ASSOCIATIVE EFFECTS IN THE RUMINANT ANIMAL

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CHAPTER I

INTRODUCTION

Starch is the main storage carbohydrate of plants and provides much of the energy required for the animal kingdom. Hence, starch digestibility is of utmost importance for animal growth. Availability of starch to a ruminant animal can be influenced by grain processing, roughage level, roughage source, intake level, age of the animal and amount of rumination. There also is a wide variation in ability of of individuals within a species to digest starch. Starch composition varies with plant source and maturity (French, 1973). Cereal grains are the major source of starch in diets for domestic livestock. High concentrate diets contain 60 to 70% starch on a dry matter basis.

Several investigators have demonstrated the benefits in cattle performance derived from grain processing (Buchanan-Smith, 1976; Gill, 1980; Hale, 1980). Increasing the surface area and access to the starch granules improves efficiency of feed use for weight gain by 5 to 10%. Some evidence indicates that the ability to digest starch decreases with age (Blaxter, 1962); however, this may be a result of an increased rumen volume, increased intake and faster outflow from the rumen. Also, aged animals may digest food less completely due to dental problems. The time spent ruminating may be critical for whole grain diets since post-ruminal digestion is limited by particle size (Owens and Zinn, 1981).

Increased food consumption reduces time spent in the GIT and may limit the extent of digestion (Entringer et al., 1974; Kass et al., 1980). NRC (1980) and ARC (1980) currently adjust TDN and energy values for level of intake. A four percent reduction in DMD is applied for every multiple of maintenance increase in intake. Digestibility of starch decreases as feed intake increases (Orskov, et al., 1969; Galyean, 1975).

The final two factors which influence starch digestion are roughage level and roughage source. At times, mixtures of grain and roughage have digestibilities or produce performance which differs from the mean of that obtained from the individual feedstuffs fed alone. This deviation from linearity has been termed an "associative effect." Researchers disagree about the validity or magnitude of causes for this effect (Garret, 1979; Moe, 1980). The scientists which favor the concept disagree as to which chemical constituent is involved in the altered digestibility. Deviations from linearity have been positive and negative in different experiments. Certain researchers attribute the associative effect to a reduction in starch digestibility in the total tract (Wheeler et al., 1975; Joanning et al., 1981) while others maintain that cell wall digestion is the primary component involved (Van Soest, 1973). Teeter (1981) attributed the increased starch digestibility with cottonseed hull supplementation to greater mastication of the diet. Causes for the associative effect and variation in its magnitude have not been elucidated and were explored in this thesis. Chemical constituents which reduce digestibility under various circumstances may differ. The impact of source of roughage and level of intake on the associative effect have not been thoroughly

investigated. How various types of roughages alter rate of passage and site of digestion remain undefined.

These studies were designed to evaluate 1) the significance and magnitude of associative effects and 2) which dietary factors contribute to this phenomena. The effects of various roughage sources on rate of passage and site of digestion were evaluated and the relative energetic efficiency of ruminal versus intestinal digestion of glucose was determined.

The results of this doctoral dissertation (Chapter III-VIII) will be submitted for publication in the Journal of Animal Science. The format of these chapters will comply with publication requirements of the journal. Chapters I and II were written to fulfill format requirements put forth by the graduate college.

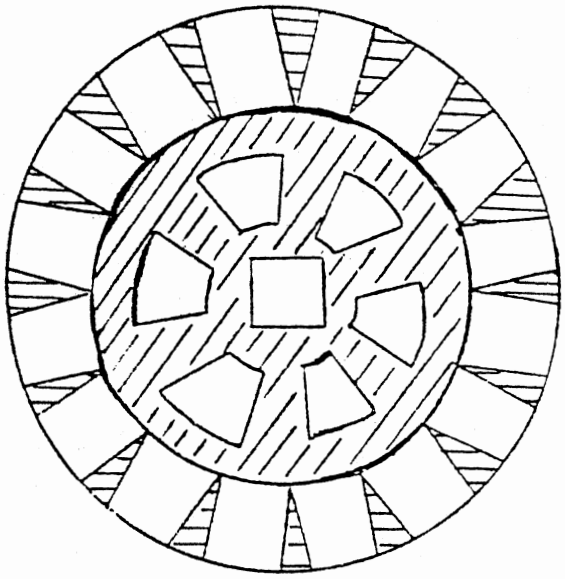
CHAPTER II

REVIEW OF LITERATURE

Properties of Starch

Starch is the predominant storage form of carbohydrate in plants (Morrison, 1979). Storage depots are found in stems, leaves, roots, fruit and leaves. Two types of polymers are present in starch: 1) a linear component consists of a-1-4 glucopyranosidic chains (amylose) and 2) a branched portion (amylopectin) attached to the core of starch molecule by an a-1-6 glycosidic linkage (Stryer, 1981). The relative proportion of amylose and amylopectin differs with type of grain and is controlled genetically. In commercial corn grain, amylose and amylopectin comprise 25 and 75 percent of the total starch, respectively (French, 1973). Generally, amylose percentage increases with maturity. The greater the amylopectin content, the less crystalline the structure. A less crystalline structure is more soluble in H_2O. Starch molecules greater than 500 glucose units in length are insoluble in cold water, however, application of heat solubilized starch (French, 1973).

Plants package starch molecules into granules. Starch granules consist of approximately equal proportions of high organized (crystalline) and amorphous or gel-like regions (Figure 1). During irreversible swelling, water enters and swells the gel regions. Upon drying, the granule returns to its original amorphous structure. However, high



Source: French (1973).

Figure 1. Physical Structure of the Starch Granule. Cross-hatched Area-gel WHITE Area-Crystalline Starch

temperatures in the presence of water swell and melt the crystalline areas and disrupt the starch granule (French, 1973). This characteristic of starch has been used to increase starch availability of grains such as milo and corn by steam flaking. Acid hydrolysis of the starch granule erodes the gel-like amorphous region.

The amorphous region has a fine texture which prevents amylase from entering. Therefore, amylase must act on the surface of the granule, at fissures, or at structural imperfections. Alpha amylase is an endoenzyme which attacks starch molecules randomly, creating oligosaccharides and glucose. Beta-amylase is an exoenzyme which sequentially cleaves maltose units from the non-reducing end of the starch molecule.

Corn Kernel Structure

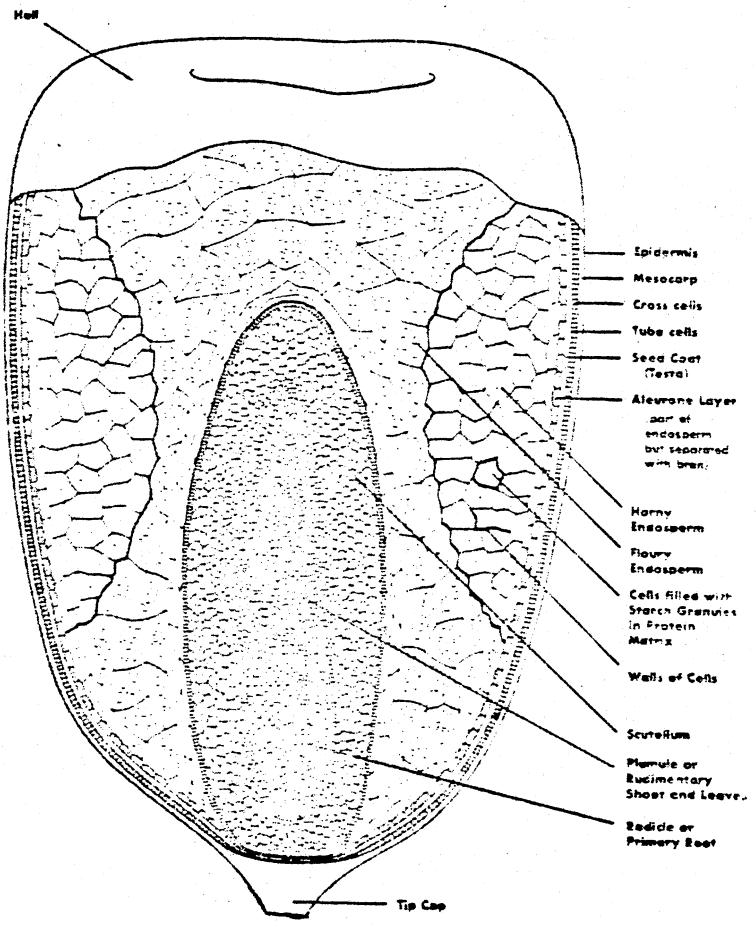
This summary of corn kernel structure was obtained primarily from published material from Matz (1969) and Inglett (1970). Mature corn kernels are composed of four major parts: 1) pericarp, 2) germ, 3) endosperm and 4) tip cap (Figure 2). The corn kernel consists of approximately 82% endosperm, 12% germ, 5% pericarp and 10% tip cap. Another portion of the corn kernel of nutritional interest is the horn-like gluten layer between the pericarp and the endosperm. The chemical composition of the kernel and these four major parts are presented in Table I.

Endosperm

The endosperm fraction of the corn kernel is of major nutritional importance since it contains most of the digestible carbohydrate. The

endosperm is composed of floury and horny regions. The ratio of horny to floury endosperm is 2:1 in normal dent kernels. The floury endosperm region consists of larger (10-20 μm diameter) cells, large round starch granules within a thin protein matrix. Upon drying, the thin protein matrix ruptures leaving void areas. These void areas produce the white color typical of floury endosperm. The horny endosperm is tightly packed. Starch granules in this region assume angular surface (polyhedron) characteristics. The protein matrix of this fraction is much thicker (1-2% more protein) and does not rupture upon drying. On the outer edge of the endosperm is the gluten layer. This layer can contain as much as 28% protein. The minute starch granules in this fraction are covered by a thick protein matrix.

The endosperm contains two distinct proteins: a matrix protein and a granular component embedded in the matrix. The protein bodies are large and more numerous in the subaleurone layer and become fewer and smaller as one progresses to the inner endosperm. The American Physiological Society has separated the various protein types in the kernel based on solubility: albumins (water soluble), globulins (salt soluble), prolamines (70-80% ethanol soluble), glutelins (sodium hydroxide soluble) and scleroproteins (insoluble in aqueous solvents). The relative amounts of each protein fraction in the endosperm are presented in Table II. The prolamine fraction (zein) is the major protein fraction in the endosperm. Zein alone has low nutritional value because it contains little lysine and tryptophan. Small amounts (2% of total) of non-protein nitrogen are present in dry, mature corn grain (Christianson et al. 1965). Over half of this NPN is amino acid-nitrogen.



Source: Inglett (1970).

Figure 2. Diagram of Longitudinal Section of a Kernel of Corn

Starch comprises the largest portion of the endosperm. Starch granules in normal dent corn exists in two forms differing in size - amylose (1000 glucose units) and amylopectin (40000 glucose units). Amylose makes up 27% and amylopectin 73% of starch granule in typical corn grain though "waxy" grain contains more amylose. The free sugar content of the endosperm is 10%. The major sugar present is sucrose, while small amounts of glucose, fructose and raffinose are found. The major pigments of the endosperm are β carotone, lutein and zeaxanthin. These pigments are associated with the protein fraction and their concentration is greatest in the horny endosperm.

Germ

The germ comprises about 11.5% of the dry weight of the kernel. The two major parts of the germ are the scutellum and the embryonic axis. The scutellum stores nutrients which are moblized during germination. The germ contains the highest concentrations of the free sugar, lipid, protein and ash content of the kernel. Sucrose is the major free sugar present in the germ. The major lipids found in the germ are linoleic (56%), and oleic (30%) acids with smaller amounts of linolenic, stearic, palmitic and arachidic acids (0.7%) present. Proteins present in the germ are types similar to those of the endosperm fraction. Approximately 80 percent of the minerals and vitamins of the total kernel are found in the germ.

Pericarp

The pericarp (bran) comprises about 5% of the weight of the kernel and is composed of four layers. The outer layer has dead, elongated,

thick walled cells forming a tough dense shell. The second layer has spongy cells which are called cross and tube cells. The next layer is the seed coat or testa. The innermost layer, one cell in thickness, known as the aleurone cell layer, comprises about 3% of the kernel weight. The cell walls of the pericarp contain cellulose and pentaglycans (hemicellulose).

Tip Cap

The tip cap is the remnant of tissue connecting the kernel to the cob. This spongy structure is composed of star-shaped cells which aid in rapid moisture absorption. The hilum is a black tissue at the point of attachment to the germ which seals the kernel upon maturation. The tip cap contributes very little to kernel weight making chemical composition nutritionally unimportant.

