THE BIOLOGY AND MANAGEMENT OF WILD RUMINANTS

CHAPTER ELEVEN

FORAGE CHARACTERISTICS AND THE DIGESTIBILITY
OF PLANT TISSUE

by

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CHAPTER 11. FORAGE CHARACTERISTICS AND THE DIGESTIBILITY OF PLANT TISSUE

Life on earth depends on the process of photosynthesis. Plants are called primary producers, using light energy to synthesize carbon dioxide, water, and minerals into new plant material. Animals that eat plant materials are called primary consumers, and animals that eat the primary consumers are called secondary consumers. They are also dependent on plants even though they do not eat plant material directly.

The nutrients in forage are the substrate for metabolic processes. The annual pattern of ecological metabolism reflects the timing and costs of metabolic processes that result in maintenance, growth, and reproduction in relation to the changing nutrient characteristics of the range forage over the annual cycle.

Metabolic patterns were discussed in CHAPTER 7. An understanding of these patterns is essential for an understanding of animal-range interactions. How can nutritive relations between animal and range be understood if the metabolic characteristics of the animals and nutritive characteristics of the range are not both known?

The nutrients in ingested food are partitioned into several pathways as food traverses the gastro-intestinal tract and nutrients are extracted and metabolized. This is so because mechanical, chemical, and metabolic processes are not 100% efficient. The idea of a process being less than 100% efficient implies a "waste," but that is not a good term for describing pathways in biological systems. Heat energy, for example, is part of the "waste" by microflora involved in rumen fermentation, but the heat dissipated by the microflora is useful to the host in the regulation of body temperature.

The efficiencies of nutrient pathways are related to specific nutrients and their specialized roles in physiological functions. There is a general pattern, however, beginning with the gross amount ingested, to the amount present in the urine and feces. Some of the forage is digested and metabolized, converted to body tissue, and then broken down and incorporated into urine and feces. Some of the fecal material is undigested forage residue, left intact from ingestion to defecation. Thus some ingested nutrients go through the gastrointestinal tract without being broken down and assimilated, and others are assimilated into new tissue that is broken down later and its constituents eliminated.

The major nutrient pathways of energy and protein are illustrated in the diagrams pages 2 and 4. Note that the basic format is very similar for the pathways of energy and protein breakdown from gross to net.
Definitions of the four-letter symbols are given below, and the categories on the upper left side of the flow diagram are discussed in the paragraphs that follow.

GREN = Gross energy  
APDE = Apparent digestible energy  
UFOR = Undigested forage residue  
MFEN = Metabolic fecal energy  
FEEN = Fecal energy  
TRDE = True digestible energy  
HEFE = Heat of fermentation  
AUUE = Absorbed but unused urinary energy  
MEEN = Metabolizable energy  
MUEN = Metabolic urinary energy  
UREN = Urinary energy  
NEEN = Net energy  
HNUM = Heat of nutrient metabolism  
MAIN = Maintenance  
ACTI = Activity  
PROD = Production  
REGU = Regulation

ENERGY

Energy is a very basic nutrient that is necessary for all of the life functions. The pathways of energy partitioning from gross to net are discussed in the paragraphs that follow.
Gross energy. The gross energy in any combustible material can be expressed in kcal per unit weight or kcal per unit volume. Firewood is sold on the basis of volume, where one cord = 128 cubic feet, equal to a stack 8 by 4 by 4 feet. Ther energy in this cord varies. A cord of white oak, a very dense wood, gives off 7,700,000 kcal when burned, and of white pine, a light porous wood, 4,100,000 kcal when burned.

The gross energy in a forage is the amount of energy released when that forage is completely oxidized in a bomb calorimeter (See Moen 1973: 172). It is an initial nutritive measurement of the energy in the product of primary production. The energy content per unit dry weight, or kcal per kg, is not widely different for different forages: 4500 KCAL PER KG is a good approximation of gross energy in many forages. Complete oxidation and the yield of gross energy is not necessarily related to the nutritive energy as a result of the biochemical functions in the gastrointestinal tract. The amount of energy available as a result of digestion is dependent on the effectiveness of the rumen microflora in breaking down the forage ingested and releasing the nutrients.

Apparent digestible energy. The apparent digestible energy is the gross energy in ingested food minus the energy in the feces. It is easily determined by measuring fecal energy and subtracting it from the gross energy, but it is of limited value since feces also contain tissues of metabolic origin. These tissues have been assimilated and broken down, and are not the same as undigested food residue. These two sources of fecal energy--undigested forage residue and metabolic fecal energy--must be separated before nutritive pathways can be quantified properly.

Apparent digestibility, expressed as a percent, may be calculated with the formula:

\[
\text{Apparent digestibility} = \left( \frac{\text{Intake energy} - \text{Fecal energy}}{\text{Intake energy}} \right) \times 100
\]

True digestible energy. True digestible energy is determined by subtracting metabolic fecal energy from fecal energy, and subtracting that from gross energy. Metabolic products in the feces include such things as mucous, digestive juices, intestinal cell walls, bacteria, and protozoa. True digestibility, expressed as a percent, may be calculated with the formula:

\[
\text{True digestibility} = \left( \frac{\text{Intake energy} - (\text{Fecal energy} - \text{Metabolic fecal energy})}{\text{Intake energy}} \right) \times 100
\]

Numerically, true digestibility is greater than apparent digestibility.

