged to develop the broad view of quality which includes consideration of usefulness of forage constituents (nutritive value) for particular productive purposes in animals as proposed above. This section discusses systems of nutritional description of forages and the classification of forage types for application in grazing management.

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Nutritional Description of Forages

A useful description of forages must somehow relate to the nutrient groups required by animals. These groups were enumerated as energy, protein, vitamins and minerals. The **Proximate Analysis System** was developed over 100 years ago in an attempt to use chemical determinations to describe the value of feeds for animals. The proximate factors used as components are crude fiber (CF); crude protein (CP); crude fat, often stated as ether extract, EE; nitrogen-free extract, NFE; and ash. The most widely used proximate component analysis has been for crude protein.

$$(3)\ CP\ (\%) = \%\ Nitrogen \times 6.25$$

The protein contained in a wide array of forages averages about 16% nitrogen. So the standard procedure is to determine the nitrogen content of a forage, multiply that value by 6.25 (100/16) and refer to the product as **crude protein**. Crude fiber (CF) and NFE fractions were intended to estimate the less and more easily digested portions of feeds, respectively. When applied to forages this arbitrary partitioning does not adequately differentiate the digestibilities of these fractions.

The adoption of the proximate analysis system to describe feed fractions led to the development of Total Digestible Nutrients (TDN) approach. The latter was an attempt to more adequately describe the energy value in feeds. **Total digestible nutrients** are defined as the sum of the digestible portion (% composition x coefficient of digestibility, COD) of each of the proximate organic components with an adjustment factor of 2.25 for EE. Ash is not included because it contains no energy, while EE is increased because fat contains about 2.25 times the energy per unit weight compared with carbohydrates. The TDN system has been very useful over a long period of time in assigning values to feedstuffs that are relatively constant in composition but is less adequate for forages, especially range forages which vary widely in chemical components within the proximate fraction.

The detergent fiber analysis system (Van Soest 1967) was a major improvement in the evaluation of the nutritional characteristics of forages. Partitioning cell content (NDS) from cell wall (NDF) distinguishes that portion that is essentially totally digestible from that which is partially and variably digestible, respectively. Further fractionation of the NDF into its components including acid detergent fiber (ADF), acid insoluble ash (AIA), lignin and silica has refined the analysis of the fibrous portion. A very useful adjunct to this system of analysis was the development of a two-stage, micro-digestion technique (Van Soest et al. 1966). This technique, in vitro digestion of dry matter (IVDDM), provides an approximation of the digestibility of plants and plant parts. Further computorial correction to an organic matter basis provides an estimate of digestible energy content in megacalories.

However, IVDDM does not take into account the variable effects of rate of fermentation, digesta flow rate and retention time on digestive efficiency (Huston et al. 1986). These factors vary among animal species and in response to **associative effects** of companion dietary constituents. That is, the nutritional value of a dietary constituent can be enhanced by the addition of another dietary constituent which supplies a limiting nutrient.

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Determinants of Nutritive Value

Forage quality is determined by various combinations of micro- and macro- scale biotic and abiotic factors (Morley 1981, Wheeler and Mochrie 1981, Van Soest 1982). The inherent morphological, anatomical, physiological and chemical characteristics of each plant species determine its potential nutritive value. Abiotic and temporal factors modify this potential.

Examples of biotic factors can be found in the differences in quality between grasses utilizing three-carbon (C_3) versus four carbon (C_4) photosynthetic pathways and between monocotyledonous (monocots) and dicotyledonous (dicots) plants (Table 2.3). In the first example the C_4 plants, commonly termed warm-season species, contain less mesophyll and greater proportions of schlerenchyma, epidermis and vascular tissue than C_3 plants, cool-season species (Fig. 2.12). Vascular bundles are densely packed and parenchyma bundle sheaths are thick-walled in C_4 grasses (high NDF), therefore inhibiting microbial digestion in the rumen, while reduced mesophyll (low NDS) provides less protein and soluble carbohydrates. Lignin concentrations are higher and leaf:stem ratios lower in warm-season grasses than in cool-season grasses. Stems have significantly greater proportions of structural carbohydrates and lignin (high NDF) in all forages, while leaves have greater proportions of cell contents (high NDS) and crude protein than stems.