Cell Wall Anatomy

The following review of cell wall anatomy was summarized largely from material published by Pigden and Heaney (1968) and by Wood (1970). Forage plants contain non-protoplasmic cell walls which provide support and protection and assist in absorption, transpiration, translocation and secretion. The cell wall has little metabolic activity once it is formed. Nevertheless, cell walls determine the shape of the cell and texture of the tissue. The nutritional value of a forage is dictated primarily by the amount and composition of the cell wall fraction. Generally, young cells have thin cell walls which are more digestible. Most plant cell walls have three distinct layers: 1) the middle lamella (intercellular substance), 2) the primary wall and 3) the

TABLE I

COMPOSITION OF WHOLE CORN KERNEL AND ITS MAJOR FRACTIONS

Fraction	Kernel %	Starch %	Protein %	Lipid %	Sugar %	Ash %
Kernel	-	71.5	10.3	4.8	2.0	1.4
Endosperm	82.3	86.4	9.4	0.8	0.6	0.3
Germ	11.5	8.2	18.8	34.5	10.8	10.1
Pericarp	5.3	7.3	3.7	1.0	0.3	0.8
Tip Cap	0.8	5.3	9.1	3.8	1.6	1.6

TABLE II

PROTEIN FRACTIONS IN ENDOSPERM OF YELLOW DENT MATURE CORN

Protein	Percent of Endosperm Protein
Albumins	3.2
Globulins	1.5
Prolamine (Zein)	47.2
Glutelins	35.1
Scleroproteins-NPN	13.0

secondary wall. The middle lamella is located between the primary walls of two adjacent cells. In some plants, the middle lamella is called the cuticle. The cuticle serves as a cementing agent and is composed of pectic compounds combined with calcium. As a plant matures, the middle lamella becomes lignified. The primary wall, the first wall formed, undergoes periods of growth in surface area and thickness. It is composed of cellulose, hemicellulose and pectic acid compounds. Secondary walls form when the primary wall ceases to expand. The secondary wall is comprised mainly of hemicellulose and cellulose.

Secondary walls are not present in certain plants. The secondary wall contains three distinct layers designated S_1, S_2, and S_3. The S_2 layer forms the bulk of the secondary layer. Cellulose units are organized into elementary fibrils which aggregate to form microfibrils. Regions of cell walls with highly oriented cellulose molecules are referred to as crystalline regions whereas less structured regions are called paracrystalline or amorphous regions. Highly organized cellulose chains form crystalline cores which are surrounded by less ordered cellulose chains forming the amorphous regions. Cellulose microfibils are oriented in a helical fashion around a fiber axis. Each layer can be distinguished by the direction of the helix and the angle of orientation with respect to the fiber axis. Hydrogen bonding occurs between the cellulose units in the helical structure. Besides the amorphous regions around the elementary fibrils, each microfibril has intermittent regions of crystalline and amorphous organization.

Cellulose has its highest concentration in the secondary wall. Cellulose concentration diminishes toward the outer surface while

hemicellulose predominates in the outer portion of the cell wall and decreases in concentration nearer the lumen. Hemicellulose and lignin form a matrix surrounding cellulose units in the amorphous regions of microfibrils. The three layers of the cell wall (middle lamella, primary and secondary walls) become heavily lignified as the plant matures. As the cell wall becomes lignified, the middle lamella, primary wall and possibly portions of the secondary wall become indiscernible.

The most common chemical constituent of the cell wall is cellulose, however, substantial amounts of hemicellulose, pectin and lignin may be present. Minor constituents include cutin, suberin, waxes, some protein and ash.

Chemical Constituents of Cell Walls

Cellulose is a hydrophilic crystalline compound $(C_6H_{10}O_5)_n$ composed of glucose molecules linked by oxygen bridges with B-1, 4 glucosidic bonds. This ribbon-like structure contains more than 1000 glucose units. Hemicelluloses are a heterogenous group of polysaccharides composed of xylans, mannans, galactans and glucans. Pectic compounds are related to hemicellulose but differ in solubility. Pectic acid, pectin and protopectin comprise the three forms of pectic compounds which are polymers of mainly uronic acid. Gums and mucilages are compound carbohydrates similar to pectic compounds. Gums appear in plants due to physiological or pathological disturbance which damage cell walls and cell contents. Mucilages are generally associated with aquatic plant species and seed coats. Lignin is a polymer of phenylpropanoid units. Lignin give cell walls rigidity. Lignification occurs in the

middle lamella and primary wall before the secondary wall has finished growing. The amount of lignification of plant cell walls dictates the digestibility of the forage. Suberin and cutin are highly polymerized compounds consisting of fatty acids. Cutin forms the cuticle layer on the external surface of the epidermis of aerial parts of forages. Suberin is associated with cork cells of the periderm in certain plants. Waxes generally cover the outer surface of the cuticle layer. The waxy compounds reduce transpiration, protect foliage from hard rains or mechanical injury and prevent penetration by parasites. Minor constituents which may impregnate cell walls include silica, calcium carbonate, tannins, resins, fatty substances, volatile oils and acids and certain pigments. Silica can accumulate in cell walls and interfere with digestibility. Tannins are bitter tasting polyphenol compounds which can reduce palatability. Tannins also may inhibit cellulolytic digestion. Some of the volatile compounds and pigments also may influence palatability.

Differences in Forage Cell Walls

The type and composition of cell wall differs greatly between types of plants. The cell wall morphology of typical forages fed to livestock have not been extensively studied. However, gross anatomical differences are discussed below. Cell walls of legumes generally contain more lignin and less hemicellulose than cell walls of grasses. At the same relative digestibility, grasses contain less lignin but more total cell wall than legumes. Differences in lignin distribution or exposure of sites for digestion may be responsible for the generally greater rate of digestion of legume cell walls. Grasses accumulate

more silica than legumes. Silica reduces organic matter digestibility. Grasses store considerable amounts of fructosan in their leaves and stems. Certain legumes contain coumestrol which possesses estrogenic activity. Indolalkylamine bases in certain grasses can be toxic or effect palatability. Legumes generally contain more protein, calcium, phosphorus, and potassium than grasses.

Physiology of Carbohydrate Digestion

Carbohydrate digestion by ruminants has been reviewed (Kronfeld and Van Soest, 1976; Morrison, 1979; Van Soest, 1982) but is summarized below. Carbohydrates can be digested by two different processes; fermentation and hydrolysis. The type and mode of digestion for different carbohydrates are shown in Table III. Hydrolytic digestion by the ruminant animal occurs in the abomasum and small intestines. Certain glycosidic bonds, as in fructosans, are cleaved by gastric acids produced in the abomasum. However, the majority of the hydrolytic digestion occurs in the small intestine through specific enzymes. Hydrolytic digestion also occurs in microorganisms present in the gastrointestinal tract.

Starch Digestion

The general sequence of starch digestion involves hydrolysis of starch into oligosaccharides which are further degraded to glucose. Amylase is the enzyme responsible for hydrolysis of starch into oligosaccharides. Two types of amylase have been isolated. Beta-amylase is found in plants and hydrolyzes $\alpha(1-4)$ glucosidic linkages. Alpha-amylase is an animal enzyme which can hydrolyze both $\alpha(1-4)$ and $\alpha(1-6)$

TABLE III

SUMMARY OF MODE, EXTENT AND ENDPRODUCTS OF DIGESTION

Substance	Simple sugar components	Mode of digestion	Approximate digestibility	Major digestive endproducts	Linkages
Maltose	glucose	maltase[a]	complete	glucose	α 1-4
Sucrose	glucose, fructose	sucrase[a]	complete	glucose, fructose	α 1-2
Lactose	glucose, galactose	lactase[a]	complete	glucose, galactose	β 1-4
Starch	glucose	amylase[a]	high	glucose	α 1-4 α 1-6
Fructosans (grass)	fructose	gastric acid	high	fructose	β 2-6
Galactans	galactose	fermentative	high	VFA and bacteria	α 1-6
Cereal gums	glucose	fermentative	?	?	β 1-3 β 1-4
Pectin	galacturonic acid, arabinose, galactose	fermentative	high	VFA and bacteria	Mixed
Cellulose	glucose	fermentative	variable	VFA and bacteria	β 1-4
Hemicellulose	arabinose, xylose, mannose, galactose, glucuronic acids	fermentative	variable	VFA and bacteria	Mixed
Mannon	mannose	fermentative	high	VFA and bacteria	β 1-4

[a]In ruminant animals, these substances can be digested through fermentation yielding VFA and bacteria.

Source: Van Soest 1982.

linkages. There are four sources of α-amylase in animal systems: 1) salivary, 2) pancreatic, 3) intestinal mucosa, and 4) microbial. Non-ruminant animals generally obtain amylase from all four sources, but ruminants lack salivary amylase.

Ruminal Digestion

Since ruminant digestion is the topic of this thesis, ruminant carbohydrate digestion will be summarized. Ruminal starch digestion begins with solubilization through bacterial extracellular α amylase hydrolysis (French, 1973). The soluble oligosaccharides and dextrins are further degraded to glucose by maltase or other oligosaccharidases. The oligosaccharidases may be extracellular or attached to microbial cell wall membranes. Glucose is absorbed by ruminal microbes and metabolized to volatile fatty acids and methane or incorporated directly into microbial mass. Many bacteria contain isomaltase (a debranching enzyme) which further degrades α (1-6) linkages. Alpha amylase has only limited ability to degrade the α (1-6) linkage.

Intestinal Digestion

Carbohydrates may be solubilized by action of hydrochloric acid in the abomasum or rendered more acessible through the action of proteolytic enzymes. Pancreatic α-amylase is the first starch digesting enzyme encountered in the small intestine. The endproducts of amylase digestion include: 1) maltose, 2) maltotriose and 3) dextrins. Pancreatic amylase may act intraluminally or bound to the mucosal cells of the small intestine. Intestinal mucosa glycoamylase and bacterial amylases also contribute to intestinal starch digestion. Theoretically,

any enzymatical starch digestion in the ileum or large intestine would occur by enzymes from lysed bacterial cells however, such digestion is minimal. Starch is also fermented by microorganisms present in the ileum and large intestine.

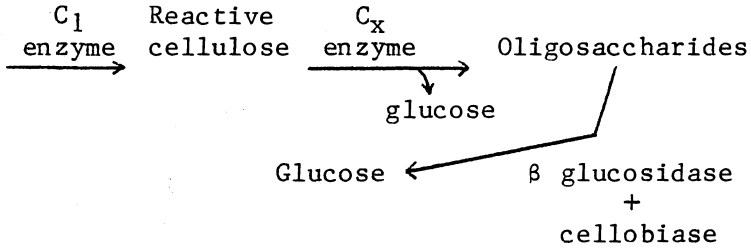
Intestinal oligo- and disaccharidases hydrolyze the intermediate endproducts of starch hydrolysis to glucose and glucose is absorbed. Intestinal oligosaccharides common to most animals include maltase, isomaltase, sucrose, lactase and trehalase. These enzymes are generally associated with the mucosa of the small intestine. Sucrose digestion in the intestine of the mature ruminant may result from bacterial fermentation as some evidence suggests that sucrase is lacking (Orskov et al., 1972).

Fiber Digestion

Cellulose, hemicellulose and pectin must be digested by microorganisms since mammals lack enzymes to degrade these complex polymers. Microbial populations are greatest in the rumen, lower ileum, cecum and colon. Structural carbohydrates are degraded by enzymes secreted by bacteria into the intestinal medium. Further hydrolysis or phosphorylative cleavage occurs inside bacterial cells. Certain protozoa also can engulf and digest cellulose. Cellulolytic bacteria attach to fibers and etch pits into cell walls. Many cellulolytic bacteria are encased in a gelatinous coat of glycoprotein which aids in attachment. The cellulases and hemicellulases are found in close proximity to this glycoprotein layer. Adhesion of bacteria to cell walls is greatly enhanced by mechanical damage to the wall (Latham et al., 1978). This damage could occur with physical processing of feeds or with mastication.

The type of cell wall also influences the readiness with which bacteria adhere. This dictates the length of the delay or lag time prior to the start of digestion.

