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Chapter 2

NUTRITIONAL VALUES OF FORAGES

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NUTRITIONAL VALUES OF FORAGES

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The nutritional values of forages are determined by the extent to which they provide nutrients required by animals for maintenance and for performance of productive functions (growth, lactation, fattening, etc.) at given rates. A number of factors influence the quantity of forage consumed and the animal's efficiency in digesting and utilizing (metabolizing) the 40 or more required nutrients contained in the forage. Thus, the description of nutritive value could be a complex one if the content, digestibility, and efficiency of utilization of each of these nutrients had to be considered. Fortunately, most of these nutrients are present in more than adequate concentrations in essentially all forages. Of primary concern then are those nutrients most commonly deficient in forages. These are discussed in order of decreasing quantitative importance.

NUTRIENT REQUIREMENTS OF ANIMALS

Nutritive Energy

Energy deficiency occurs as a consequence of the relatively low digestibility of structural carbohydrates (cellulose and hemicellulose, also referred to simply as fiber) which comprise from 45 to 85 percent of forage dry matter. The intake of forages is frequently limited by their digestibility, thus further compounding the deficiency of nutritive energy intake. Not only is energy the most common deficiency of forages, but it is quantitatively the largest and, as a consequence, the most expensive to correct by supplementation.

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Animals store energy which can be drawn upon in times of dietary energy deficits. These stores are important and economical alternatives to supplementation, provided they are not overtaxed and are replaced in reasonable time.

Protein

Protein is required for the construction of new body tissues (growth), milk production, and replacement of body tissues constantly being degraded (maintenance). The body has limited stores of protein which can be drawn on to balance deficits in the diet. A deficit of dietary protein for 2 days or more will result in depletion of these stores and an accentuated degradation of body structural (muscle) tissue. Therefore, in contrast to energy, a protein deficiency is generally not advisable. Protein deficiencies of forages are not nearly so large quantitatively as energy and can therefore be more economically supplemented.

Phosphorus

Grasses are almost invariably deficient in phosphorus for all but the least productive animals or except when grown on high levels of soil phosphorus (or fertilization). As legumes are considerably higher in phosphorus, young growing legumes generally adequately provide for the requirements of all but young, rapidly growing animals. Although the phosphorus content of grasses can be increased by fertilization to achieve adequate nutritional concentrations, this is a less efficient and more expensive route than providing supplemental phosphorus directly to the animal. Due to the commonness of this deficiency and the relatively small quantity of phosphorus required, it is generally recommended that phosphorus supplement be provided free choice year around. Thus, phosphorus content of forages is not an important component of forage nutritive value for economic reasons.

Other Minerals

Other minerals are occasionally deficient in forages and their deficiency can be linked to either (a) specific deficiencies in the soil, and consequently in the plant, or (b) to conditions in the plant and/or its utilization by the animal which limit the availability of some minerals, such as in grass tetany. In the first case, certain soil types are deficient in and produce forages deficient in copper, cobalt, zinc,

manganese, iodine, and/or magnesium. Unless this soil deficiency limits plant growth, it is more efficient to provide supplemental mineral directly to the animal rather than via the soil, as in the case of phosphorus. Quantitatively, these mineral deficiencies are minor. Hence self-fed supplements are recommended when such deficiencies are recognized. Again, these are not economically important components of the forages' nutritive value complex.

Vitamins

Provided with a forage adequate in protein, energy, and cobalt, ruminants can synthesize enough of all vitamins, except A and E, to meet their requirements. Vitamin E is very abundant in forages. Thus, only vitamin A is likely to become deficient and then only under well recognized conditions. Quantitatively, deficiencies of vitamin A are small and economically corrected by supplementation. Therefore vitamins are, as a group, not economically important components of the nutritive value complex.

Other Factors

A number of other factors influence the value of a forage; they are substances which produce undesirable physiological consequences in the animal. Examples are (a) bloat producing factors in most legumes, (b) toxic alkaloids in certain forages such as fescue, and (c) toxic levels of certain minerals such as selenium, fluorine, and molybdenum in plants and/or in response to soil conditions. Although these may severely limit the value of a forage, they will not here be considered components of the forages' nutritive value.

Nutritive Content

Economically, the most important determinants of a forage's nutritive value are its contents of protein and nutritive energy. The nutritive energy of forages is commonly expressed as digestible energy, digestible dry matter, or digestible organic matter which indicates a ruminant's ability to digest these forages. Losses of energy due to indigestibility are the largest and most variable of the energy losses involved in utilization of forages. Thus, in most cases, digestibility is an adequate relative description of its nutritive energy potential. Accounting for further losses of digestible energy in urine, combustible gases and heat of fermentation yield metabolizable energy. The magnitude (15-20 percent) and variation of these losses are relatively small and are related to and can be predicted from digestibility (Blaxter, 1962). Similarly, efficiency of utilization of metabolizable energy for net energy purposes appears to be related to and predicted from digestibility (Blaxter, 1962). Therefore, digestibility appears an adequate measure of the relative nutritive energy potentials of forages.

Except where a forage has been subjected to higher temperatures (>60°C) in the presence of high moisture (>30 percent), the true digestibility of forage crude protein is essentially 100 percent (Van Soest, 1964, 1967; Buentello, 1972). Thus, with the exceptions to be subsequently discussed, forage crude protein is an adequate measure of the nutritive protein values of forages.

Expression of Nutrient Requirements

Nutrient requirements of an animal vary as functions of the size and activity of the animal (maintenance), the type of product (growth, fattening, lactation, etc.) being produced, and its level of production. With an accurate knowledge of these functions, one can predict the animal's daily requirement for digestible energy and protein. The ability of an animal to obtain these requirements from a forage depends upon the content of digestible nutrients in the forage and its level of consumption. If forage intake can be accurately predicted, then nutrient requirements of the animal can be expressed as the concentration of digestible energy (kilocalories per pound of forage) or crude protein (percentage) required in the forage. This is a most useful expression as it permits direct comparisons of nutrient contents of various forages to nutrient requirements for various functions.

Prediction of voluntary intake is subject to much greater uncertainty than prediction of daily nutrient requirements. Within the usual ranges of dry matter digestibilities for forages, intake is limited by and may be predicted from digestibility (Conrad _et al._, 1964). Thus, digestibility is the first consideration in comparing nutritive values of forages.

FACTORS AFFECTING DIGESTIBILITY

Classes of Forage

Forages of different general agronomic classifications differ widely in their nutritive value. Figures 1 and 2, with digestibility data obtained primarily at the Angleton Station (Riewe and Lippke, 1970), summarize the ranges in digestible energy found in various representatives of five agronomic classes of forages and compare those to the concentration of digestible energy required by various classes of livestock to perform at different levels (Lippke, 1968).

The range in digestible energy content within each forage class is the result of a number of conditions, such as maturity (to be discussed later). Under the most favorable conditions it is obvious that, in terms of energy digestibility, legumes, as a class, are higher than warm-season grasses and warm-season perennial grasses are lowest.

Figures 1 and 2 also provide a basis for selecting the class of forage required to meet the nutrient requirements for specific animals and levels of production. For example, warm-season perennials can be used for mature beef cows but are of limited value in meeting the digestible energy requirements of a 300-400 pound stocker steer (or developing heifer).

The crude protein of various classes of forages during different times of the year is shown in Figure 3. As a class, cool-season grasses and legumes are the highest in protein, with warm-season grasses the lowest. A comparison of protein content with requirement for different classes of animals (Figure 3) reveals that protein is deficient only in the warm-season grasses and then only (a) late in the growing season under conditions of low nitrogen fertilization or (b) after frost. Comparison of Figure 3 with Figures 1 and 2 also supports the generalization that deficiencies of digestible energy are more common and quantitatively more important than protein.