Metabolizable energy. Metabolizable energy is that which is available for the nutrient metabolism that supports maintenance, activity, and production. It is the energy left after true digestible energy, heat energy of fermentation, energy in the methane, and urinary energy have been partitioned out of the gross energy. Methane, plus a few other gases in
trace amounts, are produced in the digestive tract as a result of rumen fermentation. They are eliminated by eructation. The heat energy of fermentation is due to the exothermic metabolic reactions of rumen microflora. This heat energy contributes to the regulation of body temperature, and indirectly, at least, affects levels of activity and production.

Net energy. Net energy for maintenance, activity and heat production is the metabolizable energy less the heat of nutrient metabolism. It is a high-level distinction in the series of energy pathways, surpassed only by the further division into net energy for specific body functions, such as contraction of heart muscle, net energy for the muscular contraction necessary for walking, net energy for the growth of fetal tissue, and many other specific functions. These distinctions are beyond the considerations for wild ruminants in this book; metabolizable energy is the finest division that will be applied directly to ecological situations.

PROTEIN

Ingested protein is partitioned into different sequences of metabolic processes just as energy is. Some is left intact as it traverses the gastrointestinal tract. Digested protein is broken down into amino acids and synthesized into new protein tissue. Some of this new tissue is in the form of rumen microflora, and some is new host tissue. The pathways are illustrated below.

```
  +
  CRPR  PIUF
  /   /   \
 APDP MFNT FEPR
  |     |     \
 TDIP ABUP
  |     |     |
 EURN URNI
  |     |
 MNIC NENS
```

Definitions of the four-letter symbols are given on the next page, and the categories on the upper left of the flow diagram are discussed in the paragraphs that follow.
Crude protein. Crude protein is the gross protein content of forage. It is an expression of the total protein in the forage, whether or not it may become metabolically available to a primary consumer.

Apparent digestible protein. The apparent digestible protein is the crude protein minus the protein in the feces. The feces, however, contain some protein of metabolic origin. Epithelial linings of the gastrointestinal tract, for example, are found in the feces. Thus the apparent digestible protein fraction of the crude protein is higher than the true digestible protein fraction.

True digestible protein. The true digestible protein fraction includes not only the undigested protein in the forage but also the fecal nitrogen of metabolic origin (MFEN). The true digestible protein fraction of the crude protein is higher than the apparent digestible protein, indicating that more protein was digested than at the apparent digestible protein level.

Metabolizable nitrogenous compounds. The nitrogenous compounds that actually end up being metabolized are available for synthesis, with some of the nitrogen ending up as endogenous urinary nitrogen (EURN) and some as net nitrogen synthesized (NENS) as new tissue. Endogenous urinary nitrogen is eliminated, though some is subject to resorption and recycling.

Net nitrogen synthesized. The nitrogen in the metabolizable nitrogenous compounds that actually ends up in new tissue represents the net nitrogen synthesized, becoming part of the protein tissue in the body.

FORAGE ANALYSES

An understanding of the nutrient pathways begins with an understanding of digestion. Food ingested must first be broken down into chemical forms that can be absorbed, metabolized, and synthesized. Since forage characteristics are very important in determining digestion, forage analyses are of definite interest.

What factors determine the digestibility of a forage for a ruminant animal? How does forage quality change as the range goes from the dormant winter condition, through various stages in phenology during the growing season, and back to the dormant winter condition? The nutritive use of the
range by consumers ultimately occurs at the cellular and molecular level. Digestibilities are affected by the molecular structure of plant cell walls. Their complex molecular structure is hard to break down; the cell walls are often quite indigestible. Materials within the cell have fairly simple molecular structures, however, and are usually very digestible. Visualize the structure and volume of the cell wall in relation to the volume of intracellular space as the growing season passes. Cell walls of emerging plant tissues are thin, and as the tissues mature, the cell walls become thicker. The cell walls of mature tissues, especially structural tissues, are thick.

As the cell walls increase in thickness, the amount of intracellular material decreases. Since highly lignified thick cells walls provide structural support to the plants, they also are an effective barrier to structural and chemical breakdown by rumen microflora. Since thicker cell walls are more resistant to chemical breakdown than thinner ones, the digestibility pattern over the annual cycle follows plant maturation patterns; the general pattern of plant development at the cellular level is the basis for variations in digestibility.

A method of nutrient analyses called "Proximate analysis" has been used for over 100 years. Unfortunately, the results of this chemical method are not always closely aligned with the biological processes going on in the ruminant animal. Short (1966:163) states: "The proximate analysis of important species of deer browse has many times been shown to have little value in predicting how a deer digests a particular forage item." Why is this statement true? Because proximate analysis is an analysis of the chemical characteristics of forages, and these chemical characteristics are not always related to the digestion process of living organisms. These considerations are discussed further in Moen (1973:136-139).

How, then, should forage analyses be conducted to be of greatest value in evaluating nutritive relationships of wild ruminants? What factors determine the digestibility of a forage for a ruminant animal? How does forage quality change as the range goes from the dormant winter condition, through various stages in phenology during the growing season, and back to the dormant winter condition? Cell characteristics and digestibilities are considered in TOPIC 1. Chemical characteristics, sorted according to nutrients, genus and species of plants, and different plant parts are given in TOPIC 2. Diet digestibilities, determined by in vivo, in vitro, and calculations are given in TOPIC 3.

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