Table 2.3

Figure 2.12

Shrubs and most forbs are dicots and their leaf biomass is generally of higher nutritive value than that of grasses (monocots) (Table 2.3). Non-woody plant parts of dicots have greater quantities of cell solubles than monocots and lower levels of structural carbohydrate and lignin. This apparent advantage is often offset, however, by biologically significant proportions of secondary compounds (tannins, volatile oils, alkaloids etc.) in a number of shrub and forb species. Many of these secondary compounds produce inhibitory and/or toxic effects on the microbial fermentation (Hegarty 1982). Hence, even if the quality of a particular plant species is comparatively high, inhibitory factors may reduce the utilization of the metabolizable nutrients (Burns 1978).

Food materials of the highest quality are found in metabolically active tissues (live leaves, stems, flowers, etc.) or storage tissue (seeds, fruits and roots). Live plant tissue is of higher quality then dead. Similarly, younger live tissue by virtue of its greater metabolic activity is of higher quality than older live tissue. Generally, live leaf is of higher quality than live stem because of its greater photosynthetic activity. Nutrient quality declines as the rate of development or recruitment of new leaf tissue decreases and the rate of senescence increases (see Chapter 4). While the overall quality of live leaf material may not change drastically with age, increasing amounts of senescent material dilute nutrient density (Greene et al. 1987). Concurrent changes in the leaf to stem ratio also occur as a plant matures. In terms of the energy flow (see Chapter 1) and standing crop (g/m^2), available gross energy ($Kcal/m^2$), usually peaks when stems have elongated in mid-anthesis. However, maximum available net energy (NE $Kcal/m^2$) occurs earlier in the late vegetative and early anthesis stages before significant reproductive culm elongation occurs (see Chapter 4).

Turning to the abiotic factors which affect forage quality the most important are air temperature and soil moisture. These environmental conditions modify the rates at which live material is accumulated and senescence occurs. Generally, the leaf and stem tissue of grasses grown at high temperatures is lower in both digestibility and crude protein content. Lignification and the formation of structural carbohydrates (NDF) occur rapidly at elevated temperatures causing a concomitant reduction in the cell soluble fraction. Shrubs and forbs usually exhibit little change in leaf quality until senescence; however, stems of forbs and juvenile leaders of shrubs exhibit exaggerated declines in quality with advancing age (Petersen et al. 1987). Below normal ambient temperatures that occur during the growing period frequently reduce growth rate and respiration rate, thereby reducing the rates of senescence, stem elongation and lignification. These reduced rates effectively extend vegetative growth further into the growing season so the resultant standing crop maintains greater proportions of digestible dry matter and protein than the same forage crop under normal temperature conditions.

Restricted soil moisture can either increase or decrease forage quality. If moisture is restricted during the vegetative growth stage creating slowed growth, but not senescence, delayed maturation maintains forage quality in a manner similar to lower ambient temperature. However, if restriction progresses to severe water stress, forage quality decreases in response to nutrient translocation and senescence of plant parts. In most rangeland environments, drought is often accompanied by above normal ambient temperatures which exacerbate the plant's growing conditions by increasing the rateof evapotranspiration.

In summary, the primary factors influencing the quality of forage are the plant species present and their level of metabolic activity. The more active a particular tissue is the greater its quality. Environmental conditions in turn modify this activity by affecting the rate at which it occurs.

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Practical Classification of Range Forages

A variety of plant communities, each having a unique assemblage of plant species, occurs in rangeland ecosystems. Intra- and interspecific competition among plants for resources and interactions with prevailing climatic conditions lead to formation of plant communities (see Chapter 5). Animals, however, are neither plant taxonomists nor community ecologists and consume plants according to availability and preference (see Chapter 3). Whether a plant is an increaser, decreaser or invader (see Chapter 4 and Chapter 5) is immaterial to the animal. Instead, the amount of live-to-dead and leaf-to-stem material available, presence or absence of inhibitory factors, etc., in various species or species groups are the only matters of concern (see Chapter 3).