Species Within Each Class of Forage

There are important differences in digestible energy content of different species within classes of forages. Differences due to species appear to be greatest in the warm-season perennial grasses which, as a class, are of the lowest digestibility. For example, other factors such as season and maturity being equal, kleingrass (_Panicum coloratum_ _L._) and Dallisgrass (_Paspalum_ _dilatatum_) are consistently higher in digest-

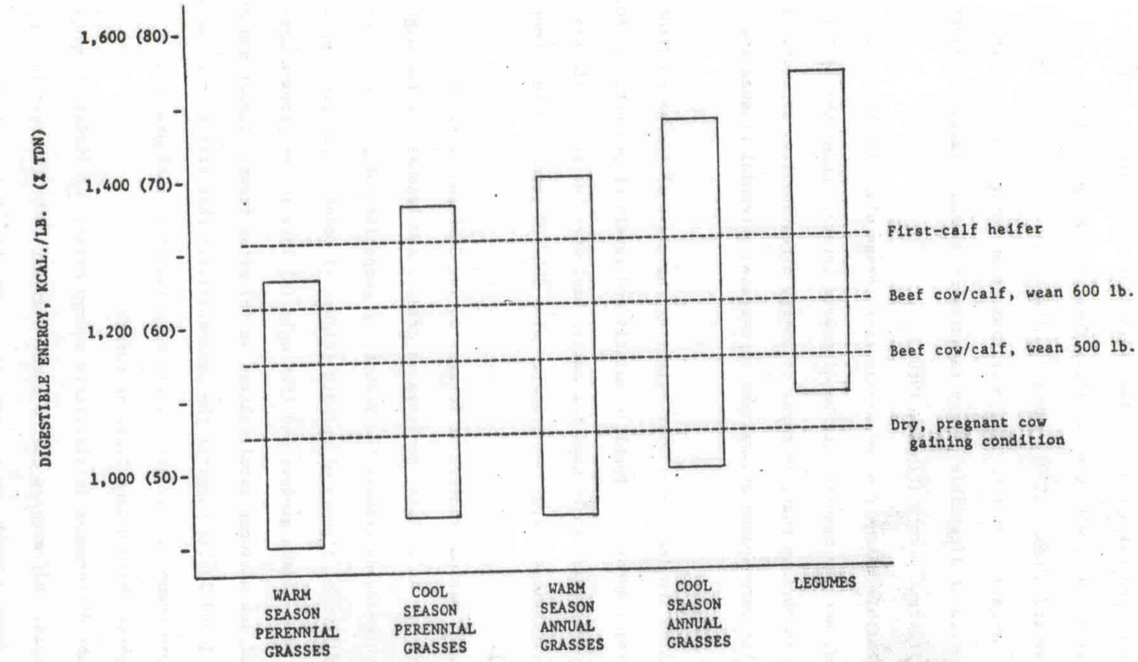

Figure 2-1. **Ranges in digestible energy of several classes of forages and the ability of the forages to meet the needs of cows.**

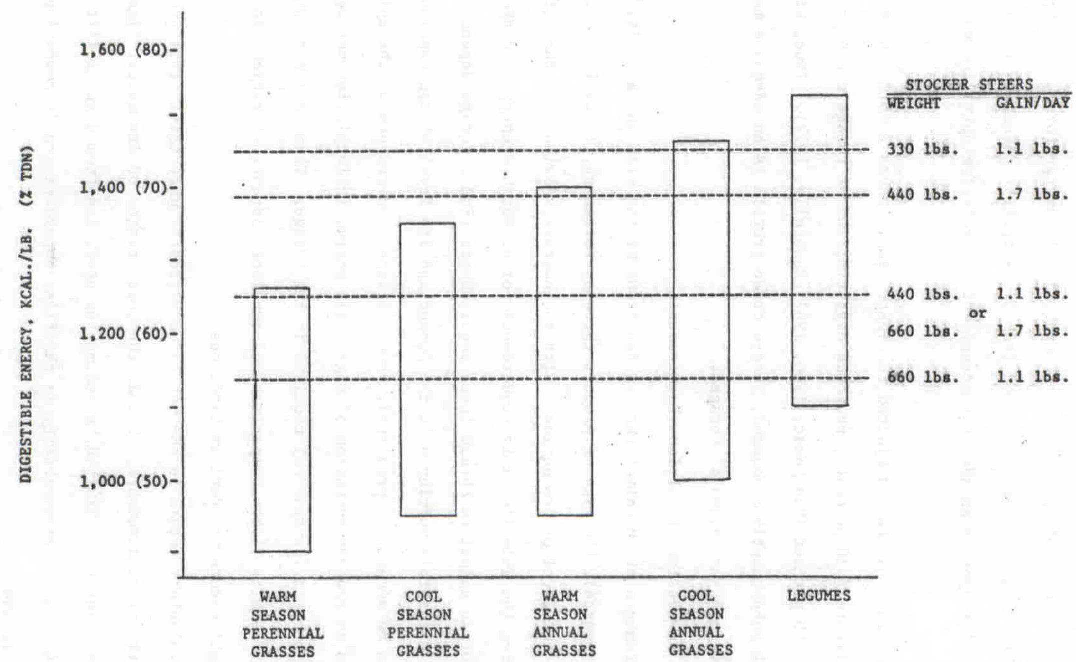

Figure 2-2. **Ranges in digestible energy of several classes of forages and the ability of the forages to meet the needs of stocker calves and yearlings.**

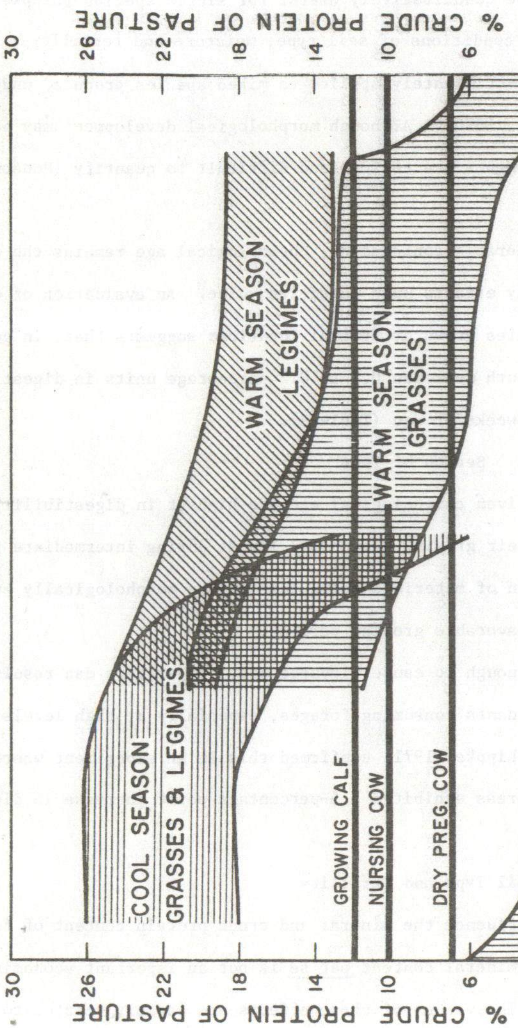

Figure 2-3. Crude protein content as related to class of forage and season.

ibility than Coastal bermuda (Cynodon dactylon (L.) Pers) (Riewe and Lippke, 1970; Conrad, 1971). In contrast, there is little difference in digestibility of species of cool season annuals, all being in the order of 60-75 percent during vegetative stages of maturity. This includes varieties of oats, wheat, barley, rye, ryegrass and triticale (Ellis and Stasney, 1971; Allen and Ellzey, 1970).

Differences in protein content due to species within agronomically similar classes of forages are small relative to differences in energy digestibility.

Variety of Forage

Variations in digestibility exist among varieties. This has been extensively studied for ryegrass and cocksfoot (Cooper et al., 1962; Julen and Lager, 1966), bromegrass (Mowat, 1969) and the Bermudas (Burton, 1970). The digestibility of four varieties of bermudagrass is shown in Table 1. Coastcross-1 bermudagrass was selected

Table 2-1. Organic Matter Digestibility of Bermudagrass Varieties[1]

Cutting	Variety			
	"Alicia"[2]	Coastal	Coastcross-1	Common
May	55.7[3]	61.9	68.7	---
June	51.6	52.0	59.9	54.8
July	46.1	53.0	53.1	49.4
August	50.2	52.6	55.2	---
October	45.9	48.8	51.4	45.9
Average	49.9	53.7	57.7	50.0
Value relative to Coastal, %	93	100	107	97

[1]Grown at the North Louisiana Hill Farm Experiment Station, Homer, Louisiana; analyzed by the Texas Forage Digestibility Laboratory.