Bacteria readily attach to cell walls of the epidermis, sclerenchyma, phloem and mesophyll tissue. Attachment to the walls of bundle sheath cells or metaxylem or protoxylem tissue is less extensive and occurs slowly. Bacteria cannot attach to the cuticle or chloroplast tissues. Epidermal and phloem cells are more rapidly digested than other cell wall tissues. The factor usually limiting cellulose digestion is the amount of lignification (Pigden and Hearney 1968). Each individual forage has a specific degree of lignification. Cellulose digestion is complex (Reese et al., 1950) and involves a multiple enzyme system. This system involves at least two specific steps: 1) solubilization and 2) degradation. The generalized scheme is:



The C_1 enzyme solubilizes the cellulose in some manner so the resulting cellulose can be further hydrolyzed by a C_x -enzyme complex. The C_1 and C_x enzymes may work in unison to solubilize native cellulose (Wood, 1970). The chemical and physical alterations which the C_1 enzyme produces have been elusive. Possible modes of action include: 1) a random acting C_x component, 2) a C_x enzyme which penetrates the cellulose lattice of the crystalline areas or 3) an enzyme capable of attacking atypical bonds in components other than D-glucose present in the cellulose molecule. It has been suggested the C_1 component of the

cellulose complex attacks the amorphous regions thereby solubilizing the crystalline cellulose. Proteolytic and lipogenic enzymes also may be involved in solublizing fiber.

The C_X enzyme hydrolyzes β (1-4) linkages between glucose units yielding oligosaccharides and disaccharides. The endproducts of the C_X enzyme catalyzed reactions are absorbed by bacterial cells and degraded by β-glucosidases or cellobiase. Some non-cellulolytic bacteria can absorb C_X endproducts for metabolism to glucose.

Protozoa also may digest cellulose. Diplodinia may partially digest large particles of cellulose or contain cellulolytic bacteria engulfed with the forage particle to digest cellulose. Hemicellulose and small amounts of lignin appear to be digested by similar enzyme mechanisms as the cellulose complex. However, different oligosaccharidases are involved in the final step. Cellulolytic and non-cellulolytic bacteria exhibit synergistic effects on fiber digestion (Dehority and Scott, 1967). Structural carbohydrates which escape digestion in the rumen may be degraded in the cecum and colon. Passage of the cell wall material through the acidic conditions of the abomasum may hydrolyze certain chemical bonds, thereby allowing further fermentation in the lower gut. Van Soest (1982) suggested that passage of hemicellulose through the abomasum hydrolyzes the arabinofuranosidic linkages, thereby exposing xylan to further degradation. Likewise, it seems feasible that some hemicellulose may be released from the glycoproteins by pepsin. Substanial amounts of hemicellulose and cellulose can be digested in the large intestine (Van Soest, 1982).

The extracellular cellulose enzymes are exposed on the microbial cell surface in two ways: 1) bound to the surface of the organism to

act on attached fiber or 2) secreted into the environment, allowing the free enzyme to attack and degrade fiber particles in the rumen media. The latter enzymes may solubilize cellulose for engulfment by protozoa. However, isolation of free cellulase has proven difficult (Akin 1978). Degradation of cellulose by bound enzymes can be categorized in three ways: 1) surface pitting, as with cotton fibers, 2) cylindrical cavities parallel to the microfilaments or 3) formation of bore holes. The last two methods have been observed with fungi in wood cells while bacteria and fungi cause surface pits in cotton fibers.

In biochemical terms, the more complex the substrate, the more enzymes and enzymatic cooperativity is required. To provide optimal cooperativity between enzymes, many metabolic sequences are catalyzed by a series of enzymes associated together in a complex. Microbial cellulose enzymes may be grouped into such a complex to degrade plant cell walls. Some of the structural features which determine cell wall susceptibility include:

1) moisture content of the fiber or wetability
2) size and diffusibility of the enzyme molecules
3) degree of crystallinity of the cellulose
4) unit cell dimensions
5) conformation and steric rigidity of the cellulose units
6) degree of polymerization of the cellulose
7) type of substances associated with the cellulose
8) nature, concentration and distribution of substituent groups (Cowling and Brown 1969).

The effect of each structural feature is discussed below.

Moisture Content

Moisture can influence cellulose digestion by swelling the fiber. Moisture provides a medium for diffusion and serves as a reactant during hydrolysis of the β (1-4) bond. Swelling the fiber also opens the fine structure making cellulose more susceptible to enzymes. Furthermore, sufficient moisture allows free movement of enzymes to substrates and endproduct assimilation by microbial cells. The third function of moisture in fiber degradation involves hydrolysis of the glycosidic bond between successive glucose molecules. Water is added across the glucosidic link during cleavage.

Diffusibility of the Enzymes

The amount of cell wall degradation that occurs is limited by the accessibility of the cell wall carbohydrates. There are two capillary sytems by which cellulose enzymes can enter the cellulose fibers; gross capillaries (pores and apertures in membranes) and cell wall capillaries (spaces between microfibrils or cellulose molecules in the amorphous region). Most of the cellulose enzymes can enter through the gross capillary system. Cell wall capillaries are much smaller and enzymes can enter only by enlarging the size of the pore. Cell wall capillaries are closed when fiber is dry. Adsorption of water opens the fine structure capillaries. However, as discussed earlier, the amorphous region of cellulose fibers contain hemicellulose and lignin which can reduce enzyme movement. Therefore, entry of enzymes into the capillary structure of the cell wall does not guarantee extensive cellulose degradation. The size, shape and binding affinities of

cellulose enzymes can limit cellulose degradation. These properties of cellulases differ depending on the microbial origin. Brown rot fungus depolymerizes both crystalline and amorphous regions of wood fibers simultaneously whereas white rot fungus degrades the amorphous region first and then attacks the crystalline core. Cowling and Brown (1969) postulate that the size and shape of the cellulase enzyme is responsible for differences in rate and extent of cellulose fiber degradation between the two species of fungi.

Crystallinity

Cellulose fibers with a high degree of crystallinity in the central core have much smaller capillary sytems. This reduces access of cellulose enzymes. Generally, greater crystallinity forces enzymes to degrade the amorphous regions to gain entry into the core.

Cellulose occurs in four recognized crystal structures based on its repeating three-dimensional structure. The crystal lattice structure of the cellulose limits the degree of association at the active site of the enzyme. However, fungi can modify the structure of the active site on the enzyme to accomodate the specific lattice structure of the cellulose. Steric rigidity and conformation of the glucose units in the cellulose chain also contribute to the inaccessability of crystalline cellulose as compared to the amorphous regions. Glucose units are orientated in a chain conformation in the amorphous region which may optimize the degree of association at the active site. The degree of polymerization (chain length) also can influence susceptibility if glucose units are cleaved sequentially from the end of the

chain. However, most cellulases appear to attack cellulose chains at random.

Associated Substances

Chemical constituents within fiber sources can limit the degree of cellulose degradation. Certain metals, as Co, Mg and Ca have been classified as stimulators of cellulases whereas Hg, Ag, Cu, Cr and Zn are inhibitory. Inherent materials can influence cellulose accessibility by 1) blocking capillary systems, 2) inhibiting cellulolytic bacterial through toxic substances (phenols), 3) inhibiting enzymes, 4) promoting bacterial growth (thiamine) or 5) containing insufficient nutrients (nitrogen and phosphorus) in fiber. Association of cellulose with lignin and possibly hemicellulose also can limit the susceptibility to enzymatic digestion.

Substituent Groups

Modification of glucose units within a cellulose chain can influence the degradability of the cellulose. Substituent groups which increase cellulose solubility will improve the accessibility of cellulose. However, larger or more numerous groups can effectively block the cellulose fiber from the enzyme. A free hydroxyl group is required for enzymatic hydrolysis to occur. Acetyl groups inhibit cell wall digestion and may become more prevalent with stage of maturity (Bacon et al., 1975). Therefore, any structural feature or chemical entity which limits mobility of the cellulase enzyme will reduce the degradability of the cellulose fiber. The origin, size and shape of the enzyme can influence how effectively it will digest cellulose.

Post-Ruminal Carbohydrate Digestion

The outline of post-ruminal digestion below is summarized from reviews (Armstrong and Beever, 1969; Armstrong and Smithard, 1970). Glandular tissue in the fundus of the abomasum secretes hydrochloric acid and pepsin. Pepsin solubilizes the protein matrix liberating oligosaccharides in corn or structural carbohydrates of cell walls for enzymatic degradation. In non-ruminant animals, substantial dry matter may disappear in the stomach due to microbial fermentation (Argenzio and Southworth, 1974). Acidic conditions of the abomasum may enhance digestion of certain carbohydrate fractions such as hemicellulose and soluble carbohydrates. Exposure of hemicellulose to the acid conditions in the abomasum may increase the degradability of xylan by hydrolyzing arabinofuranosidic linkages (Van Soest, 1982). Likewise, soluble carbohydrates may be hydrolyzed under the acid environment. However, very little soluble starch enters the abomasum in ruminant animals. Acid conditions may increase the wetability of certain types of feedstuffs (Armstrong and Beever, 1969). Protozoa and rumen bacteria are partially degraded in the abomasum. Trypsin and pepsin digest the cell wall which releases stored and structural carbohydrates of microbes for digestion.

Digestion of carbohydrate in the duodenum and jejunum is enzymatic. Amylase degrades starch to small oligosaccharides and glucose. Several factors (amylase activity, time, amylase exposure) limit digestion of starch in the small intestine. The factor which may limit starch digestion from cracked corn in the small intestine of ruminants is particle size (Zinn and Owens, 1982). Little reduction in

particle size occurs in the small intestine. A large percentage of the carbohydrate digestion occurs in the jejunum where pH is most optimum (Huber et al., 1961; Hembry, et al., 1967; Coombe and Siddons, 1973). Another possible limit to starch hydrolysis is the amount of hydrolytic enzymes present. Pancreatic amylase has strong amylase activity and a weak maltase activity (Siddons, 1968). In the rat, amylase secretion by the pancreas increases with additional dietary starch over several days (Howard and Yudkin, 1963; Abdeljbil and Desmuelle, 1964). In ruminants, pancreatic amylase activity may increase in response to increased grain intake, but adaptation may require as much as three weeks (Clary et al., 1969). This suggests that to evaluate starch digestion, a 3-4 week period may be needed for adaptation.

Starch and oligosaccharide digestion in the small intestine could occur by one of three major enzymes: amylase, maltase or isomalase. Maltase activity is constant through out the small intestine and doesn't appear to limit glucose absorption (Huber et al., 1961; Hembry et al., 1967). Amylase activity has been suggested to limit starch digestion (Huber et al., 1961, Hembry et al., 1967, Little et al., 1968). However, Mayes and Orskov (1974) suggested that isomaltase is the limiting enzyme. Factors which persuaded Nicholson and Sutton (1969) to suggest amylase is limiting include: 1) amylase secretion is low in the ruminant, 2) blood glucose levels are not greatly altered by abomasal starch infusion and 3) the high correlation between duodenal and ileal starch concentrations. Infusion of various levels of starch into the abomasum of steers indicated that a 360 kg steer can digest

approximately 275 g of starch per day in the small intestine (Karr et al., 1966). Processing of whole grain to reduce particle size increases intestinal starch digestion in the pig (Lawrence, 1970). Grinding grain removes the fibrous and proteinaceous layers surrounding the endosperm. The lower ileum contains bacteria attached to the mucosa which are capable of fermenting carbohydrates (Armstrong and Beever, 1969). The small amounts of hemicellulose and cellulose disappearance in the small intestine (Armstrong and Beever, 1969, Hintz et al., 1971; Watson et al., 1972) is attributed to bacterial fermentation. Studies with ponies suggested that fiber digestion in the small intestine occurred exclusively in the terminal ileum.

The cecum, colon and large intestine also digest carbohydrate. Armstrong and Beever (1969) reviewed the literature on post abomasal starch and cellulose digestion and concluded that 5 to 10% of those nutrients are degraded in these organs with typical feeding conditions. Feeding finely ground or whole shelled corn grain can increase the amount of starch digested postruminally (McCullough, 1973; Waldo, 1973). Cellulose and hemicellulose digestion is substantial in the large intestine and cecum (Armstrong and Beever, 1969; Hintz et al., 1971; Watson et al., 1972; Van Soest, 1982). However, the cecum and colon may play a larger role in hemicellulose than cellulose digestion. Organic matter fermented in the cecum and colon has been reported to be of limited value since volatile fatty acid absorption is limited and bacteria are excreted in the feces (Orskov et al., 1970). However, substantial VFA absorption from cecal and colonic tissue has been demonstrated in the pig, dog and horse (Stevens, 1977). Fecal material

has little buffering capacity between pH 2-4 which would suggest that volatile fatty acids are absent.

Definition of "Roughage"

A roughage according to Webster (1977, p. 1098) is a "coarse food that is relatively high in fiber and low in digestible nutrients, and that, by its bulk, stimulates peristalsis." Crude fiber in the Wende system conceptually represented the truly indigestible fraction of the diet regardless of dietary manipulation. A less strigent definition of fiber, more prevalent today (Van Soest, 1975), is a chemical estimate of the amount of cell wall material from plants. Plant cell walls can be measured by several procedures. The procedure most widely used is the Van Soest analysis (USDA, 1970).