Generally, animals select from the highest quality components of the available forage pool first. Some plant species are highly nutritious but available only in limited quantities while more readily available species are less nutritious. As the pool of highest quality plants is depleted, increasing quantities of the next highest quality components are consumed. These selection and consumption processes are integrated through space and time (see Chapter 3). Although each rangeland environment is composed of a unique agglomeration of plant communities, each with particular vegetational characteristics, the following general classification of their functional nutritional components has been proposed (Huston et al. 1981).

Semiarid and arid rangelands are usually dominated by a particular forage type that is relatively high in quality during early vegetative growth but quickly declines in quality as the forage accumulates and matures. This forage type provides the majority of organic matter consumed by grazing animals on rangeland and is termed the **production component**. On temperate and tropical rangeland, this component is comprised of perennial grasses. Characteristics limiting the nutritional value of these plants are the very same as those ensuring their availability for consumption. Their content of structural carbohydrates is quite high, they enter dormancy during unfavorable periods and reinitiate growth during favorable periods. Adult bulk feeders can maintain acceptable levels of productivity when grazing these forages, provided their reproductive cycle conforms closely to the temporal nutrient profile of the vegetation. In other ecosystems, the production component may be annual grasses as for example California annual grassland or shrubs in salt desert shrub ecosystems, but the common characteristic of the production component is that it ultimately determines the sustained animal yield potential because it is the principal stable component under existing grazing conditions.

Other plant species provide a **quality component** to diets of ruminants on rangeland. These species, which differ from one ecosystem to the next provide only a minor amount of forage, but that forage is significantly higher in nutrients CP, DE, etc. than the production component. Certain perennial forbs, shrub leaf buds and tips, mast, fruits, seeds, etc. contribute disproportionately to the productivity of bulk feeders both by raising the overall diet quality and preventing nutrient deficiencies, for example vitamin A and phosphorus. Perhaps more importantly, quality components provide a suitable diet for grazing and browsing small ruminants having higher nutritional requirements, thereby increasing the overall production potential of a specific rangeland. The quality component is also important to big game populations.

The plant species making up the **level component** of forage materials in this classification system can be characterized as those which remain green throughout the grazable portion of the year. These species rarely produce forage that is either exceptionally high nor ruinously low in nutrient content, but offer fair to good quality forage during all seasons. The level component competes with the production component in a plant community for space, moisture and nutrients, but substitutes for the quality component during periods of dormancy and can significantly reduce reliance on supplemental feed. Examples of plants in the level component include elk sedge in the Intermountain area of North America and Texas wintergrass in north and central Texas. Leaves of evergreen browse species, such as fourwinged saltbush of western North America belong to this component.

Plant species that are of exceptionally high quality and are available episodically make up the **bonus component**. These species are the antithesis of the production component species, being neither stable nor predictable. In continental climates, annual forbs and grasses commonly form this component. When present, these plants contribute significantly to the live standing crop and offer a substantial short-term opportunity for enhanced animal production. Sufficient management flexibility must exist to exploit their presence. Animals having high nutritional requirements such as growing or heavily lactating animals make the most efficient use of this component. This component is also particularly important to upland and non-game birds and big game animals.

In this classification system, **null component** plant species are those not used unless the availabilities of the other components, particularly the production component, are severely restricted. Significant animal consumption of these forages indicates a badly depleted forage resource. In Texas these plants include prickly pear, creosote bush, tarbush, honey mesquite, Texas persimmon, broomweed and croton. These species are of limited value to grazing animals yet may be an extremely important part of the diets of sympatric mammals and bird species. The presence of these plants is often mistakenly considered desirable by stockmen because they are viewed as emergency forage. But this view is incorrect. Cyclic utilization of this component is an indicator of unstable nutrient intake where nutrient demand grossly exceeds nutrient availability from alternative components.

The **toxic component** includes all species poisonous or injurious to grazing animals. Many of these species serve dual roles. They are of some value in other components but are harmful when consumed in excess or at a particular stage of growth. Examples of these dual-role plants in

Texas include kleingrass, peavine, sacahuista, oaks, johnsongrass and pricklypear. Acute effects of toxicity are obvious and can be dealt with promptly. Conversely, chronic effects, often go undetected and may even be more costly by virtue of reducing production efficiency.