[2]A patented grass reported by its grower to be of the variety called Alicia.

[3]Results are means for four replicates per variety. "Alicia" was significantly less (P<.05) digestible and Coastcross-1 significantly more (P<.05) digestible than Coastal and Common.

and developed as a variety of higher digestibility than Coastal or Common bermuda. The consistently lower digestibility of the variety reported to be Alicia, compared with Coastal bermuda, has been substantiated in Mississippi (Watson and Strachan, 1973), Florida (Ruelke et al, 1973) and Texas (Holt and Ellis, 1973).

In contrast to differences in digestible energy, no significant differences in protein content exist among these varieties (Table 2).

Table 2-2. Crude Protein Content of Bermudagrass Varieties[1]

Cutting	Variety			
	"Alicia"[2]	Coastal	Coastcross-1	Common
May	18.0	18.1	17.4	---
June	11.3	11.8	13.1	11.5
July	11.0	12.5	12.8	10.4
August	12.4	12.4	12.7	---
October	11.2	11.8	12.0	10.4
Average	12.8	13.3	13.6	

[1]Grown at the North Louisiana Hill Farm Experiment Station, Homer, Louisiana; analyzed by the Texas Forage Digestibility Laboratory.

[2]A patented grass reported by its grower to be of the variety called Alicia.

Maturity of Forage

Within a variety, age or physiological maturity is the single most important factor affecting its nutritive value. Universally, as a plant matures, its digestibility and protein content decline. This is due to (a) increased deposition of the less digestible structural carbohydrates (cellulose and hemicelluloses) in the cell walls and (b) reduction in the digestibility of cell walls due to such processes as lignification (deposition of lignin).

The ability to explain and predict the consequences of advances in maturity is presently limited by inadequately discernible measures of maturity. In practice chronological age is a convenient measure. However, factors such as fertility, mois-

ture and temperature can materially alter the physiological age (maturity) of forages grown during the same chronological span of time. Lignin/cell wall ratios and protein content of the plant may be quantitatively useful for single species (Lippke, 1973) grown under well-defined conditions of soil type, moisture and fertility but are of little value if indiscriminately applied to mixed species produced under varied conditions (Ellis et al., 1970). Although morphological development may be related to maturity, such measurements are tedious and difficult to quantify (Monson et al., 1972; Hann et al., 1973).

Although subject to considerable confounding, chronological age remains the most practical expression of maturity effects upon nutritive value. An evaluation of data from a number of different species grown at several locations suggests that, in general, perennial grasses in the south decrease 0.1 to 0.2 percentage units in digestibility per day between 4 and 8 weeks of age (Table 3).

Season of Year

In general, forages of a given chronological age are highest in digestibility during the early portions of their growing season and lowest during intermediate periods. This may be a reflection of materials being less mature morphologically per day of age during early, more favorable growing periods.

Summer temperatures high enough to cause elevated body temperature can result in increased digestibility by ruminants consuming forages, especially at high levels of intake (Graham et al., 1959). Lippke (1971) confirmed this in an experiment where cattle showing signs of heat stress exhibited a 5-percentage point increase in digestibility of alfalfa pellets.

Soil Type and Fertility

Soil type and fertility influence the mineral and crude protein content of forages. As previously reviewed, mineral content per se is not an important economic component of nutritive value. The values of these effects are largely related to yield.

Within the usual fertility levels of nitrogen, increasing levels are associated with progressive increases in forage crude protein. A minimum level of protein is re-

Table 2-3. Average Daily Change in Digestibility Between Four and Eight Weeks of Age

Month harvested	Beeville, Texas[1] Klein	Pretoria-90	Buffel	Coastal	Homer, Louisiana[2] Coastal, 1971	Coastal, 1970	Tifton, Georgia[3] Coastal	Coast-cross	Bahia	Franklinton, Louisiana[4] Bahia
May	-.02	-.07	-.14	-.17	--	--	--	--	--	--
June	--	--	--	--	-.19	-.21	-.26	-.17	-.12	-.14
July	--	--	--	--	-.17	-.13	-.39	-.80	-.69	-.07
August	-.28	-.17	-.32	-.01	--	--	-.11	-.10	-.11	-.06
September	--	--	--	--	-.14	-.12	-.24	-.27	-.20	-.16
October	-.08	-.36	-.20	-.15	-.44[5]	--	--	--	--	-.15
Mean	-.13	-.15	-.22	-.11	-.17	-.16	-.34	-.42	-.28	-.11

[1]Data of Conrad, 1971.

[2]Data of Rainwater et al., 1974, excluding August hays which were extensively rained on during drying.

[3]Data of Monson and Burton, 1973; data between four and seven weeks of age.

[4]In vitro data of Montgomery *et al.*, 1972.

[5]Omitted from mean.

quired in the forage to provide adequate protein for the growth of microorganisms involved in forage digestion. This level appears to be in the order of 7-8 percent for forages of 50-65 percent digestibility (Figure 4). When forage protein is less than this, forage digestibility and intake are reduced to less than their potential. Fertilization to increase the protein content beyond this level will not further increase digestibility and intake (Table 4).

There are numerous reports of an association between protein content and digestibility of forages where maturity is a confounding factor and appears to be the basic cause for decreases in both protein content and forage digestibility. Such relationships, then, are not a valid basis for fertilizer recommendations specifically to improve digestibility unless it can also be shown that maturity is affected. Extreme ranges in nitrogen fertilization of Coastal bermuda have consistently had no effect on its digestibility (Table 4).

Levels of forage protein in excess of the animal's requirement are of no extra-nutritional value. Since the protein requirements of most animals do not exceed 12 percent (Figure 3), levels in excess of this amount can be useful only if the forage is used to supplement some other feedstuff which is protein deficient. This is an important means of efficiently utilizing the higher protein levels sometimes achieved incidental to the use of higher levels of nitrogen fertilization.

The response in forage crude protein to nitrogen fertilizer is generally greatest on sandy type soils of East Texas. In contrast, responses are lower on other soils of Central Texas. Little or no response occurs on blackland soils during the summer and fallmonths, and only limited response occurs in the spring compared with sandy type soils (Figure 5).

Other Factors

In certain forages such as Sericea lespedeza, digestibility appears to be limited by tannin content. Breeding for lower tannin content has resulted in improved digestibility (Donnelly and Anthony, 1970).

The high alkaloid content of tall fescue may limit its digestibility (Buckner *et al.*, 1967; Bush *et al.*, 1972), and strains of lower content have been selected. Re-

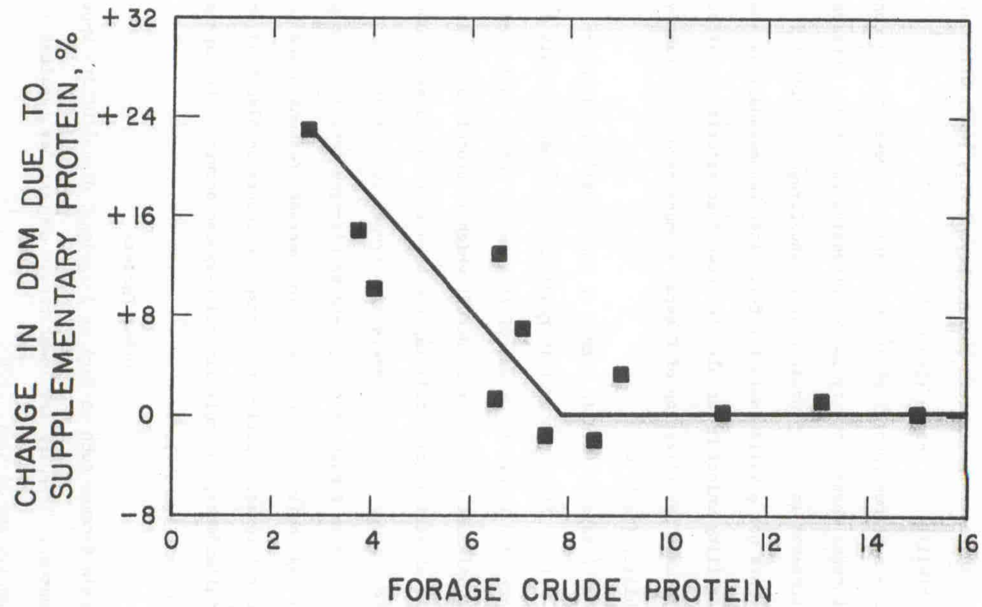

Figure 2-4. Level of forage protein below which protein supplementation improves digestibility of forage.