The term "dietary fiber" is used instead of roughage by human nutritionists. "Dietary fiber" is defined as "the remnants of plant cells resistant to hydrolysis by the alimentary enzymes of man" (Trowell, 1978). Chemically, the term fiber or roughage is difficult to define because it is comprised of several chemical fractions which differ by analytical procedures employed. Likewise, a material which serves as fiber in one segment of the alimentary tract may become digested in a subsequent segment of the tract. Since the definitions are closely related, the term fiber and roughage will be used interchangeably throughout the rest of the thesis.

Roughage is added to the diet of feedlot animals for several reasons. These include:

a. to reduce the incidence of founder, bloat and digestive upsets

b. to maintain integrity of rumen wall and reduce incidence of liver abscesses

c. to lessen management skills required

d. to reduce ingredient separation and loss of fine particles

e. to improve diet palatability

f. to add protein, minerals and/or energy to the diet

g. to induce salivation and rumination

h. to buffer ruminal contents

i. to reduce cost of available nutrients.

Roughages in high concentrate diets perform a vital role in animal production. Forages which are rapidly digested may have less "roughage effect" than more slowly digested plant material. As more roughage is fed, nutrient availability becomes of increasing concern.

Effects of Roughage on Performance and Digestibility

Animal performance is usually measured as rate of weight gain and the amount of feed needed to produce that gain. Roughage addition up to 15% of the diet may improve both components of animal performance due to a reduction in the incidence of digestive upsets, bloat and other metabolic problems. Roughage added to grain diets will not reduce daily gain if intake increases appropriately to compensate for the reduced energy density (Matsushima, 1979; Owens and Gill, 1980; Gill et al., 1981). Generally ruminants consume a constant amount of energy when diets contain over 65% TDN. Below 65% TDN, gut capacity limits energy intake (Montgomery and Baumgardt, 1965). The precise value may differ with physiological status (lactation, age).

Generally, as the amount of roughage increases, efficiency of conversion of feed energy to gain decreases (Gill et al., 1981).

The composition of plant cell walls varies with type and maturity of the roughage (Table IV). Lignification increases as plants mature rendering plants less digestible. Consequently, the influence of roughage on diet digestibility and feed efficiency can vary substantially. Generally, as the amount of roughage in the diet increases, digestibility of dry matter and nitrogen decrease, while digestibility of fiber increases (Cole et al., 1976; Reynolds et al., 1979; Price et al., 1980; Vinet et al., 1980). Effects of added roughage on starch digestion have been variable, possibly due to the various forms of the corn and types of roughage fed. Some studies have shown reduced starch digestion with added roughage (Cole et al., 1976[a]) whereas other research has shown minimal change in starch digestion (McCullough, 1973). In an Oklahoma study, Teeter et al. (1981) demonstrated that addition of 10% roughage to the diet could increase the extent of starch digestion.

At higher levels of roughage, the response in starch digestion has varied with the source of roughage. In the Oklahoma study, 40 percent alfalfa reduced starch digestion by 3.5% while the 40% cottonseed hull supplemented diet did not reduce starch digestion. This difference may be related to rumination, rate of digestion and rate of passage. The consistency of rumen fluid may determine the extent to which grain is ruminated. Whole grain must be chewed to be utilized effectively. With whole corn diets, approximately thirty percent of the kernels are broken during eating, 10% due to rumen fermentation and 46% is ground

TABLE IV

COMPOSITION OF FIBER COMPONENTS OF VARIOUS ROUGHAGES (%)

	CWC	ADF	Hemicellulose
Alfalfa	52	40	12
Barley Straw	80	59	21
Brome Grass	62	34	28
Clover, Red	56	41	15
Corn Silage	45	27	18
Cottonseed Hulls	90	71	19
Oat Straw	70	47	23
Orchard Grass	56	34	22
Sorghum Forage	62	38	24
Timothy	68	43	25
Trefoil Birdsfoot	44	34	10
Wheat Straw	85	54	31

during rumination. The residual 14% should appear in the feces (Wilson et al., 1973). Since amounts of whole corn and starch in feces vary, these figures may vary with animal and dietary factors. Since various roughages alter ruminal kinetics, the extent of grain breakdown may be altered.

Generally, as roughage in the diet increases, ruminal pH and the ratio of acetate to propionate increase (Van Soest, 1982). Diets higher in fiber favor growth of methanogenic bacteria. Methane low-- totals about 8% of the consumed gross energy with a high roughage diet (Blaxter, 1962).

Effects of Roughage Processing on Diet Digestibility

The intake of forages and other fibrous feeds can be increased substantially by pelleting and grainding (Van Soest, 1982). Osbourn et al. (1976) reviewed the effects of grainding and pelleting on feed intake and digestibility and made the following conclusions:

1. Effects on intake were greater during short term than long term experiments
2. Greater responses were apparent with sheep (45%) than with cattle (11%)
3. Greater responses in young animals (38%) than older animals (18%)
4. Greater responses with mature than immature forages
5. Increased net energy valuses of forages

6. Depressed rate and extent of ruminal digestion with grass diets but no change or enhanced ruminal digestion of legume diets.

The degree of grinding will influence the response in feed intake. Grinding to particle sizes less than approximately .75 mm for lucerne, .55 mm ryegrass and .40 mm for tall fescue will not increase intake and may instead reduce intake if the diet is dusty (Osbourn et al., 1976). The increase in net energy value of forage due to processing is due largely to the increased intake, however improvement in substrate availability and alteration in site of digestion may contribute as well (Van Soest, 1982). Generally, grinding reduces organic matter digestibility of the roughage (Van Soest, 1982). Grinding roughages decreases particle size, increases surface area and increases bulk density. The smaller particle size reduces bulkiness of diet, thus permitting greater consumption. However, ground roughage exits from the reticulorumen faster as well.

Digestion of roughages which contain rapidly fermentable cell walls and/or cell contents should benefit from grinding. But digestibility of roughages with slowly degraded cell walls could be reduced due to the reduction in time for digestion in the rumen. The association between digestibility and bulkiness for each roughage will determine which forages are hindered or benefited by grinding.

Reducing the particle size of the roughage may alter the site of digestion. Pelleting alfalfa shifted the site of gross energy digestion by sheep from the rumen to the small and large intestines (Thomson et al., 1969). In contrast to these results, Hogan and Weston (1967)

reported processing of wheaten hay did not alter site of digestion. Alfalfa has a higher content of cell solubles than wheaten hay. This may explain the pelleting response of alfalfa. Additionally, grinding of roughage decreases the work of digestion and rumination. This expense may total 8% of the total energy cost for a ruminant. Energy cost of eating a chopped grass diet is 6.4 times more than a pelleted diet (Osuji et al., 1975). The same authors compared oral with ruminal feeding of the chopped grass and reported that 92 to 98 percent of this difference in energy cost associated with consuming the diet. A reduction in the energy expended in ingestion and rumination of feed will increase the net energy value of a forage.

Effects of Roughage Maturity on Digestion

Grasses and legumes become more lignified as plants mature (Waite et al., 1964; Van Soest, 1982) and digestibility is inversely proportional to the amount of lignin present. Figure 3 illustrates the influence of maturity on the yield of dry matter and digestible dry matter. Metabolizable energy decreases after plants reach a certain physiological point. This critical stage of maturity occurs approximately at the time of incipient flowering (florescence). Part of this reduction is due to deposition of lignin. The chemical composition and structure of lignin varies with the type of plants (Van Soest, 1982). Lignin in grass contains more esters and less methoxyl groups than lignin in legumes. Ester groups render lignin more soluble in alkali. Lignin in legumes may have ether linkages.

Three theories have been proposed to describe the effects of lignin on cell wall digestibility:

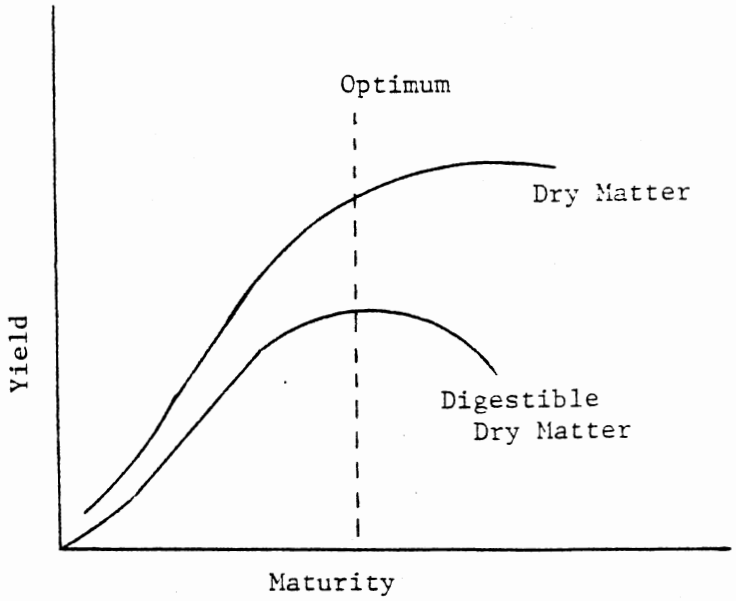
1. physical encrustation and entrapment
2. enzyme inhibition
3. linkage to carbohydrate (Van Soest, 1982).

Physical encrustation and entrapment of nutrients within lignified cell walls could drastically hinder the accessability of enzymes to structural carbohydrates. The increase in digestibility due to milling would support this premise. Cell contents are totally digested. This suggests that the inhibitory effect of lignin is limited to the cell wall carbohydrates.

Enzyme inhibitors have been found in certain browse plants and tropical legumes. These inhibitors are generally removed when tannins are removed.

Lignin-hemicellulose complexes may be inacessible to cellulolytic enzymes. This could account for the effects of lignin on fiber digestion. The chemical bonding mechanism responsible for the inaccessibility is uncertain, though it appears that lignin content limits the extent, not the rate of fiber digestion. In fiber diets typically fed to cattle in United States, the carbohydrate linkage theory has received the most attention. The encrustation theory cannot be ruled out, however, increased digestibility due to alkali or ammonia treatment of straw without removal of lignin would support the lignin carbohydrate theory.

Organic matter digestibility decreases as plants mature accelerating after flower emergence (Waite et al., 1964). Nitrogen, hemicellulose and pectin account for the largest proportion of the decrease in organic matter digestibility. Effects of level of intake on extent of



Source: Van Soest (1982).

Figure 3. Influence of Maturity on Dry Matter Digestibility

digestion are magnified as grasses mature. A Canadian study (Vinet et al., 1980) also reported that dry matter, gross energy, nitrogen, cell wall constituents and acid detergent fiber digestibilities decreased with maturity for timothy hay. Level of roughage has a more severe effect on digestibility with more mature forage. Hemicellulose and nitrogen digestibilities were increased as concentrate was added to the mature timothy diet but were unchanged with the higher quality timothy diet. In contrast, cellulose digestion decreased with added concentrate with the early cut timothy and was unaltered with the mature timothy diet.

In summary, roughages can influence utilization of various nutrients, especially if the diet contains large proportion of roughage. Generally, as roughage is added to the diet, organic matter digestibility decreases. If intake of digestible dry matter decreases, performance is reduced. Reduction of particle size of forages increases intake and rate of passage from the rumen. At high intakes, cell wall digestion may be reduced. Forage maturity, however, plays a larger role in determining diet digestibility than intake. Concentrate addition influences hemicellulose digestion to a larger degree with mature forages, but cellulose digestion may be altered to a greater extent with early cut forage.

Rate of Passage Through the Digestive Tract

The amount of time which food particles spends in the gastrointestinal tract may limit the extent of digestion (Entringer et al., 1974; Kass et al., 1980). Longer exposure to digestive enzymes, acid conditions and/or microorganisms often increase the extent of digestion.

Rate of passage appears most critical for extensive digestion of certain feed components such as fiber and protein.

Several methods have been utilized to determine rate of passage. Slaughtering animals at various time periods after feeding has been used by several researchers (Rosenthal and Nasset, 1958; Grovum and Williams, 1973; Argenzio and Southworth, 1974; Kass et al., 1980). Results with this technique are clouded by cell sloughing, rapid peristalsis at the time of slaughter and alterations in the water and electrolyte balance. The use of cannulas in various segments of the gastrointestinal tract allows direct determinations of flow rates. However, flow rates may be influenced by the presence of the cannula or surgical modifications. Rate of passage in humans has been evaluated with a triple lumen tube which is inserted orally into the gastrointestinal tract (Dillard et al., 1965). Presence of this tube also would be expected to alter motility and passage rate.

Dyed feed particles, polyethylene tubing, rare earth particulate markers, liquid markers and chromic oxide have been used to determine the rate of flow in intact and surgically altered animals. First appearance of marker, appearance of a certain percentage of the marker, total collection and ratios of different markers have been used to estimate passage rate.