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Nutrient Intake and Utilization

Ruminants optimize forage consumption to meet their nutrient requirements if no physical or metabolic restrictions are imposed (Weston and Poppi 1987). **Voluntary intake** of forage is the amount consumed by the animal when its accessibility to forage is unrestricted. In such a case, regulation of intake is dependent only on endogenous mechanisms triggered either within the animal or by some characteristic(s) of the forage (Baile and Forbes 1974, Forbes 1980, Van Soest 1982, Grovum 1986). **Forage (nutrient) intake** under grazing conditions is a modified expression of voluntary intake and is influenced by forage quality (Table 2.4), forage availability (Table 2.5), forage harvestability, environmental stress and management (Chacon and Stobbs 1976, Hodgson 1977, Arnold and Dudzinski 1978, Finch 1984, Allison 1985, Young 1986, 1987). We group environmental stress with nutrient intake in this discussion because nutrient demand for travel, diurnal and seasonal thermal fluctuations and predator avoidance are more pronounced under free-grazing than controlled feeding conditions.

Forage intake of grazing ruminants is usually controlled by distension of the reticulum and cranial sac of the rumen (Grovum 1986). Distension of this sensory region is decreased by digesta passage to the lower tract and/or by reducing ingesta volume and mass through mastication and fermentation. Mastication, primary and secondary, is the major means of particle size reduction (McLeod and Minson 1988) resulting in more dense, less bulky digesta and more rapid fermentation and passage.

Table 2.4

Table 2.5

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Animal Factors Affecting Nutrient Intake

Voluntary intake may decrease before, and increase after, parturition in both sheep and cattle (Jordan et al. 1973, Weston 1982, Warrington et al. 1988). Decreased intake during late gestation is attributed to decreased reticulorumen capacity caused by a combination of rapid fetal growth and/or increased deposition of abdominal fat and hormonal mechanisms (Forbes 197l, Baile and Della-Fera 1981). The extent to which these mechanisms ultimately control voluntary intake is not known. Voluntary intake increases post partum, but lags behind increased energy requirements for lactation by 2-6 weeks, apparently because of the time required for the rumen to increase in size and reestablish maximum volume (Weston 1982).

There is no clearly defined relationship between body condition (fatness) and nutrient intake in cattle and sheep (Freer 1981, Weston 1982). The general consensus is that abdominal fat restricts voluntary intake 3-30% (Cowan et al. 1980, Freer 1981, Fox 1987), although various effects of fatness have been reported (Bines et al. 1969, Holloway and Butts 1983, Adams et al. 1987b). Conversely animals in a depleted state, consume greater quantities of moderate to high quality forages (**compensatory intake**).

Beef cattle and sheep of different genetic backgrounds exhibit markedly different voluntary intakes (Arnold and Dudzinski 1966, Table 2.5) and efficiencies of production. Maintenance requirements of beef cattle account for 70-75% of the ME requirements through a production cycle, under pen fed conditions (Ferrell and Jenkins 1987). While limited quantitative data are available (Osuji 1974, Havstad and Malechek 1982) the maintenance energy costs of free-ranging cattle are estimated to be 20-50% greater than under pen fed conditions (Cook 1970). Therefore, the mature size and milk production capability of cows could have a marked effect on their efficiency of production under grazing conditions. Metabolizable energy intake increases as mature size and milk production increases. Similarly, Havstad and Doornbos (1987) reported voluntary intake of 3/4 Simmental cows was greater than Hereford cattle under free ranging conditions. Under conditions of low forage quantity and/or quality the production potential of 3/4 Simmental cattle was not achieved.