Table 2-4. Effect of Nitrogen Fertilization on Protein Content and Its Lack of Effect on Digestibility

Texas[1]						Homer, Louisiana[2]			Oklahoma[3]		
Kleingrass			Coastal bermuda			Coastal bermuda			Midland bermuda		
N	CP[4]	DDM[5]	N	CP	DDM	N	CP	DDM	N	CP	DDM
lb/acre[6]	%	%	lb/acre	%	%	lb/acre	%	%	lb/acre	%	%
25	5.9	56.1	25	6.7	53.8	0	10.4	51.4	0	11.5	64.9
100	6.6	57.1	100	7.6	54.8	600	15.8	53.1	400	18.4	66.0
200	9.8	55.8	200	10.6	53.4	1200	16.9	52.1	1400	18.9	65.0
300	10.8	57.4	300	10.8	55.1	--	--	--	--	--	--

[1]Data of Buentello and Ellis, 1969; one application 6 wks. prior to cutting.

[2]Data of Rainwater, 1974; six applications 4 wks. prior to cutting.

[3]*In vitro* data of Webster *et al.*, 1965; four applications.

[4]CP = crude protein.

[5]DDM = digestible dry matter

[6]lb/acre per season.

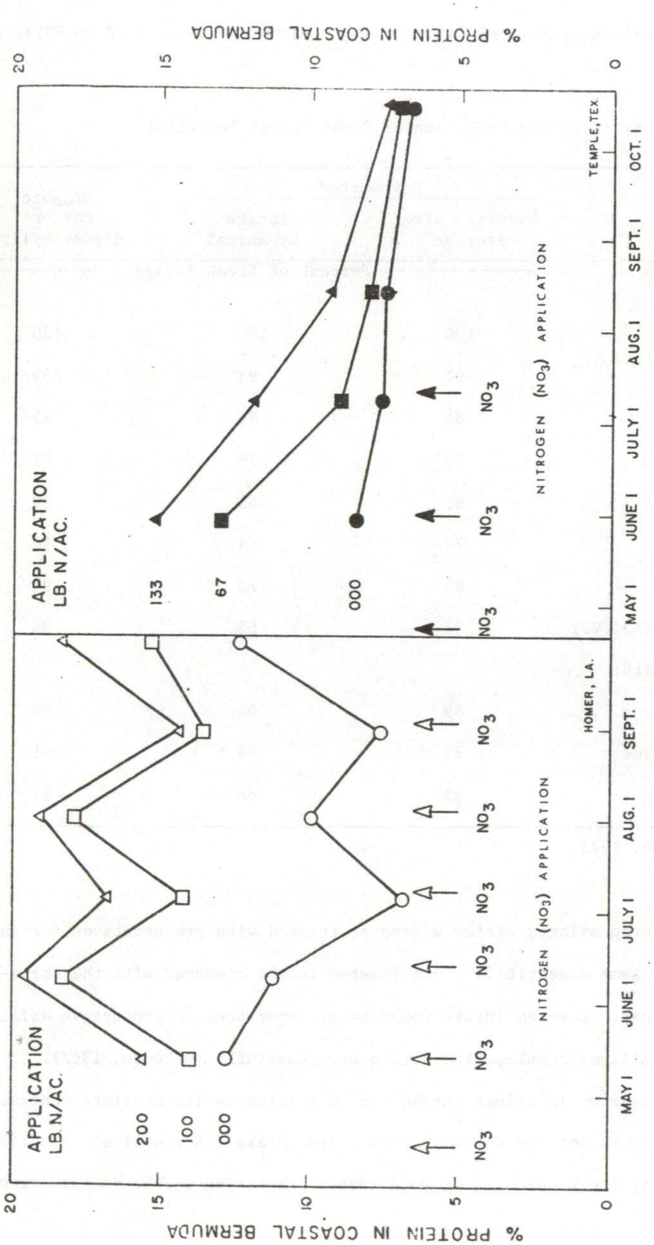

Figure 2-5. Effect of nitrogen fertilization on protein content of Coastal bermuda grown on sandy soils (left half) and on blacklands soil (right half).

search with reed canary grass in Minnesota suggests that alkaloids in this species do not impair digestibility but have an effect on limiting voluntary intake (Marten, 1973).

Level of Intake

Digestibility decreases at high levels of intake. Brown (1966) noted that although results have been somewhat contradictory, digestibility tended to decrease with increasing levels of intake for all types of rations. This effect appeared to be more pronounced for finely ground or poorer quality forages. The work by Riewe (Riewe and Lippke, 1970) leaves little doubt that this is true. The depressing effect of increasing levels of intake on organic matter digestibility was more than twice as great for sorghum hays as for alfalfa and clover hays. For most Texas forages, the range in digestibility could easily exceed four percentage points for the levels of feeding commonly encountered. Riewe and Lippke (1968) presented evidence that level of feeding exerts its influence entirely on digestibility of cell wall constituents (CWC). This is due to an increase in rate of passage of undigested CWC from the rumen with increasing levels of intake (Lippke and Ellis, 1972). Thus, CWC are subjected to fermentation in the rumen for a shorter time.

Forage Conservation

Following cutting, the plant material declines in digestibility, soluble carbohydrates (Lippke and Riewe, 1970) and protein. These losses continue until the plant material is either too dry to support further metabolism or, in the case of silages, a sufficiently low acidity is reached to inhibit further metabolism. The amount of these digestible components lost is directly proportional to the time required to achieve limiting levels of moisture or acidity (Shepperson, 1960). Even with artificial drying, appreciable amounts of these digestible components (cell contents) may be lost, leaving a dried product higher in the less digestible CWC and, as a consequence, lower in whole plant digestibility (Table 5).

Wetting of forage after cutting, such as by rain, prolongs drying time, leaches some of the more digestible nutrients from the plant and, in effect, considerably increases the proportion of CWC (Lippke and Ellis, 1972). With prolonged drying times

Table 2-5. Effect of Drying on Composition and Digestibility of Immature Ryegrass

Component	Frozen	Dried
	%	%
Cell wall constituents	50.5	59.9
Cell contents	49.5	40.1
Digestible dry matter	74.0	69.0

due to wetting, losses in nutrient values are further accentuated by overdrying and shattering of the more digestible leaves before storable moisture levels are achieved in the stems.

External wetting or prolonged drying provides favorable growing conditions for mold and fungi. Growth of mold and fungi not only removes cell contents but produces enough heat to creat a fire hazard in tightly packed hay. Poor drying conditions and high probabilities for rain coincide with most favorable forage growing seasons and especially with harvest of the more highly digestible cool-season grasses (Figures 1 and 2). Thus, some means of inhibiting mold and fungal growth and permitting storage at higher moisture levels would not only reduce nutrient losses but also facilitate hay making under the less favorable drying conditions. A number of "hay preservatives" are on the market. The most effective ones at present rely on propionic acid to inhibit mold and fungal growth and permit baling of hay with as high as 30 percent moisture without heating (Asplund, 1972). It should be emphasized that these preservatives only minimize nutrient losses and permit harvest under otherwise impossible field conditions. They do not improve the nutrient values of hay cured under favorable field curing conditions.