Several factors influence the rate of passage of feed materials in the gastrointestinal tract. These include level of feed intake, digestibility, particle size, specific gravity, animal weight, age or sex and diet composition. A three fold increase in feed intake reduced the amount of time digesta spent in the small and large intestine of sheep by 33 and 60% respectively (Grovum and Williams, 1973). The

importance of these factors in determining ruminal and post ruminal passage rates is discussed below.

Feed stuffs ingested into the rumen are distributed into pools. For simplicity, two pools, a coarse particle pool and a fine particle pool can be visualized (Hungate, 1966). The more slowly digested, coarse particles comprise one pool while the second pool includes ingesta which is small and can exit rapidly. Liquids and solids exit from the rumen at differential rates further complicating the kinetics (Grovum and Williams, 1973). Undoubtedly, proportions of the small particle pool pass out with both fractions. The ingesta in the large particle pool must be reduced to a smaller particle size and enter the second pool before leaving the rumen. Liquid outflow or dilution rate increases as level of feed intake increases (Balch and Campling, 1965; Topps et al., 1968; Galyean et al., 1979). Adding salts to the rumen fluid (Thomson et al., 1978) and cooling the animal (Kennedy and Milligan, 1978) will increase liquid outflow rates. Adding roughage to a high concentrate diet also will increase the rate of which liquids leave the rumen (Cole, 1975). Flow of solids from the rumen will increase as level of intake increases (Sutton, 1979). The reduced retention time with greater intake probably results from increased reticulo-ruminal motility (Balch and Campling, 1965).

Concentrates leave the rumen faster than roughages (Balch, 1950). Addition of finely ground hay to a long hay diet resulted in the ground hay leaving the rumen faster than long hay although variable results have been obtained when ground hay comprised the total diet (Sutton, 1979).

Rate of breakdown and specific gravity also influence the rate of flow from the rumen (Balch and Campling, 1965). Addition of urea to a low quality forage diet increased the rate of ruminal breakdown by 20% and decreased total tract retention time by 25%. Urea supplementation also increased intake by 40% in this study. Urea may have stimulated fiber digestion, thus allowing ingesta to leave the rumen faster which permitted more feed consumption. Nevertheless, urea may have other effects, such as increasing saliva flow or osmotic pressure in the rumen. Size and specific gravity of digesta particles determine the rate at which particles pass through the reticulo-omasal orifice. Particles with a specific gravity of 1.1 to 1.2 pass from the rumen and hindgut most rapidly. Particles with a specific gravity between 1.0 and 1.1 pass more slowly, while those less than 1.0 will float. Long fiber particles tend to have a low specific gravity and form a fiber mat in the dorsal portion of the rumen. Long particles tend to bind water more slowly than ground particles due to their lower surface area. Long digesta particles must be reduced top smaller sizes to pass from the rumen. Reducing particle size from 4.8 to 3.2 mm reduced retention from 91 to 80 hours in this trial. The type of forage fed can influence ruminal and total tract passage rate (Teeter, 1981). Legumes have a shorter retention time than grass hays (Church, 1976). In a Canadian study, dry corn had a slower turnover time than high moisture harvested corn (McKnight et al., 1973).

Feedstuffs, especially forages, lose many of their physical characteristics during passage through the rumen. Flow of abomasal contents to the duodenum is relatively constant (Zinn et al., 1980). Total tract rate of passage generally parallels ruminal passage rate

(Teeter, 1981). Under practical feeding situations, ruminal outflow rates appear to limit the rate of passage through the total gut in ruminants. Intestinal passage rate can be altered with substances or diets which act as duiretics. The rate of passage through the intestine of non-ruminant animals is influenced to a large degree by level of intake and level and source of roughage. Relative retention times for various species are shown in Table V.

After feeding, flow rate in the duodenum and jejunum is increased but rate in the ileum is unchanged (Low et al., 1978; Grovum and Williams, 1973). Endogenous secretions from the stomach and pancreas can comprise up to 65 percent of the total duodenal digesta (Braude et al., 1976). Intake, specific gravity, frequency of feeding, type of concentrate, and level of roughage all can influence the rate of flow through the intestines. In a study with sows, increasing feed intake from 2 to 6X maintenance increased the percentage of marker appearing in feces on the second day after dosing from 0 to 71% (Parker and Clawson, 1967). The total weight of diet consumed, rather than dry matter content of the diet, may determine the rate of passage in swine (Castle and Castle, 1957). Small and large intestinal volume and transit time increase as level of intake increases. However, intake effects on retention are more pronounced in the large intestine (Grovum and Hecker, 1973). Dense particles may pass through the large intestine faster than small particles. This is opposite of ruminal passage (Balch and Campling, 1965). Sheep which were fed hourly vs. every 24 hours showed more consistent flow to the duodenum and an increased flow per day (Thompson, 1973). Frequent feeding may eliminate duirnal variation in digestion and humoral levels and maximize animal growth rate.

TABLE V

RETENTION TIME IN THE GIT OF VARIOUS SPECIES

Species	Organ	Capacity (L)	Length (M)	Retention Time (hr)	Author
Man	SI[a]			0.3	Clemens et al 1975
	J[b]			0.2	Barreio et al 1968
Pigs	GIT	27.45	23.5		
	meal			39.9	Seerley et al 1962
	pellet			28.6	
Sheep	SI	9.0	26.2		
	400 g/d			2.25	Grovum & Williams
	1200 g/d			1.5	1973a
	SI	9.0	26.2	2.25-4.5	Coombe & Kay 1965
	LI[c]	5.6	6.53	10.2-26.5	
	R-R[d]	25.4		13.5	Grovum & Williams
	AB[e]	3.3		.5	1973b
	C&PC[f]	5.6		6.9	
				Long Fine	
	R-R&AB	28.6		51.3 53.7	Sanchez-Hemocillo
	GIT	44.2		64.8 72.5	and Kay 1979
Red Deer	R-R&AB			63.2 72.7	
	GIT			73.2 88.6	
Goats	GIT	44.2		38	Castle 1956[a]
	GIT	44.2		36.1-60	Castle 1956[b]
	D→F[g]	14.6	32.7	11-14.4	
Steers	R	252.5			
	liquid			15.8	Phillips et al
	solid			23.8	1980
Dairy Cows	GIT	356.4			
	hay			73	Campling et al
	straw			100	1961

[a]SI = small intestine
[b]J = jejunum
[c]LI = large intestine
[d]R-R = reticulo-rumen
[e]AB = abomasum
[f]C&PC = cecum & proximal colon
[g]D→F = duodenum to feces

Source: Stevens, 1977

Starch diets fed to swine produced slower passage rates than diets containing lactose or glucose (Entringer et al., 1975). The simpler carbohydrate diets may increase passage through osmotic effects. In a study comparing four types of grain in swine diets, milo and barley diets had slower duodenal and total tract passage rates than corn or wheat diets (Keys, Jr. and De Barthe, 1974). Increasing the amount of alfalfa in the diet also increased rate of passage in pigs (Kass et al., 1980). The source or type of roughage fed can influence the rate of passage through the intestines as well. A study with four fiber sources fed to humans indicated that coarse and fine wheat bran and solka floc promoted faster rates of passage through the total tract than cabbage or no additional roughage (Van Soest et al., 1978). A Michigan study with rats demonstrated that rate of passage increased as more wheat bran was added to the diet and that corn bran passes through the tract faster than wheat bran (Lee et al., 1979).

The stomach of non-ruminant animals retains fibrous digesta. It is continually mixed in the stomach (Stevens, 1977). Gastric emptying influences the composition of the digesta entering the duodenum but does not regulate the rate of movement (Poulakos and Kent, 1973). Large particle size or fibrous digesta is retained in the stomach and passes out at a slower rate than other portions of the digesta. Removal of the stomach from pigs did not alter rate of passage but reduced the digestibility of dry matter and crude protein (Cunningham, 1967). Addition of 15% corn oil to a swine diet decreased the rate of gastric emptying (Cummingham, 1967).

Digesta passes through the total tract of swine faster and more feces voided during daylight hours than during the night (Castle and Castle, 1956). Greater feed consumption and activity during daylight hours which may explain this phenomena.

As an animal ages, the rate of passage of food materials through the gastrointestinal tract decreases (Kass et al., 1980). Female mice had a faster fluid outflow but slower solid outflow from the stomach than male mice (Dawson, 1972).

Three areas of the cecum and colon may restrict digesta flow in equine (Argenzio et al., 1974). The areas in the cecum and colon where indigestible markers accumulated are at the cecal-colonic orifice, the ventral-dorsal colonic junction and dorsal-small colonic junction. High mineral and water absorption or fermentation in these areas would also concentrate the marker, however. Retrograde flow from the cecum to ileum or dorsal colon to ventral colon was not observed in the equine. Hence, flow through the large intestine of the equine appears to be undirectional.

Factors Affecting Rate of Digestion

Rate of digestion is the speed at which ingesta is physically and chemically reduced to smaller particle size in preparation for absorption. Fast rates of digestion are usually associated with faster rates of passage and, thereby, higher feed intakes. Factors which influence rate of digestion include: a) composition of the diet, b) nitrogen or mineral deficiencies and c) level of feed intake. These factors will be discussed individually.

Diet Composition

The type and maturity of the forage drastically influences the rate of digestion (Table VI). Summarization of the data by Smith et al. (1972) indicates that legumes have a faster rate of digestion than grasses. Mature plants are digested at less than half the rate of plants at the vegetative stage of growth (Table VI).

Time of exposure to ruminal organisms also will influence the rate of digestion. After seventy-two hours, ruminal digestion is considered complete (Smith et al., 1971). The rate of ruminal digestion exhibits a quadratic type function over time, however, fermentation begins at different times after ingestion for various forages (Mertens, 1977; Van Soest, 1982). This delay is called a "lag time". Cellulose sources such as Whatman filter paper and cotton have longer lag times than fibers containing other structural carbohydrates (Table VII). The duration of the lag time is not correlated with the extent of digestion in vitro. But, in vitro digestion is not limited by rate of passage. Fiber sources with long lag times may suffer reduced ruminal digestibilities if removed before digestion has been maximized.

Table VII demonstrates the vast difference in rate of digestion of various fiber sources. Vegetable fibers have uncrystalline cellulose and less lignin which results in a rapid fermentation, while alfalfa and grain brans have more crystalline structures with more lignin present. Cotton and Whatman cellulose have long lag times, little lignin and very crystalline cellulose structures. These features indicate the rumen microorganisms have difficulty gaining access to the cellulose. Nevertheless, digestion is nearly complete once enzymes attach.

TABLE VI

RATE OF DIGESTION CONSTANTS FOR CELL WALLS OF VARIOUS FORAGES AND MATURITIES

	Cell Wall Digestion Rate Constant[a] (hr^{-1})	
	Vegetative	Mature
Alfalfa	.191	.073
Birdsfoot Trefoil	.174	.060
Ladino Clover	.309	.063
Red Clover	.091	.063
Crown Vetch	.103	.097
Vetch	.118	.057
Bluegrass	.153	.048
Brome Grass	.183	.073
Tall Fescue	.131	.058
Orchardgrass	.128	.050
Reed Canarygrass	.183	.053
Barley	.119	.048
Oats	.131	.042
Rye	.160	.042
Wheat	.078	.075

[a]Rate constants for in vitro disappearances of digestible cell walls. Ln[cell walls]/hr.

Source: Smith et al. (1972)

TABLE VII

LAG TIME FOR VARIOUS FIBER SOURCES

Fiber Source	Lag time (hr)	Rate of Digestion	Extent of digestion (72 hr)	Ratio of $\frac{\text{lignin}}{\text{cellulose}}$
Cauliflower	4	.42	.94	.05
Onions	5	.23	.91	.09
Corn bran	5	.10	.94	.12
Wheat bran	3	.06	.43	.47
Alfalfa	4	.12	.59	.30
Bagasse	4	.04	.45	.31
Whatmann cellulose	9	.07	.94	.03
Cotton	17	.04	.98	.00

Source: Van Soest (1977).

Wheeler and colleagues (1979) measured rates of digestion with dacron bags. The rate constants for dry matter and cell walls with orchardgrass, barley straw, cottonseed hulls and corn stover were .0524, .0511; .0449, .0497; .0273, .0314; and .0387, .043 respectively. Cottonseed hulls proved atypical as a roughage in their study. Perhaps cottonseed hulls have a much lower water binding capacity and clear the rumen more rapidly than other forages. Sodium hydroxide treatment decreased the rate of digestion and increased the rate of passage of corn cobs (Berger et al., 1980). Osmolarity from sodium hydroxide may be responsible. Osmolarities above 400 mOSM/kg reduced cellulose digestion in vitro by 80% (Bergen, 1972).