Animal genotype and phenotype can have marked effects on voluntary intake and efficiency of production. Dairy cattle breeds have higher maintenance (Solis et al. 1988) and lactation (NRC 1978, 1984) energy requirements and intake per unit weight than beef breeds. These are attributed to differences in physiological prioritization of tissue growth and maintenance (Solis et al. 1988). Dairy breeds have a higher proportion soft tissue organ mass having high maintenance requirements. Additionally, dairy breeds store a larger proportion of fat internally than beef breeds, thereby decreasing insulatory capacity. Bos indicus cattle (Brahman type) have been found to exhibit lower maximum intakes of moderate quality diets, under minimal stress, than Bos taurus (Hunter and Siebert 1985a, 1985b). Lower intake may be the result of B. indicus having a smaller digestive tract; however, on poor quality tropical grasses, B. indicus digests forages more completely and still exhibits greater voluntary intake than B. taurus (Hunter and Siebert 1985a, 1985b). Voluntary intake of moderate to high quality forages is greater for B. taurus than for B. indicus. When low quality tropical grass diets are supplemented with nitrogen, voluntary intake of B. taurus is greater than B. indicus indicating B. indicus may have a greater capacity to recycle nitrogen (Hunter and Siebert 1985b). Adaptability of these cattle species to the thermal environment also influences intake patterns. Based upon these findings for domestic ruminants, selecting genotypes suited to a particular range setting is an important management consideration.

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Influence of Environmental Factors on Nutrient Intake

Thermal conditions affect intake more than any other environmental factor (see Chapter 3). The range of temperature and humidity where the ruminant is at relative equilibrium with the environment is the **thermal neutral zone** (TNZ). Beef cattle have a TNZ for intake of 10-25 C (Finch 1984, NRC 1981a). Below the TNZ, **cold stress**, intake increases in response to heat loss down to -25 C if fill limitations are not encountered. Above the TNZ, **heat stress**, intake decreases in response to heat loading. Abrupt changes in temperature, i.e., blizzard or sleet, may cause a transitory decrease in intake, even within the TNZ. At sustained temperatures below -25 C, grazing time and intake may be restricted under free ranging conditions to minimize energy expenditures for grazing (Young 1986, Adams et al. 1986, 1987, NRC 1981a). As would be expected from their origin, B. taurus are more cold tolerant than B. indicus animals. The reverse is true in terms of heat tolerance (Finch 1984). Intake responses follow the same trends as tolerances. Crosses of these cattle types exhibit intermediate intakes across the ranges of heat and cold stress.

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Forage Quality and Nutrient Intake

Level of forage intake and associated forage quality interactions are complex functions that vary through time and across animal and forage types (Table 2.4). Generally, short-term intake responds in positive manner to increasing digestibility up to 80% (Hodgson 1977, Freer 1981). However, because ruminants tend to consume forage in response to physiological requirements, long-term intake regulation is relative to a certain level of homeostasis in body condition. Hence, the treatment which follows is an attempt to blend both short- and long-term intake responses to forage quality relative to physiological requirements.

Long-term voluntary intake patterns are determined by the amount of food needed to meet the physiological requirements but modified by the amount which can be consumed before physical constraints are encountered. Both are affected by forage quality, in that less food is needed if the food items have higher concentrations of nutrients, and more food can be physically consumed if the bulky, indigestible fraction is lower. Figure 2.13 illustrates the relationship between forage digestibility and intake assuming no other restrictions. The descending curve represents forage intake needed for maintenance requirements for digestible dry matter, 4.3 kg (9.5 lb) DDM, for a 500 kg (1200 lb) beef cow (NRC 1984). At 20% digestibility, 21.5 kg (47 lb)/day of forage must be consumed to permit the cow to extract the required 4.3 kg of DDM. However, only 5.4 kg/day of an 80% digestible forage must be consumed to supply the same 4.3 kg DDM. The ascending curve depicts the theoretical maximum consumption of forages within the range of 20-80% digestibility, assuming a constant 1% body weight of feces (Conrad et al. 1964). The two curves intersect at approximately 46% forage digestibility and 9.3 kg/day forage intake. Note that to the left of the point of intersect, maximum intake falls below required intake. In the above example, the cow fed a forage that is less than 46% digestible cannot consume enough to reach the required amount of DDM. In the right-hand portion of the figure, maximum intake rises above required intake, so the cow can consume greater amounts of forage at these digestibility levels than are required to meet DDM maintenance needs. The model proposed by Conrad et al. (1964), postulated that voluntary intake tends to take on the pattern formed by the area below both curves. In which case, voluntary intake of forage increases as the digestibility of the forage increases to the point of intersect. Further increases in digestibility lead to decreased food intake and so no change in DDM intake occurs.