The higher the moisture content when ensiled, the longer the time required to achieve a preserving level of acidity. As a consequence, losses of nutrient value during storage are quite high for hay crop silages. These losses can be reduced by wilting before ensiling or by use of certain silage preservatives. The most effective preservatives are acids (A.I.V. process, formic acid) or formic acid formaldehyde mixtures. The relative values of several preservation methods are summarized in Table 6.

Table 2-6. Relative Retention of Fresh Forage Potential[1]

Preservation method	Dry matter: Recovery after storage	Dry matter: Intake by animal	Organic matter digestibility
	Percent of fresh forage		
Fresh	100	100	100
Dehydrated	91	93	99
Barn dried hay	84	86	93
Field cured hay	73	79	91
Unwilted hay silage	81	61	89
Molasses hay silage	77	64	94
Wilted hay silage	85	70	94
Acidified hay silage (A.I.V.)	87	65	94
Unwilted hay silage with:			
Formic acid	89	64	90
Formic-formaldehyde	87	68	91
Paraformaldehyde	83	68	91

[1]Summarized from Waldo, 1973.

In general, hay crop silages either wilted or treated with preservatives for ensiling have about the same digestibility but lowered intake compared with the corresponding field cured hay. Lowered intake would be of importance to productive animals fed solely silage or silages supplemented with other feedstuffs (Osbourn, 1967).

Although the depression in silage intake can be related to its moisture content, moisture content *per se* is not the factor limiting its intake (Thomas *et al.*, 1961). Rather, it appears that the production of some factor depressing intake is associated with the higher moisture levels (Raymond, 1969).

Excessive temperature during artificial drying or from ensiling over-wilted forages can reduce digestibility of protein (Goering et al., 1972; Yu Yu et al., 1973). Further, fermentative changes to the proteins during ensiling may reduce the value of the digested protein and contribute to the lower utilization of nitrogen in silage compared with fresh forage (Conrad et al., 1960).

Preservatives such as formaldehyde (and paraformaldehyde) not only reduce nutrient losses during ensiling but also may react with forage protein so that it is digested in forms more nutiritous to the animal (Waldo, 1973).

The nutritive values of forages preserved in oxygen-limiting structures, in general, are not superior in digestibility and intake to the same materials preserved as ordinary silage or by field curing under good drying conditions.

Processing

When a forage of relatively low digestibility (below 60 percent) is finely ground and pelleted, voluntary intake and performance by the animal consuming it are generally increased compared with the same forage in the long, coarsely chopped or finely ground form alone. This is apparently the consequence of more rapid flow of the finely ground forage particles through the animal's gastrointestinal tract. This in turn permits a greater daily intake when the finely ground forage is also pelleted. Increased intake is not accomplished for the unpelleted, finely ground material either due to its dustiness or uncompressed bulkiness.

Because of the more rapid passage through the gastrointestinal tract and higher intake, the digestibility of the fiber is reduced compared with that of long hay. Restricted intakes of finely ground and pelleted forages reduce rate of passage and yield higher digestibilities.

Thus, the primary benefit of fine grinding and pelleting is to increase voluntary intake and allow for greater daily consumption of digestible nutrients for productive purposes. The improvement due to fine grinding and pelleting increases with forages of lower digestibility. Obviously, nothing is achieved if the pelleted forage is fed at restrictive levels. Processing, such as cubing, where the forage is not finely ground does not increase its nutritive value.

The digestibility of forages is limited by the lignification and consequent physical arrangement of the fibrous cell wall and intercellular materials. Removal of these physical limitations by chemical and physical treatment would improve digestibility. Such treatments can most economically be justified for high fiber-low digestible forages. Alkali has been effective in partially solubilizing lignin and increasing digestibility, but the cost of alkali and its removal from the final product has limited its use. Treatments with steam and ammonia under pressure and gaseous oxidizing agents have effected only small improvements. In general, the expense involved for such treatments, the limited increases in digestibility, and the handling costs of bulky products have limited the practical significance of such chemical procedures.

MEASURING AND PREDICTING NUTRITIVE VALUE

Proximate Analysis

The present official methods of feedstuff analysis is essentially the proximate analysis system first proposed in 1864 by Henneberg and Stohmann. The proximate analysis system includes the following determinations:

Crude protein - total plant nitrogen multiplied by 6.25. The term crude implies that some of the determined nitrogen may be in forms other than protein. The factor 6.25 implies that the weight of protein is 6.25 times the weight of nitrogen or that the protein contains 16 percent nitrogen.

Crude fat - the material extracted by ether. The term crude implies that materials other than fat (triglycerides and fatty acids) are extracted by ether. These include plant pigments and waxes which are highly indigestible.

Ash - inorganic residues remaining after burning the sample at approximately 550° C.

Moisture - the weight loss on drying.

Crude fiber - the ash free residue remaining after extracting a fat free sample successively for 0.5 hour with 1.25 percent H_2SO_4 and 0.5 hour with 1.25 percent NaOH. This procedure is used to determine the fibrous, structural carbohydrate portion of the plant; the soluble protein and nonstructural carbohydrates being extracted by refluxing with the acid and base.

Nitrogen free extract (NFE) - determined arithmetically as 100 percent less the sum of percent crude protein, percent crude fiber, percent crude fat, percent ash, and percent moisture. This fraction is abbreviated NFE and is conceived to represent the nonstructural carbohydrates. The abbreviation could as appropriately stand for "not found elsewhere."

The requirements for a suitable method of feedstuff analysis and an early evaluation of the proximate analysis system is found in Dr. Henneberg's lecture notes as collected by Tollens in 1897 and translated by Hanson et al.(1958).

> "In order to ascertain the value of a feeding stuff for nutrition, it is necessary to determine the content of all the separate constituents, or at least of all the groups of similar value, and, so far as the cellulose is concerned, the various modifications of the same. These requirements the customary analysis of vegetable feedingstuffs by no means fulfills ... The present method of fodder analysis needs greatly to be perfected but in many respects accomplishes more than would be expected from their defectiveness."

This statement of requirement and evaluation of methods accurately summarizes the status of the proximate analysis system almost 110 years later. Although there are analytical imperfections in analysis for protein, these are not of major practical importance for forages since it determines "--- groups of similar value ---" to the ruminant. Although the varied components determined in the crude fat are not "--- groups of similar value ---," crude fat of most forages is in the order of 2-3 percent and therefore, quantitatively, of minor importance.

The major limitation of the proximate analysis systems occurs when it is applied to forages which are high in structural carbohydrates (cellulose) having various modifications not of similar nutritive value to the animal. The proximate analysis has persisted for over a century because (a) it "--- accomplishes more than would be expected from their defectiveness ---" and (b) no suitable replacements have been developed until recently.

According to Paloheimo (1953), Henneberg and Stohmann realized the limitations of the crude fiber determination by concluding:

"1. That in the crude fibre determination, the cell wall substances are rather arbitrarily divided into two portions, the one constituting the crude fibre and the other belonging, together with sugar and starch, to the N-free extract;

2. That the crude fibre is not pure cellulose but contains also encrusts rich in carbon (lignin, suberin and cutin are names), which remain among the faces together with the indigestible part of cellulose, whereas the digestible part of crude fibre is pure cellulose;
3. That in the crude fibre determination the bulk of the lignin and a part of the cellulose are dissolved and thus fall into the N-free extract; and
4. That the indigestible part of the N-free extract is composed mainly of lignin."

The effect of the crude fiber procedure on various feedstuff constituents is summarized in Table 7. Inspection of this table confirms that all the structural carbo-

Table 2-7. Effect of the Crude Fiber Procedure on a Fat-Free Feedstuff

Feedstuff constituent	Refluxing with 1.25% H_2SO_4	Subsequent refluxing with 1.25% NaOH
Protein	Partial extraction	Extensive extraction
Sugars and starches	Complete extraction	-
Cellulose	nil	nil
Hemicellulose	Variable extraction	Extensive but variable extraction
Lignin	nil	Extensive but highly variable extraction

hydrates are not determined as crude fiber and that many modifications of the same (hemicellulose and lignin) are determined as NFE as a mathematical consequence. As a result, the NFE is frequently less digestible than the crude fiber fraction of many forages (Crampton and Maynard, 1938).