Particle size of the roughage also can influence the rate of digestion. Reduction of particle size from 12 mm to 1 mm in length increased the digestion rate constant from .0415 to .0672 with alfalfa but the rate constants of orchardgrass were unchanged by grinding (Robles et al., 1980). Rate of digestion of various concentrates and mixed diets has received very little research attention. A study by Teeter (1981), indicated that alfalfa increased rate of dry matter digestion from whole shelled corn or ground corn. Cottonseed hull addition did not alter rate of digestion with either corn type. Rate of starch digestion was similar with all treatments.

Nutrient deficiencies

Nutrient deficiencies can interfere with the rate of digestion. Addition of urea to low quality forage often increases rate of digestion, rate of passage and intake (Hemsley and Moir, 1963). Urea addition usually increases volatile fatty acid concentrations and rumen

ammonia levels. When deficient, supplementation with branch chain fatty acids increase rate of growth of cellulolytic organisms and rate of cellulose digestion (El-Shazly, 1961; Hemsley and Moir, 1963; Hungate, 1966). Low ruminal pH values reduce the rate of cellulose digestion (Terry et al., 1969; Stewart 1977; Slyter, 1981). Certain inorganic minerals can stimulate digestion rate as well (Hungate, 1966; Martinez and Church, 1970). Phosphorus deficiency may limit microbial digestion of cereal straws.

Mertens (1977) developed a model to predict digestion and passage through the ruminal ecosystems. His model separates ruminal digestion into four component parts: digestion rate, digestion lag, potential extent of digestion and passage rate. Each component of the model is influenced by additional factors discussed below.

Lignin content was poorly correlated with rate of digestion but influences extent of digestion. Mertens indicated that present chemical methods do not measure the chemical entity which limits rate of digestion. The role of physical and morphological characteristics of the plants which are not detectible by chemical procedures may be controlling rate of digestion. Some of these physical characteristics include fragility of plant tissue, degree of crystallinity, surface area and wetability. Another aspect influencing rate of digestion is the effect of various external factors on the ruminal ecosystem.

The factors which influence lag time are unidentified however, some possible factors include:

a. wetability

b. particle size and surface area

c. susceptibility to microbial attachment and

d. amount of soluble substrate.

The factors limiting the digestion of potentially digested cell walls are not well studied. Lignin and silica may limit the extent of digestion. Crystallinity of the cellulose may limit cell wall digestion, as well. The last component of the Mertens model is rate of passage. Two factors which influence rate of passage are level of feed intake and particle size. Simulation of various levels of these four components on cell wall digestibility for grasses and legumes is shown in Table VIII. As rate of digestion and potential cell wall digestibility increase, dry matter digestion increases. Increasing digestion lag time or rate of passage lowers the extent of dry matter digestion. The lag time effects on digestion predicted by this model contradict the results of Van Soest (1977) as discussed earlier. Van Soest's data includes several roughage sources whereas Mertens modeled data from grass and legume hays. Similarly, the ruminal ecosystem could alter the length of lag time. The extent of ruminal digestibility of a fiber is the product of these four components.

Nutritional Significance of Rumination

This overview of rumination was gleaned from reviews by Church (1976) and Van Soest (1982). Rumination serves to reduce particle size of ingesta to facilitate passage to the lower gut and to add saliva to ingesta. Particle size reduction increases rate of passage allowing the animal to consume more feed. Rechewing food at a time considerably after consumption, as occurs during rumination, may be an evolutionary phenomena which allowed ruminants to consume food during periods when

TABLE VIII

MATHEMATICAL SIMULATION OF MERTENS MODEL

	Dry matter digestibility (%)	
	Grass	Legume
a) Rate of digestion (hr^{-1})		
-.08	63.4	59.6
-.10	64.7	60.0
-.12	65.7	60.4
-.14	66.4	60.7
-.16		
b) Digestion lag time (hr)		
0	67.9	61.8
2	66.3	61.0
4	64.7	60.2
6	63.2	59.5
8	61.8	58.8
c) Potential cell wall digestibility (%)		
40	46.8	55.0
50	51.9	58.5
60	57.0	62.0
70	62.2	65.5
80	67.3	69.0
d) Rate of passage (hr^{-1})		
.01	67.2	61.3
.02	64.7	60.2
.03	62.5	59.3
.04	60.4	58.4
.05	58.4	57.5

the risk of predation was low. A further advantage of rumination includes soaking of the fibrous portion of the diet to maximize the effect of chewing. Rumination also adds saliva to help maintain a pH optimal for fermentation and to prevent bloat.

Rumination involves the following five steps:

a. regurgitation of ingesta

b. reswallowing of regurgitated liquids

c. remastication of solids

d. re-insalivation

e. reswallowing

Grinding or pelleting hay reduces the amount of time spent ruminating, while long fibrous feeds increase the time of rumination to a maximum. Ruminant animals chew more thoroughly during rumination than during eating. However, the maximum amount of time spent chewing (eating plus ruminating) is 10-11 hours per day (Bae et al., 1979). Time spent eating and ruminating varies depending on the feedstuff (Table IX). Summarization of Table IX ranks classes of feedstuffs according to the amount of time spent ruminating oat straw (100), hays and silages (60) and finely ground forages and concentrates (12). Due to the variation between animals, genetic selection for chewing efficiency may be feasible (Balch, 1971). Urea addition reduced the time spent eating and ruminating with oat straw (Table IX).

The amount of energy expended during eating is 12 times greater than during rumination. Therefore, the amount of time spent eating is the major difference in energy expenditure between animals fed chopped and pelleted diets and animals fed long forage (Osuji et al., 1975). Pelleted diets are consumed twice as fast as chopped diets.

TABLE IX

TIME SPENT CHEWING FOR VARIOUS FEEDSTUFFS

Diet			Eating	Ruminating (minutes/KgDM)	Total
Oat straw			41-58	94-133	145-191
Oat straw & Urea			23-24	67-79	98-117
Finely ground oat straw (pelleted)			11-24	0-20	11-31
Finely ground oat straw			15-18	0-22	15-37
Dried grass			8-18	33-39	44-53
Finely ground dried grass (pelleted)					
Medium quality hay			20-40	63-87	103-109
Good quality hay			27-31	55-74	87-105
Finely ground hay (pelleted)			13	0-6	13-19
Grass silage			31-58	60-83	99-120
Concentrates (pelleted)			4-10	0-25	4-29
Hay %	Concentrate %				
67	33		19	47	66
44	56		18	42	60
31	69		15	37	52
17	83		11	24	35
8	92		21	19	40
7	93		16	20	36
0	0		10	0	10
Barley straw %	Concentrate %				
60	40		18	44	62
40	60		17	36	53
20	80		16	20	36
0	100		21	0	21

Source: Balch, 1971

Concentrate diets are consumed rapidly as well. Rate of eating may be limited by the rate of saliva flow. Feeds which require little insalivation for swallowing can be consumed more rapidly.

Corn Processing

Corn kernels can be altered by several methods to increase nutrient digestibility. More common processing methods include grinding, rolling, steam flaking, high moisture harvesting, acid treating and reconstitution. Benefits of high moisture harvest include earlier harvest, with less field loss, and avoiding the expense of drying. Corn processing can improve bunk management and reduce sorting of dietary components. Most processing methods increase surface area of the grain allowing more rapid and extensive bacterial or enzymatic digestion. Several of the wet processing methods, such as with high moisture harvested, reconstituted and steam flaked corn increase starch availability from the grain. This may be due to increased surface area. Grain is processed in feedyards for two basic reasons: 1) increase the energy value and 2) improve the appearance of the diet in the bunk for visiting cattle consigners. The decision to process grain must be a compromise between processing costs, added energy value and diet appeal. Under 1982 economic conditions, the increased energy value derived from steam flaking corn may not cover the processing cost. Harvesting corn with a higher moisture content is economically beneficial provided the corn is available locally. The economic benefits of reconstituting corn have not been conclusively determined. The benefit of rolling or grinding whole corn depends on the size and facilities available in a feed yard and cost and type of roughage used.

Effects of Corn Processing on Performance

Fifty feed trials were reviewed to examine the effects of corn processing on performance of feedlot cattle by Hale (1980). Results are show in Table X. He concluded:

1. gain was 3% greater for cattle fed high moisture harvested or reconstituted corn than for cattle fed corn processed by other methods
2. feed intake of cattle was similar with whole shelled and dry rolled corn but was 7.8 and 3.3% lower with steam flaked and high moisture or reconstituted corn, respectively
3. feed required per unit of gain was similar for whole and dry rolled corn but was reduced 8.1 and 6.5 per cent for steam flaked and high moisture or reconstituted corn, respectively
4. processing improved grain utilization by 10.1 per cent (assuming no associative effects).

The level of corn in the diets was variable. The authors assumed the advantage of processing did not interact with roughage level or source. Typically processed corn diets are fed with slightly higher levels of roughage which may have biased the results in favor of the processed corn.

Whole corn may have some "roughage" effect, thereby allowing lower roughage levels to be fed. Gill et al., (1980) fed whole shelled corn with 5% silage, steam flaked corn or high moisture harvested corn with 14% corn silage. The steers fed whole shelled corn gained faster and more efficiently than steers fed high moisture or steam flaked grain. Net energy values for the whole shelled, high moisture and

steam flaked corn diets were 60.4, 58.5 and 64.3 Mcal/100 lbs of feed, respectively. Corn grain required per unit of gain for whole shelled, steam flaked and high moisture corn were 5.3, 5.6 and 5.3, respectively, indicating that steam flaked corn was utilized least efficiently. Colorado State University recommends that when diets contain greater than 50 or 60% concentrate corn should be in the whole shelled form (Matsushima, 1979). Utilization of whole shelled corn allows cattlemen to feed all concentrate diets. McCullough and Matsushima (1974) fed whole shelled (WSC) or steam flaked corn (SFC) with 0 or 15% corn silage to feedlot steers. Daily gains were similar at both roughage levels with either corn type however gains were slightly lower with the SFC than WSC diets. Feed required per unit gain was slightly greater for diets containing 15% silage. Summarizing the above trials, one can conclude that the effect of level of roughage on performance can vary with the method of corn processing. As level of roughage decreases, the advantage of whole shelled corn increases. However, data comparing corn processing methods at higher roughage levels is lacking.

Feeding corn processed by different methods together or in combination also may influence performance. Steers fed high moisture harvested corn for the first 70 days and then switched to whole shelled corn had more rapid gains than cattle switched to steam flaked corn or continued on high moisture corn (Gill et al., 1980). In that study, steers finished on whole shelled corn gained faster than steers fed either high moisture or steam flaked regardless of corn processing method fed the first seventy days. Cattle fed whole shelled corn

TABLE X

COMPARISON OF CORN PROCESSING SYSTEMS

	Processing method			
	Whole shelled	Dry rolled	Steam flaked	High moisture or reconstituted
Daily gain, (Kg)	1.25	1.25	1.25	1.29
Daily feed, (Kg)	8.60	8.62	7.93	8.32
Reduction (%)	----	+.2	-7.8	+3.3
Feed/gain	6.88	6.90	6.34	6.45
Improvement (%)	----	-.3	+7.8	+6.3
Grain Level	78	74	74	80
Improvement (%) in grain efficiency	----	----	10.1	8.1

outperformed cattle fed corn processed by methods tested during the latter half. This may be due to the lower roughage level in the diet.

Addition of dry ground corn to high moisture harvested corn diets increased gain and decreased feed required per unit of gain in a Colorado trial. However, dry ground corn addition to steam flaked corn did not alter gains and increased feed required per unit of gain (Butterbaugh and Matsushima, 1974). The authors concluded that addition of dry ground corn to a high moisture corn increased intake while addition of steam flaked corn decreased intake. In an Oklahoma trial, steers fed a mixture of steam flaked and high moisture corn were more efficient than steers receiving only high moisture corn but less efficient than steers receiving only steam flaked corn (Gill et al., 1981). Gains were similar for the three diets in that study. The optimum roughage levels in that study for steam flaked, high moisture or the mixture of the two corns were 8, 12 and 8%, respectively. A 50:50 mixture of whole shelled and cracked corn or whole shelled and finely ground corn fed to steers produced 6.3% greater gains and required 5% less feed per unit of gain than either of the corn types fed individually (Turgeon and Brink, 1981).