Figure 2.13

This model has been challenged in recent years as being inaccurate and too simplistic (Freer 1981, Grovum 1986), and in some cases with good reason. For example, low digestibility forages are, almost without exception, also low in protein. A small addition of protein to the diet dramatically increases intake of a low quality forage indicating that its inherent low digestibility alone did not lead the animal to consume less. On the other side of the scale, grazing animals do not abruptly quit eating the moment their daily nutrient requirements for on-going physiologic processes are met. This fact is easily seen in cows becoming overly fat after the loss of an infant calf or failure to breed. Animals clearly initiate and terminate feeding in response to an array of physical, chemical and humoral signals (Grovum 1986). In the lower digestibility range, physical factors are most important, although ruminal nitrogen status is certainly involved. At higher diet digestibility, physical factors are less important so internal chemical and humoral factors become more important in producing hunger and satiety signals. Although the model shown in Figure 2.13 does not account for all factors modifying forage intake, it does depict generalized long-term forage intake patterns of grazing ruminants.

The area to the left of the point of intersect, below 46% digestibility in this example, forms the **zone of response**. As forage quality increases, nutrient intake (Ventura et al. 1975) and productivity increase. If a cow which is not lactating and at mid-pregnancy, consumes 9.3 kg of forage, normal growth of fetus and some accumulation of fat for later use after parturition occurs. However, if she consumes forage of lower quality, < 46% digestibility, little or no fat accumulates and fetal development is retarded. Once born, the calf will be smaller and weaker. The cow will produce less milk, wean a lighter calf and have a reduced probability of rebreeding on schedule. In the extreme case, < 30% digestibility, the cow is malnourished and will eventually die.

The area to the right of the point of intersect, above 46% digestibility in the example, forms the **zone of adequacy**. As forage quality increases above the 46% digestibility level, the model indicates that the cow is correspondingly less stimulated to consume the forage, thus intake declines. Because requirements are met at a lower level of intake of a more digestible diet, no decline in productivity accompanies the decline in intake. An animal previously restricted by either quantity or quality of diet to the point of nutrient depletion increases intake to a greater level than depicted. Once recovered from the depleted state, voluntary intake is adjusted lower.

Adequate data on forage intake in free-grazing ruminants in different physiological states and over a wide range of forage digestibility is limited due to the difficulty of making such measurements. However, sustained access to forages in the higher range of digestibility is rare under range conditions. If this occurs, animals having higher nutrient requirements (stockers, replacement heifers) should be grazed to make the most efficient use of this resource. The art and science of grazing management is matching the nutrient supply in the forage to the nutrient requirements of the foraging animal to reach sustained optimal productivity. In that spirit we submit the Huston - Pinchak Theorem:

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GOOD ENOUGH IS EXCELLENT!

Diets of range animals typically fluctuate above and below the theoretical point of intersect (Fig. 2.13) in a more or less cyclic fashion based upon short-term intake responses to quality of forage consumed (Table 2.4). During periods of high physiological requirements such as early to mid-lactation, the animal may not be capable of consuming adequate amounts of forage to prevent tissue loss. Whereas during periods of low physiological requirements and on occasion higher forage quality, nutrient intake may greatly exceed current requirements and result in substantial tissue accretion. We define this spectrum of forage quality as the **normal range** of forage quality and intake. This spectrum is specific for each of the animal species, types, ages and uses in production systems and is reflected in Table 2.4. The data in this table illustrate a wide array of seasonal trends of intake in response to forage quality over an equally wide array of forage type-animal species combinations, i.e., "a spectrum of normal ranges". A forage or assemblage of forages providing a diet in the normal range is therefore correct for that production system. Good enough is excellent.