Newer Chemical Methods

Numerous investigators have worked toward improving methods to replace the crude fiber procedure. A major problem is to extract effectively the protein and lignin from the structural carbohydrates so they can be routinely determined gravimetrically (Hanson et al., 1958). Paloheimo et al.(1961) suggested the determination of "cell walls" to include structural carbohydrates and lignin. Ellis (1962) suggested the colorimetric determination of structural carbohydrates which would avoid the contaminating protein and lignin detected gravimetrically.

"Detergent Fiber"

Van Soest (1963) suggested the use of appropriate detergents to more effectively remove protein and other nonstructural carbohydrates from plant material and permit the gravimetric determination of structural carbohydrates and lignin. When plant material is refluxed with a buffered, neutral detergent solution, the residue is rather pure structural carbohydrates and lignin which is referred to as cell wall constituents (CWC). When refluxed with an acidic detergent solution, the predominance of the hemicellulose are also removed, leaving an acid detergent fiber residue containing predominantly lignocellulose (acid detergent fiber, ADF). Details of these analyses and their application to forages have been summarized in Agricultural Handbook form (Goering and Van Soest, 1970).

It has been established that the neutral detergent soluble material (100%-% neutral detergent fiber) is essentially 100 percent truly digestible (98 ± 2.5). This high digestibility together with the solubility characteristics of cellular protein, starch, sugars and lipids, justifies referring to this extracted material as cellular contents as has been done by Van Soest. Its value then is in determining, according to Henneberg's standard, groups of similar value (digestibility) and, when corrected for protein and lipids, would be a suitable replacement for NFE to express the nonstructural carbohydrates.

Application of the neutral detergent fiber method divides the plant into a completely truly digestible portion (cell contents) and an incomplete and variable digestible portion (cell walls). The remaining problem then is to estimate the digestibility of cell walls. Based on data from a variety of forage classes, Van Soest (1967) proposed that digestibility of cell wall constituents could be predicted as a function of the lignin/acid detergent fiber ratio (Agricultural Handbook No. 379 by Goering and Van Soest). More recent data (Ellis et al., 1970; Buentello, 1972) suggest that this relationship may not be generally applicable to all forages and may be especially limiting for warm-season perennials.

Lignin

There is little doubt that lignin is the major factor altering digestibility with advancing maturity in all forages. However, a unit of lignin deposited at one locale may be far more limiting to digestibility than at another locale in or between the cell walls. The site of deposition and the amount of lignin directly limiting digestibility may be more important than the total lignin as determined by present chemical methods (Buentello, 1972). The structural configuration of plant tissues is an important factor determining digestibility as implied by Baker and Harriss (1947). Monson et al. (1972) have indicated that cutin acts as an effective barrier to microbial attack of leaves. Hanna et al. (1973) demonstrated the importance of certain cell layers surrounding the parenchyma bundle sheath in determining the digestibility of this major component of leaf tissue. These important structural considerations are not reflected by chemical analysis and point up the limitations of chemical methods in ultimately predicting digestibility of such a heterogeneous and complex tissue as forage.

Predicting Digestibility

Thus, the problem of predicting the digestibility of cell walls remains, especially in warm-season perennials. The Texas Forage Testing program utilizes the determination of cell contents and cell walls, which are assumed to be 90 and 55 percent digestible, respectively, to calculate total plant digestibility. This is considered to be more accurate than the crude fiber procedure (Buentello, 1972) and of sufficient accuracy for practical purposes at present.

A number of other chemical entities have been demonstrated to be related to digestibility but are less consistent than lignin in their presence in forages. Van Soest and Jones (1968) demonstrated a correlation between digestibility and the plant's content of metabolically deposited silica (in contrast to extraneous soil silica). The digestibility of total plant dry matter decreased by approximately 3 percentage units for each percentage unit increase in metabolically deposited silica beyond a concentration of 2 percent. The depressive effect is related to the total forage dry matter in contrast to lignin which specifically affects digestibility of the cell walls. Certain plants such as rice appear to accumulate unusually high levels of such silica.

Various components of the cell wall have characteristically different digestibilities. An easily hydrolyzable hemicellulose (solubilized in 0.1 N H_2SO_4) is characteristically higher and a difficult hydrolyzable hemicellulose (solubilized in 1 N H_2SO_4) characteristically lower in digestibility than is cellulose (Ellis et al., 1967). However, the proportion of these compounds in the cell wall apparently do not vary sufficiently and consistently enough to account for variations in digestibility of the cell wall (Ellis et al., 1970).

In Vitro Digestion

In vitro digestion methods attempt to simulate the digestive processes occurring in the animal (in vivo). These methods are also variously referred to as "artificial rumens," "laboratory digestion" and "micro-digestion techniques." In vitro methods have long been used to study qualitatively microbial digestion as carried out by rumen microorganisms. However, it was not until the development of a "two stage" method by Tilley and Terry (1963) that such methods have been used extensively in a quantitative fashion. These investigators employed a 48 hour "fermentation stage" to simulate rumen digestion followed by a second stage involving a proteolytic enzyme to simulate intestinal digestion of the microorganisms produced in the first stage. With such two stage procedures, in vitro results closely approach in vivo apparent dry matter digestibility. The second stage does not completely digest all microbial dry matter, thus some appears in the residue together with undigested forage dry matter. The same occurs in vivo, and digestibility calculated as feed minus feces (undigested feed plus undigested microbial dry matter) actually underestimates feed digestibility and is referred to as apparent digestibility.

Van Soest et al. (1966) proposed an in vitro procedure in which the second stage employs a neutral detergent solution rather than a proteolytic enzyme. The neutral detergent solution is very efficient in removing microbial dry matter so that the final residue is composed of almost pure undigested forage. Thus digestibility determined by this procedure appraoches true digestibility and is higher than the apparent digestibility as measured in the Tilley and Terry method (1963) and most in vivo methods.

Either method gives dependable and accurate ranking of forages as to their relative digestibilities. They are less accurate in estimating absolute digestibility due to variations within the method and variations relative to the in vivo process. These variations can be largely removed by the inclusion of a standard forage of known in vivo digestibility to adjust for within variations and correct to an in vivo basis. This is done in the Texas Forage Development Research program. As an example of this method's accuracy, a correlation coefficient of 0.92 was found between in vitro and in vivo digestibility of 15 samples of Coastal bermuda. The mean deviation between in vivo digestibility and corrected in vitro values for 70 different forages was -1.7 (Buentello, 1972), indicating the high accuracy of the method.

In Situ Digestion

In situ methods of digestion involve the use of a container to suspend a forage sample in the rumen for digestion in situ. This is also referred to as the "nylon bag" technique since nylon is impervious to rumen digestion and hence a useful container. This procedure was used in the selection of the higher digestible bermudagrass hybrid, Coastcross I (Burton et al., 1967). Fabrics containing a pore size greater than approximately 10 microns will permit entrance of fiber from the rumen into the bag (Van Hellen and Ellis, 1973). This can confound results, especially for in situ times of less than 12 hours, when digestion is small compared to entrance of fiber from the rumen.

VOLUNTARY INTAKE

The voluntary intake of a forage is an important determinant of its nutritive value when intake limits performance, as commonly occurs for forage fed animals. This is true since the greater the intake, the greater the proportion of the forage's nutrients which exceed the animal's fixed maintenance requirement and which is available for productive functions. Increases in intake above that required for maintenance result in progressive increases in feed efficiency (decreases in feed required per unit gain) as exemplified for a 440-pound steer in Table 8.

As in the case of other mammals, feed intake by the ruminant is mediated by the frequency and size of meals which are in turn controlled by the feeding and satiety

Table 2-8. Influence of Feed Intake on Feed Efficiency of a 440 lb. Steer

Feed intake	Feed for maintenance	Average daily gain	Feed Efficiency
lb/day	lb/day	lb/day	feed/gain
7.3	7.3	0	0
9.9	7.3	.5	20
12.1	7.3	1.0	12
14.4	7.3	1.5	10

center of the brain. These centers respond to various signals generated as a result of the animal's tissue metabolism or gut fill. When consuming diets of low nutrient density (low digestibility), the capacity of the gastrointestinal tract to process undigestible residues (gut fill) is reached and generates signals to limit meal size. In contrast, when diets of high nutrient density are consumed, gut capacity is not limiting, and intake is then regulated by signals derived from metabolism and the productive ability of the animal. Thus, in general, the control of intake due to gut fill is related to the rations' digestibility, and control due to metabolism is related to the productive abilities of the animal. This is illustrated graphically for mature cows in Figure 6.