The level of corn moisture can influence how efficiently corn grain will be utilized. Several reviews (Buchanan-Smith, 1976; Corah, 1976; Goodrich and Meiske, 1976) have suggested that high moisture harvested (67 - 73% DM) corn is used more efficiently than dry corn (85% DM). This advantage is the result of similar gains with lower feed intake. Feeding corn with 86% and 73% DM provided similar animal performance, whereas an 80% DM ration yielded a reduced response in a study by Teeter et al. (1979). A combination of the 86 and 73% DM corns

gave animal responses similar to the mean of cattle fed the two feeds alone. In high concentrate diets, corn which is steamed and rolled into a thin flake will increase gains 4-5% and reduce feed required per unit gain by 8-10% as compared with corn processed to a thicker flake (Matsushima, 1979).

Influence of Corn Processing on Digestibility

Processing whole corn, whether by reducing particle size or adding moisture, increases digestibility of organic matter and starch (McCullough, 1973; McKnight et al., 1973; Galyean et al., 1976; Moe and Tyrrell, 1977). Effects of corn processing on protein digestion are more variable. Some researchers have reported increased protein digestibility (McKnight et al., 1973) while others have reported no change in protein digestibility with corn processing (Galyean et al., 1976; Prigge et al., 1976; Moe and Tyrrell, 1977). There is a tendency for fiber digestion to be reduced with more extensive corn processing (McKnight et al., 1973 and Moe and Tyrrell, 1977).

The increased digestion of organic matter and starch occurs before digesta reaches the small intestine (McKnight et al., 1973; Galyean, 1976). Digesta from steam flaked corn diets had 9% faster dilution rates than cracked corn diets (Johnson et al., 1968). Liquid outflow from the rumen is slower with ground high moisture corn than dry ground corn (McKnight et al., 1973); however, in contrast to these results, Prigge et al. (1978) reported a greater dilution rate with high moisture harvested than dry rolled corn. It appears that high moisture or steam flaked corn leaves the rumen faster than dry rolled corn but slower than ground corn. This is in agreement with the low digestion

of starch in the rumen reported for ground corn by Waldo (1973). Based on the review of 30 trials by Waldo (1973), the rank of corn processing methods for ruminal starch digestion, from least to most, is: whole shelled and ground corn < dry rolled < steam flaked and high moisture harvested.

A review (Buchanan-Smith, 1976) of the mechanism whereby additional moisture may increase nutrient availability from corn may enhance our understanding of the high digestiblity of organic matter, starch and crude protein from high moisture harvested corn. During reconstitution, water penetrates the amorphous region of the grain kernel. This disrupts the aleurone layer and releases the starch granules. Disrupting the aleurone layer stimulates it to secrete amylolytic enzymes. Protein solubility may parallel increased starch availability provided heat damage to the protein does not occur. Corn processing, whether by particle size reduction or addition of heat and/or moisture, increases the ability of amylase to attack the starch molecule.

Several researchers have suggested that processing of corn increases the net energy value. Work by Moe et al. (1974) and Moe and Tyrrell (1977) suggests that corn meal has a larger NE_L value than cracked corn while whole shelled corn has the lowest NE_L. Likewise, a study from Oklahoma in which corn was processed by several methods ranked NE_g of processed corn greatest to least as whole shelled, high moisture harvested and steam flaked corn (Gill et al., 1980). The reason whole shelled corn had the highest NE value for beef but the lowest for dairy can be explained by level of intake. The dairy cattle were limit fed a 40% hay diet whereas the feedlot cattle had ad libitum

access to a very low roughage diet. Also, at the 40% roughage level, the digestibility of the whole shelled corn may have been reduced due to ruminal kinetics.

Processing of corn increases total volatile fatty acid content (VFA) and increases the molar proportion of propionate in the rumen (Galyean, et al., 1977 and McKnight et al., 1973). Acetate production tends to be higher with unprocessed grain. Rumen pH is lower with ground high moisture than steam flaked or dry rolled corn diets (Galyean et al., 1977). Energy losses as methane are reduced with highly processed feeds (Johnson et al., 1968 and Moe and Tyrrell, 1977). Heat increment appears similar regardless of corn processing method (Johnson et al., 1968). Highly processed feeds, such as steam flaked or high moisture harvested corn, leave the rumen at a slower rate than dry rolled corn (McKnight et al., 1973; Cole et al., 1976; Galyean et al., 1977). Dry corn passes out of the rumen at faster rates as particle size is reduced (Galyean et al., 1979).

Intake Effects

Effect of Intake Level on Energy Availability

Energy retention increases with increasing intake. But energy utilization above the point of zero energy retention (for growth and fat deposition) is less efficient than energy use for maintenance. The sum of these two gives a curvilinear relationship of energy retention to level of feed or energy intake. Reasons for this curvilinearity are not well understood. Some explanations include differences in:

1. rumen fermentation and rate of passage

2. efficiency of energy utilization for synthesis of body protein and fat versus oxidation of body tissue
3. efficiency of protein or fat synthesis
4. metabolism due to temperature changes (Orskov et al., 1969).

This curvilinearity forms the basis for the European metabolizable energy and the California net energy systems. Metabolizability of a diet decreases with level of intake. The magnitude of the change depends on the overall balance between fecal, urine and methane loss. For diets with metabolizability values of 1.8 Mcal/Kg, doubling intake reduces metabolizable energy 10%, whereas diets with an energy value of 3.0 Mcal/Kg increase in metabolizable energy concentration when intake is doubled (McDonald et al., 1973). Blaxter (1962) suggested that diets below 62% metabolizable energy will decrease in ME value as intake increases. In contrast to these results, a feeding study conducted at Oklahoma State University (Owens and Gill, 1982) demonstrated a reduction in metabolizability of high concentrate diets as intake increased. As level of feeding increases, energy lost in feces increases. Therefore, metabolizable energy of a feed may not change in a similar manner or extent as apparent digestibility. For this reason, one must be careful in predicting animal performance from digestibility and intake data alone. The California net energy system takes the energy scheme one step further and accounts for heat loss. Heat loss reduces the amount of energy available for production unless the animal is in a cold environment.

Intake Effects on Digestibility

Generally, apparent organic matter digestibility (OMD) decreases

as level of intake increases (Van Soest, 1980). This decrease in digestibility is a result of an altered rate and extent of digestion and passage rate. The NRC (1980) for dairy incorporates a 4 percent reduction in OMD for every multiple of maintenance increase in intake. Blaxter, as cited by the ARC (1980), indicated that OMD was depressed 2.9 and 8.2 percentage units per multiple of maintenance increase in intake with feeds having apparent digestibilities of 75 and 55%, respectively. Schiemann, as cited by the same author, showed a 3% depression in digestibility per unit of maintenance intake increase. Diets consisting of 50 per cent roughage and concentrate exhibit a linear decrease in OMD as intake is increased, however, a 20% roughage and 80% concentrate diet yielded a curvilinear relationship in OMD due to intake (Leaver et al., 1969). Intake depressions in OMD are greater for finely ground roughages and mixed diets than long forages (Brown, 1966).

The portion of the diet which is digested least rapidly will be influenced to the largest degree by level of intake. Structural carbohydrates are generally more slowly digested because of their low solubility and their complex chemical structure. Several researchers have attributed reduced dry matter digestibility to the cellulose and hemicellulose fractions (Rodrique and Allen, 1960; Leaver et al., 1969; Robertson and Van Soest, 1972; Tyrrell and Moe, 1975; Van Soest, 1982). A large portion of dietary cell walls in high concentrate diets is contributed by the grain. For example, in a diet containing 90% corn (13% cell walls) and 10% alfalfa (52% cell walls), 69% of the dietary cell wall is from the corn. Grain cell walls in these diets are highly susceptible to digestibility depression with increased intake (Van

Soest, 1973; Van Soest, 1982). Likewise, byproduct feeds are very susceptible to digestibility depressions at high intake levels. Cellulose and hemicellulose digestibilties were reduced 8% while soluble cell contents were reduced only 3% per multiple of maintenance increase in a 60% grain - 40% corn silage ration (Tyrrell and Moe, 1975). Results by Wagner, as cited by Kromann (1973), reported the rate of depression in digestibility at higher intake levels increases as grain is added to the diet. Digestible energy content of the diet was similar at 4.5 X maintenance level of intake for diets containing different levels of grain (25, 37.5, 50, 62.5 and 75%). A substantial amount of this depression with high intake levels may be attributed to starch digestion (Wheeler et al., 1975; Joanning et al., 1981); however, lower cell wall digestion can account for some depression also. With a ration containing 37.5% grain, the maximum digestive efficiency occurred at 3.2 X maintenance level of intake (Wagner, 1965, as cited by Kromann, 1973). Intake beyond 3.2 X maintenance had little effect on diet digestibility. This data suggests there may be a level of intake between maintenance and full feed which yields maximum energetic efficiency and intake. Beyond this point, energetic efficiency is reduced while performance continued to increase due to greater dilution of maintenance.

Cell walls must be digestible before high intake will depress digestibility. The digestibility depression may be proportional to the digestible cell wall content and rate of passage but inversely related to the rate of digestion and lignification (Van Soest, 1982). Based on these assumptions, one would expect differences in intake depression of organic matter digestion with different roughage sources, different processing methods and different forms of grain in the diet. Rate of depression in

digestibility due to intake will increase as grain is added to hay or hay crop silages. In contrast, grain addition to corn silage diets has a smaller effect on digestibility (Tyrrell and Moe, 1975). Similarly, Andersen et al. (1959) demonstrated no effect of intake on digestibility with ground corn addition to long or chopped hay rations, but corn addition to ground hay diets depressed digestibility at higher intakes. Increased intake of a diet of whole shelled corn had little effect on cellulose digestibility whereas greater intake with cracked or ground corn diets decreased cellulose digestion (Moe and Tyrrell, 1977).

Starch digestion is influenced by level of feed intake. Studies in Oklahoma demonstrated that starch digestion decreased 9.3% as intake was increased from 1X to 2X maintenance (Galyean, 1975). Approximately 60% of the decreased starch digestion in his study occurred in the rumen. A study with sheep at two intake levels (70 vs 100% of ad lib) showed that ruminal starch digestion decreased as intake increased (Orskov et al., 1969). Joanning et al. (1981) reported that starch digestion in the total tract decreased as starch intake increased with corn-corn silage diets. In contrast, starch digestibility in diets containing only grain remained similar as intake increased. Total tract starch digestion was shown to decrease as level of corn intake increased (Russel et al., 1981); however, relative proportions of total starch digestion disappearing in the reticulorumen or small plus large intestine remained the same.

As mentioned earlier, the influence of various forms of corn and roughage is supposedly through alteration of fermentation and rate of passage. Diets which reduce rate of starch fermentation may increase ruminal protozoal numbers and may alter the type of endproducts absorbed (Hungate, 1966). Ruminal pH also can influence the predominant

type of bacteria present in the rumen. The presence of grain allows preferential digestion of starch and reduced ruminal digestion of cellulose (Van Soest, 1982).

In summary, intake influences diet digestibility through altering digestive patterns and rate of passage. For every multiple of maintenance increase in intake, organic matter digestibility is reduced by about 4%. This effect can be attributed largely to reduced cell wall digestion. There appears to be an interaction between level of intake and composition and processing of diet ingredients.

Associative Effects of Feedstuffs

Associative effects have been defined as the non linear response in digestibility and net energy value when two feedstuffs are fed together. Researchers disagree on the validity of this concept. Certain researchers suggest that observed "associative effects" are the result of improperly balanced diets (Moe, 1980) or artifacts of an experimental design (Garret, 1979). Defining "associative effects" as the results of improperly balanced diets obviates the concept by definition. Certain nutrient deficiencies can drastically alter diet digestibility as evidenced by the following examples:

1. urea addition to low quality forage diets adds ammonia and improves feed intake and forage utilization
2. soybean addition to corn diets for growing swine adds lysine and increases rate and efficiency of gain
3. excessive amounts of fat or molasses in the diet reduce digestiblity and

4. soluble carbohydrates in roughage diets for ruminants will reduce fiber digestibility (Moe, 1980).

Several studies have reported the existence of detectable associative effects (Forbes et al., 1931; Forbes, 1933; Kriss et al., 1943; Blaxter and Wainman, 1964; Vance et al., 1972; Byers et al., 1975; Joanning et al., 1981; Teeter, 1981). From a theoretical viewpoint, one may expect associative effects to exist under certain feeding conditions such as addition of feedstuffs which increase rumination or decrease rate of passage and thereby alter digestibility and performance.