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Influence of Forage Availability and Structure on Nutrient Intake

An obvious interaction exists between the quantity and quality of available and consumed forage (see Chapter 1). Selective utilization of areas within pastures as well as selective utilization of plants and plant parts within these areas (see Chapter 3) make it difficult to determine which component of available forage is regulating intake. Table 2.5 is an overview of the dynamic interactions between forage and animal type demonstrating the relationships between forage intake and forage availability. Generally, standing grass crops below 1000 kg/ha restrict forage intake by sheep and cattle on temperate native grasslands of North America. However, on improved pasture, temperate and tropical, standing crops become limiting between 1000 and 4000 kg/ha (Stobbs 1973, Forbes and Coleman 1987). Differences within and between regions are related to forage species or species mix of the pastures. The vertical distribution of leaf and stem biomass and their live and dead fractions ultimately limits intake (Chacon and Stobbs 1976, Poppi et al. 1980, Freer 1981, Forbes and Coleman 1987). Hence the amount of available live leaf biomass (kg/ha) within an exploitable zone (see Chapter 3) determines maximum rate of intake. Departure from maximum rate of intake results from the decline of live leaf within this zone below a critical threshold. The point at which this threshold is reached varies with forage species, growing season, length of grazing period and animal species.

Historically the relationships between forage availability and intake have been described in relation to forage standing crop (Table 2.5). However, overwhelming evidence exists that the amount of leaf and the ratio of leaf to stem within harvest horizons ultimately determines the upper limit of intake, and therefore production, for a given set of forage conditions at a specific point in time. The frequency, severity and duration of periods of restricted intake determine the sustained animal yield capacity of any land area. Short-term conditions can be overcome through supplemental (substitutional) feeding. Chronic intake restriction can be overcome by destocking and/or increasing forage production and/or increasing of the amount of leaf material. The latter two remedies depend on increased cultural inputs.

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Supplemental Nutrition Management

Supplemental nutrition management is defined as the implementation of practices specifically aimed at improving the nutritional status and/or efficiency of converting available forage into animal products in a given circumstance. Supplemental nutrition is an option when the forage base fails in quantity and/or quality of nutrients to meet the physiological requirements of the grazing animal. Supplemental feeding is targeted at correcting nutrient deficiencies or providing nutrients to stimulate intake, digestion and/or utilization of forage (Table 2.6). In a broader sense, supplemental nutrition management includes corrective practices to align nutrient supply with nutrient demand. Replacing a quantity of forage that would otherwise have been consumed by feeding an alternate feed supply is called substitution. Supplying a limited nutrient, i.e., protein, to animals having unrestricted forage available of poor quality is called **supplementation**. Huston et al. (1988) (Fig. 2.14) clearly demonstrated the potential stimulation in forage intake of low quality forages by sheep with low levels of protein supple-mentation. Generally, field experiments have been less conclusive (Table 2.6) although low levels of protein supplementation on poor quality, (< 6% crude protein) diets can stimulate forage intake (Caton et al. 1988a).

Table 2.6

Figure 2.14

Grazing management is a primary means of achieving a balance between animal demand and nutrient supply. Decisions on animal populations (species, breeds and classes), stocking rates, breeding dates, pasture sizes, rotation schedules, etc. (see Chapter 7) set the degree of match or mismatch between the supply of and demand for nutrients. Supplemental nutrition management in this context is then the fine adjustment in the balance between supply and demand. The following discussion describes four general categories of mismatches of nutrient supply and demand. The difference between high and low quantities relates an animal's ability or inability to achieve adequate intake of forage in a reasonable length of grazing time (see Chapter 3). High and low quality refers to the normal range defined in the previous section.

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Quantity and Quality High

This range condition is seldom found on a sustained basis but often occurs on a short-term basis. Seasonally, such a condition occurs on temperate rangelands during the late spring growth period. Small grain pastures, wheat, oats, rye, provide forage of this type until mid-anthesis. This is an important interval for animals matched to forage within the **normal range** as this "up" period follows and precedes a "down" period. Therefore, it is essential for recovery from a past depletion period and preparation for future depletion.