When gut fill regulates feed intake, feed intake of lactating dairy cows can be estimated quite accurately from digestibility (COD) and body weight (pounds) according to the following formula by Conrad et al. (.964).

$$\text{Intake, lb/day} = \frac{\text{body weight}}{1000} \times \frac{9.4}{100 - \text{COD}/100}$$

This equation implies that the gastrointestinal tract of a 1000-pound cow can process an intake which will yield 9.4 pounds of indigestible dry matter per day.

It should be noted that the point distinguishing gut fill versus metabolic control of intake is variable and dependent upon the productive abilities of the animal

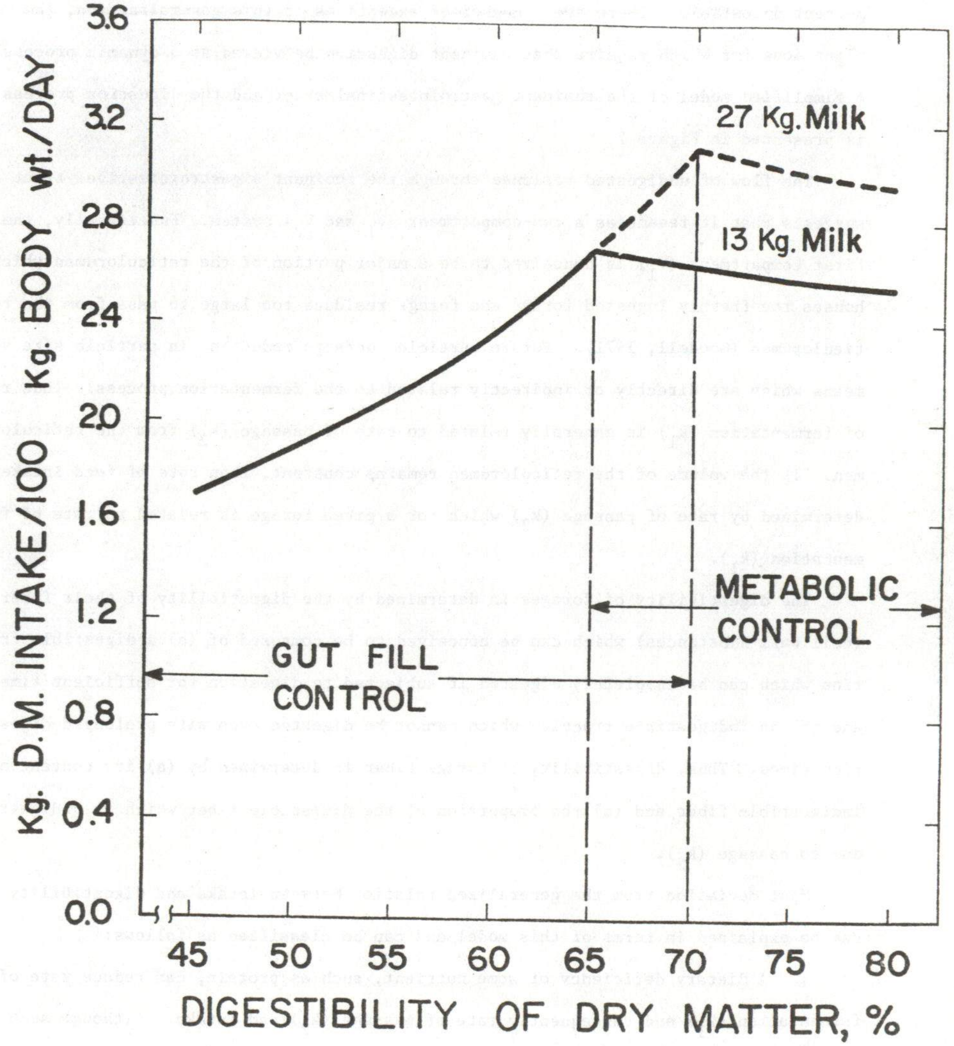

Figure 2-6. Relationship between intake and digestibility.

as portrayed in Figure 6. As a general rule, feed intake by mature beef cows appears related to gut fill (and hence digestibility) when the feedstuffs are less than 65 p percent digestible. There are a number of exceptions to this generalization, the explanations for which require that ruminant digestion be viewed as a dynamic process. A simplified model of the ruminant gastrointestinal tract and the digestion process is presented in Figure 7.

The flow of undigested residues through the ruminant's gastrointestinal tract suggests that it resembles a two-compartment (V_1 and V_2) system. Functionally, the first compartment (V_1) is conceived to be a major portion of the reticulorumen which houses the freshly ingested forage and forage residues too large to pass from the reticulorumen (Goodell, 1971). Forage particles undergo reduction in particle size via means which are directly or indirectly related to the fermentation process. Thus rate of fermentation (k_1) is generally related to rate of passage (k_2) from the reticulorumen. If the volume of the reticulorumen remains constant, then rate of feed intake is determined by rate of passage (k_2) which for a given forage is related to rate of fermentation (k_1).

The digestibility of forages is determined by the digestibility of their fiber (cell wall substances) which can be conceived to be composed of (a) a digestible fraction which can be completely digested if subjected to digestion for sufficient time and (b) an indigestible fraction which cannot be digested even with prolonged digestion times. Thus, digestibility of forage fiber is determined by (a) its content of indigestible fiber and (b) the proportion of the digestible fiber which is undigested due to passage (k_2).

Most deviation from the generalized relation between intake and digestibility can be explained in terms of this model and can be classified as follows:

1. A dietary deficiency of some nutrient, such as protein, can reduce rate of fermentation (k_1) and consequently rate of passage (k_2) and intake. Although such a deficiency reduces digestibility (Figure 4) via reduced rate of digestion of the digestible fiber fraction (k_1), the greater effect is on reducing rate of passage (k_2) and, as a consequence, rate of feed intake. Protein supplementation can restore nor-

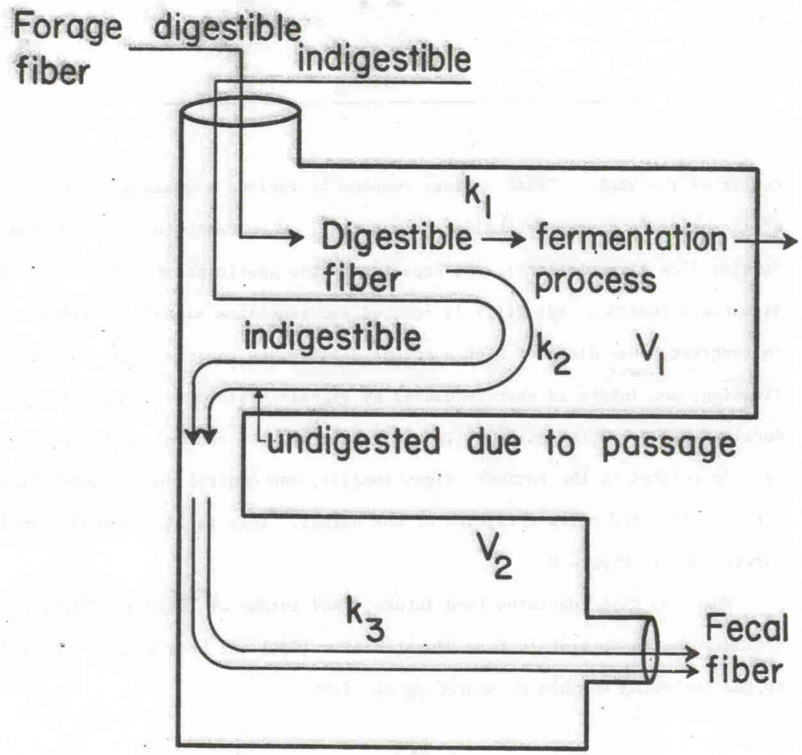

Figure 2-7. Dynamic model of fiber digestion in gastrointestinal tract.

malized relations between rates of digestion and passage and hence normalized relations between intake and tract digestibility.