It is conceivable that under some conditions both diet quantity and quality consistently, or at least frequently exceed requirements. In such cases, forage quality and nutrient intake rise above the **normal range**. The expected result is overly fat animals, reduced efficiency in transferring dietary nutrients into animal products and possibly reduced individual animal performance. The corrective management strategy is to restructure the grazing population. That is, animals having greater productive potential and a greater capability for utilizing the high quality forage should be selected or the stocking rate of existing animals should be increased.

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Quantity High and Quality Low

This range condition commonly occurs when abundant plant growth is followed by an extended period of temperature and/or moisture induced dormancy. This condition is characteristic of the dormant season in the temperate region. The residual forage contains comparatively high proportions of structural carbohydrates, thereby diluting its energy and protein value. The key concern is whether the digestibility of the forage fluctuates within the **normal range**. Remember that forages that fall in the lower region of the normal range for dry cows virtually always are below the normal range for lactating cows and small ruminants, sheep, goats, deer, etc. A supplemental nutrition program should provide the limiting nutrients (e.g., protein, phosphorus, vitamin A). This supplemental feeding program may stimulate forage consumption if protein and/or phosphorus are critically low or may decrease forage consumption by substitution (Fig. 2.14). Assuming that protein and/or phosphorus are not limiting in the forage, forage consumption decreases by approximately one-half of the amount of concentrates fed.

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Quantity Low and Quality High

The converse of the previous range profile, this condition favors small ruminants, especially goats and deer, which are flexible in their foraging behavior. This condition is characteristic of shrub dominated landscapes and often results from overgrazing and/or protection from fire (see Chapter 5). Supplemental feeding can be used to increase the stocking rate, but if the range is properly stocked with the correct animal types, supplemental feeding does not improve the productivity of the individual grazing animals.

Special use pastures can also be assigned to this category such as small grain pastures of extremely high quality, especially in protein. Feeding grains to growing animals, lambs and calves, on small grain pastures allows an increase in stocking rate without altering animal performance. In this case, an almost exact substitution occurs, the small grain forage intake is reduced by the amount of the grain fed. Benefit is realized because the high concentration of protein is more efficiently distributed to a larger number of animals resulting in greater net secondary productivity.

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Quantity Low and Quality Low

This range condition is best typified by desert or arid landscapes. The limited standing crop typically contains an abundance of structural carbohydrates, lignin and/or secondary plant chemicals that reduce palat-bility, intake and utilization. The proper nutritional strategy in this circumstance is to encourage high plant selectivity by maintaining a low stocking density. Feeding during dormant interim periods provides a balance of nutrients when little or no alternative natural supply is available.

Similar seasonal conditions exist on rangelands overstocked during periods of dormancy. Very little forage is available and that which remains is low in quality. For best results in the short term, a good quality hay or a complete feed should be provided. Heavy rates of stocking on yearlong range lead to similar nutritional conditions during winter dormancy (Heitschmidt et al. 1987, Greene et al. 1987) hence establishing a cyclic pattern. The range between the highs and lows in nutritional adequacy is too broad to fit within the nutritional state characterized earlier as the **normal range**. The lows are too low for adequate recovery during the highs; thus, productivity is substantially reduced. Management alternatives include reduced stocking to increase quantity and quality of diet or liberal feeding which rarely yields economic returns and only prolongs an unsustainable ecological condition.

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Conclusions

So, what have we said? Ruminant animals are placed on rangeland as primary consumers of the vegetation formed by the capture of solar energy. In a natural state, these animals would in turn adapt spatially and in proper numbers for more or less sustained survival. However, the human demand for the offtake of consumable products (food and fiber) imposes a requirement in excess of survival and so creates an equilibrium that is less than a natural balance. Restricted movement, altered numbers and controlled breeding impose an unnatural match between what is offered by the vegetation and what is required by the grazing animal.

Through an understanding of what nutrients are important, their probable concentrations and fluctuations in forages and their requirements by animals, management can partially align nutrient supply and demand on rangeland. Supplemental nutrition management is then required to provide a fine adjustment for optimal productivity. Perhaps the most important aspect of management is the recognition of what is involved in grazing behavior and diet selection, the topic of Chapter 3.