2. A reduction in dietary particle size can result in a more rapid rate of flow through the reticulorumen independent of rate of fermentation. This occurs when a forage is finely ground. Compared with long or unchopped form, its rate of passage (k_2) is increased, and a greater proportion of the digestible fiber is undigested due to the more rapid passage. Increases in forage intake by this means would be inversely related to changes in digestibility, such change in digestibility being effected by the treatment. The intake of different forages whose particle size had been reduced by grinding would still be related to differences in their digestibility in this ground form, but the quantitative relationship between digestibility and intake would be changed as indicated in Figure 8. Figure 8 also indicates that the greatest benefit of reducing particle size would occur for forages of lower digestibility (Lippke, 1973; McCrosky, 1972).

3. Forages may differ in the physical ease with which they fragment to sufficiently small size to pass from the reticulorumen (Troelson and Bigsby, 1964; Chenost, 1966). In such cases rate of passage may be only partially related to rate of fermentation and digestibility. That such factors may be important is indicated by observation that variations in intake are generally greater than variations in digestibility (Crampton et al., 1960; Heaney et al., 1968).

4. Factors such as pregnancy in sheep reduce intra-abdominal space available for the reticulorumen and its volume (V_1). As a consequence, the daily flow from ($V_1 \times k_2$) is reduced and thereby reduces daily feed intake.

Environmental temperature also influences intake. The Missouri Station has, for a number of years, investigated the effects of heat stress on animal performance. In one of the early reports, Ragsdale et al. (1950) noted the detrimental effect of heat stress on intake. Riewe (1967) confirmed this effect of high temperature on the intake of several forages. A subsequent study by Lippke (1971) implicated a much reduced rate of passage from the rumen as being a major cause of this phenomenon.

Young animals have high nutrient requirements and less developed gastrointesti-

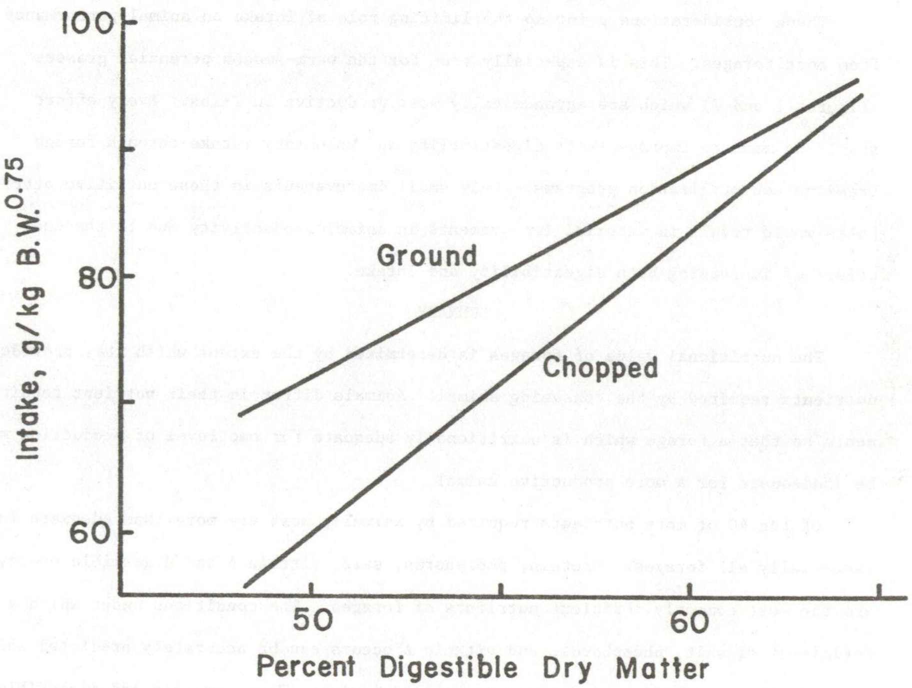

Figure 2-8. Effect of physical form on the intake-digestibility relationship.

nal function. As a consequence, their voluntary intake is more sensitive to gut fill and forage digestibility than is that of mature animals. Hodgson (1968) found a close linear relationship between forage (ryegrass) digestibility and amount eaten by 3-6 month old calves over the digestibility range of 68-82 percent. The equation describing forage organic matter intake (y, g/$W^{.73}_{kg}$) as a function of organic matter digestibility "as grazed" (x) was

$$Y - 3.0x - 143.3 \qquad R^2 = 0.92$$

These considerations point up the limiting role of intake on animal performance from most forages. This is especially true for the warm-season perennial grasses (Figures 1 and 2) which are agronomically most productive in Texas. Every effort should be made to improve their digestibility and voluntary intake through forage breeding and utilization programs. Only small improvements in these nutritive attributes would result in material improvements in animal productivity due to the dual effect of increasing both digestibility and intake.

SUMMARY

The nutritional value of forages is determined by the extent which they provide nutrients required by the consuming animal. Animals differ in their nutrient requirements so that a forage which is nutritionally adequate for one level of production may be inadequate for a more productive animal

Of the 40 or more nutrients required by animals, most are more than adequate in essentially all forages. Protein, phosphorus, salt, vitamin A and digestible energy are the most commonly deficient nutrients of forages. The conditions under which a deficiency of salt, phosphorus, and vitamin A occurs can be accurately predicted and economically prevented by appropriate supplementation. Thus, protein and digestible energy are quantitatively and economically the most improtant determinants of nutritional value. Of these two, deficiencies of digestible energy are quantitatively the most common and largest and, hence, economically the most important determinant of nutritional value. Further deficiencies of digestible energy limit total forage intake. Forages which are adequate in digestible energy are generally also adequate in protein. Thus, a forage's content of digestible energy (or, simply, digestibility) is

generally the most important indication of its nutritive value.

From a nutritional standpoint, forages may be conceived to consist of (a) cell contents (mostly protein, lipids, soluble carbohydrates and minerals and starch) which are completely digestible and (b) cell wall constituents (cellulose, hemicellulose and lignin) which are incompletely and variably digested. Methods have now been developed to determine these conceptual and nutritional entities analytically in contrast to the inadequate crude fiber procedure. A major problem remains in predicting the digestibility of the cell wall. Physical and chemical changes within the cell wall associated with aging and the progressive deposition of lignin (lignification) appear to be determinants of the cell walls' digestibility. The morphological location of such changes is important in that, for example, lignification in certain areas may serve to encompass materials which would otherwise be highly digestible. Such morphological differences vary by species and genotype within specie.

The digestibility of cell walls can be predicted as a function of its lignin content where wide ranges in lignin content exist such as between species and maturity extremes within species. However, it is unreliable when applied indiscriminately within the usual maturities encountered in practice.

Due to limitations of chemical methods in predicting digestibility, laboratory biological methods have been developed which rather accurately estimate a forage's digestibility. These are (a) <u>in vitro</u> digestion methods which simulate a part or all of gastrointestinal digestion or (b) <u>in situ</u> digestion methods which measure extent of digestion during a specified time in one segment of the gastrointestinal tract. Both methods are useful for specific objectives where rate of digestion is the major variable under consideration, as is usually the case. The usual laboratory biological methods are time-constant measurements (amount per 48 hours) of a time-dependent process in that digestion in the animal (<u>in vivo</u>) is the net result of rate of digestion and rate of passage (or conversely, residence time at the digestive site).

Another important nutritional attribute of forages is rate of voluntary consumption. The greater the intake relative to the animal's weight, the greater the proportion of forage nutrients used for production (i.e., the greater the feed efficiency).

Forages vary quite widely in this attribute, and such variation can generally be explained by a model which considera (a) rate of digestion and factors affecting such; (b) rate of passage and factors affecting such; and (c) volume of the gastrointestinal tract and especially portions of the reticulorumen.

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