To determine the presence and significance of associative effects under feeding practices, data on cattle performance, intake and carcasses were compiled from 18 different feeding trials with three or more levels of roughage. These were programmed by the net energy equations to calculate metabolizable energy content (ME) of the diet from performance (Owens and Gill, 1980). Non-linearity of the ME values at various roughage levels indicates that associative effects were present. Analysis of net energy values will remove some of the differences in performance due to intake but considers the metabolizable energy values to be additive. Data from the 18 feedlot trials at several different locations (Table XI) indicate that associative effects exist when data are averaged across all forages (Table XII). With corn grain-corn silage diets (12 trials), quadratic effects of forage level on energy availability as well as on intake were detected (Table XII). A positive quadratic effect indicates that the midpoint on the curve was below a straight line between the endpoints suggesting that the associative effect on energy availability was negative. Diets of sorghum silage, alfalfa, alfalfa-sudan hay mixtures or rice hulls

exhibited no associative effects. However, two points must be emphasized. The rice hull diets contained 0 to 9 percent roughage and no linear effect of roughage was detected. With so little roughage present, detecting an associative effect would be difficult. Secondly, the literature contains few studies with sufficient data reported to determine ME values for these forages other than corn silage.

Several digestibility studies have detected non-linear effects of roughage level on diet digestibility (Forbes, 1931; Forbes, 1933; Kriss, 1943; Blaxter and Wainman, 1964; Byers et al., 1975; Joanning et al., 1981; Teeter, 1981). Corn silage diets typically exhibit a negative associative effect on digestibility. That is, the mixture of grain and corn silage is less digestible than the arithmetic mean of the grain and corn silage when fed singly (Byers et al., 1975; Joanning, 1981). Negative associative effects on OMD also have been reported for grain diets supplemented with alfalfa hay (Forbes et al., 1931; Forbes etal., 1933; Teeter, 1981) and grass hay (Blaxter and Wainman, 1964; Leaver et al., 1969). In contrast, Garret (1979) observed no significant associative effect with a sudan grass - alfalfa hay diet. Similarly, a mixture beet pulp and alfalfa hay produced no associative effect of dry matter on energy digestibility (Asplund and Harris, 1971). Nitrogen free extract and ether extract digestibility were greater than predicted from digestibility values of the individual feeds while crude fiber digestibility was less. Teeter (1981) reported a positive associative effect with the addition of cottonseed hulls to whole corn diets. Generally, reductions in dry matter digestibility with different roughage levels have been attributed to starch digestion (Wheeler et al., 1975; Joanning et al., 1981) while the reduction in

TABLE XI

PERFORMANCE AND ENERGY VALUES OF DIETS
FROM FEEDING TRIALS

Author	Roughage Source	Roughage Level	ADG	TOTFI	ME	NE_m	NE_G
Brethour and Duitsman, (1973)	Sorghum silage	73	2.04	18.0	2.42	1.46	0.89
		26	2.74	20.0	2.85	1.82	1.21
		21	2.93	19.9	2.99	1.96	1.30
Danner et al., (1978)	Corn silage	99	1.06	11.7	2.16	1.28	0.64
		93	1.77	13.7	2.41	1.46	0.88
		86	1.85	14.1	2.49	1.51	0.94
		71	1.62	12.9	2.43	1.47	0.89
		69	2.04	13.6	2.54	1.56	0.98
		66	2.10	13.7	2.58	1.58	1.01
		2	2.22	12.9	2.81	1.78	1.18
Furr et al., (1969)	Rice hulls	0	2.87	18.9	2.97	1.93	1.29
		3	2.90	19.1	2.98	1.94	1.29
		6	2.88	19.1	2.98	1.95	1.30
		9	3.09	19.8	2.93	1.89	1.26
Garrett, (1979)	69% Alfalfa 31% Sudan hay	78	1.72	18.0	2.57	1.57	1.00
		66	2.05	18.0	2.78	1.76	1.16
		51	2.11	17.0	2.95	1.91	1.28
		37	2.27	16.3	3.09	2.05	1.36
		23	2.40	16.8	3.12	2.09	1.38
		9	2.46	14.9	3.53	2.66	1.60

TABLE XI (Continued)

Author	Roughage Source	Roughage Level	ADG	TOTFI	ME	NE_m	NE_G
Gill et al., (1976)	Corn silage	75	2.42	17.8	2.83	1.80	1.19
		30	2.68	18.3	3.21	2.19	1.43
		14	2.77	16.6	3.33	2.32	1.50
Hansen et al., (1969)	Alfalfa	15	2.86	18.3	2.62	1.62	1.04
		8	2.88	17.9	2.74	1.72	1.13
		0	3.03	17.5	2.90	1.86	1.24
	Paper	15	3.13	19.8	2.56	1.57	1.00
		8	3.04	18.8	2.69	1.67	1.09
		0	3.03	19.5	2.90	1.86	1.24
	Feedlot waste	15	2.50	18.6	2.42	1.46	0.88
		8	2.79	19.1	2.61	1.61	1.03
		0	3.03	17.5	2.90	1.86	1.24
Harrison and Riley, (1974)	Sorghum silage	25	2.39	20.3	2.31	1.38	0.78
		18	2.34	20.5	2.31	1.38	0.79
		10	2.47	20.2	2.38	1.43	0.85
Henderson et al., (1971)	Corn silage	96	2.36	15.1	2.79	1.77	1.17
		59	2.84	18.7	2.86	1.83	1.21
		40	3.16	20.7	2.78	1.76	1.16
		21	2.66	18.8	2.74	1.71	1.13

TABLE XI (Continued)

Author	Roughage Source	Roughage Level	ADG	TOTFI	ME	NE_m	NE_G
Larson et al., (1976)	Corn silage	86	2.22	17.4	2.78	1.76	1.16
		77	2.54	18.2	2.84	1.81	1.20
		65	2.74	17.3	3.07	2.03	1.35
		54	3.02	16.9	3.28	2.27	1.47
		42	3.80	15.6	3.30	2.29	1.48
		29	3.51	17.8	3.51	2.54	1.59
		16	3.24	16.8	3.53	2.57	1.60
		0	2.92	14.7	3.51	2.54	1.58
Miller et al., (1972)	Corn silage	86	2.08	15.2	2.43	1.47	0.89
		55	2.76	16.6	2.62	1.61	1.04
		29	3.05	16.8	2.71	1.69	1.11
Minish et al., (1966)	Corn silage	92	2.20	15.4	2.47	1.50	0.93
		78	2.29	16.5	2.52	1.54	0.97
		62	2.54	17.9	2.50	1.52	0.95
		51	2.65	18.3	2.52	1.54	0.96
Newland et al., (1965)	Corn silage	95	2.21	15.6	2.62	1.62	1.04
		78	2.38	16.1	2.64	1.65	1.08
		62	2.66	17.8	2.58	1.58	1.01
		45	2.62	18.3	2.57	1.58	1.01

TABLE XI (Continued)

Author	Roughage Source	Roughage Level	ADG	TOTFI	ME	NE_m	NE_G
Newland (con't)	Alfalfa	50	2.07	20.2	2.08	1.23	0.57
		39	2.21	19.0	2.21	1.31	0.69
		29	3.17	20.2	2.44	1.47	0.90
		18	3.29	18.4	2.65	1.64	1.07
Peterson and Hatfield, (1970)	Corn silage	86	2.61	19.3	2.55	1.56	0.99
		57	2.76	19.5	2.63	1.62	1.05
		29	3.07	19.0	2.78	1.76	1.16
		0	3.25	16.3	3.17	2.15	1.41
Preston et al., (1972)	Corn silage	59	2.72	16.1	3.00	1.96	1.31
		38	2.68	15.4	3.07	2.03	1.35
		16	2.77	14.4	3.32	2.31	1.49
		3	2.71	13.7	3.33	2.32	1.50
Vance et al., (1971)	Corn silage	58	2.46	16.5	2.85	1.82	1.21
		44	2.51	17.3	2.79	1.76	1.17
		30	2.54	18.0	2.73	1.71	1.12
		22	2.76	18.7	2.81	1.78	1.18
		12	2.66	18.0	2.85	1.81	1.21
		2	2.65	16.3	3.02	1.98	1.32

TABLE XI (Continued)

Author	Roughage Source	Roughage Level	ADG	TOTFI	ME	NE_m	NE_G
Woody et al., (1978)	Corn silage	93	2.11	18.7	2.51	1.53	0.96
		59	2.48	19.7	2.63	1.63	1.05
		12	3.24	18.2	3.15	2.12	1.40
		0	2.68	16.4	3.09	2.06	1.36
	Corn silage	92	2.02	17.1		1.59	1.02
		60	2.37	17.4		1.74	1.15
		12	2.69	15.1		2.37	1.52
		0	2.60	14.3		2.44	1.55

TABLE XII

SUMMARY OF REGRESSION ANALYSIS OF ROUGHAGE LEVEL OR ENERGY VALUE WITH DIFFERENT ROUGHAGE SOURCES

	Significant effect[a]					Number of studies
	ME	NE_m	NE_G	MEI[b]	TOTFI[c]	
Across all roughages	LQ (.87)[d]	LQ (.87)	LQ (.86)	LQ (.86)	LQ (.85)	18
Within roughage source						
Alfalfa	L (.99)	L (.99)	L (.99)	L (.85)	NS (.80)	2
Alfalfa-sudan hay	L (.94)	L (.93)	L (.95)	L (.84)	L (.85)	1
Rice Hulls	NS (.50)	NS (.50)	NS (.50)	NS (.71)	NS (.82)	1
Corn silage	LQ+ (.86)	LQ+ (.85)	LQ+ (.86)	LQ- (.89)	LQ+ (.83)	12
Sorghum silage	L (.94)	L (.93)	L (.94)	LQ (.98)	L (.82)	2

[a]Statistically significant effects ($P<.05$)
NS = not significant
L = linear effect
Q = quadratic effect
+ = positive Q
- = negative Q

[b]Metabolizable energy intake

[c]Total feed intake

[d]Regression coefficient

dry matter digestibility with increased intake has been attributed to cell wall fractions (Van Soest, 1973). In the studies of Joanning and of Wheeler, differences in intake were more closely associated with starch digestion (R^2=.90) than with level of roughage (R^2=.25).

The above trials allowed animals free access to diets. This resulted in a positive associative effect on feed intake. Differences in intake could account for the reduced digestibility observed in these studies. Reduced cell wall, starch and protein digestibilities accounted for nearly all the reduction in DMD with increased intake. Altered starch digestion accounted for most of the reduced DMD in some studies (Wheeler et al., 1975; Joanning et al., 1981) while cell wall constituents predominated in others (Van Soest, 1973).

Contrary to the above results, a limited number of studies have examined associative effects with fixed intake levels. The metabolizable energy value of corn meal differed depending on the level of intake and type of roughage added (Forbes et al., 1933). Similarly, starch digestion was unaltered with 40% cottonseed hulls added to a whole corn diet while 40% alfalfa severely reduced starch digestion (Teeter, 1981). Scrutiny of the results of trials reported by Forbes and by Teeter indicate that associative effects may be positive or negative depending upon the type of roughage and grain processing utilized.

Blaxter and Wainman (1964) fed six levels of mixed hay (5, 20, 40, 60, 80 and 100%) to fattening cattle and concluded that the net energy value of a feed depended on the level of intake and nature of the diet. Omission of the 5% roughage level increased the regression coefficient

for digested (.98 vs .72) and metabolizable energy (.98 vs .91) and urinary energy losses (.99 vs .90). Removal of the 100% roughage level from the regression of roughage level on methane production increased the regression coefficient from .67 to .83. These regression analyses indicate non-linearity of digestive function at very high levels of roughage or concentrate. Therefore, studies which do not encompass the total spectrum of roughage levels may fail to detect non-linear effects.

The manifestation and magnitude of an associative effect probably is a result of the interaction between level of intake, rate of passage and rate of digestion (Byers, 1980). As shown above, the associative effects reported in many trials can be explained by differences in level of feed intake. Addition of small amounts of roughage to all grain diets generally increases feed intake (Rust et al., 1979; Joanning et al., 1981). Increased intake in turn accelerates rate of passage which reduces digestibility of slowly digested residues such as cell walls. Maintenance requirements are diluted at higher levels of intake, thereby permitting more of the metabolizable energy to be utilized for gain.

Rate of digestion can influence the extent of cell wall digestion if time for digestion is limited. Addition of soluble carbohydrates such as simple sugars or oligosaccharides reduce the rate of ruminal fiber digestion. This shifts the site and may reduce the extent of organic matter digestion.

The effects of level of intake, rate of passage and rate of digestion are more critical for certain forages than for others. Roughages which contain high amounts of soluble cell contents (alfalfa) or

are high in lignin and indigestible (rice hulls) should suffer little reduction in digestiblity upon addition to high grain diets. Supporting this conclusion are the results of Newland et al., (1965), Hansen et al., (1969) and Furr et al., (1969). Newland and Hansen fed alfalfa at various levels. Metabolizable energy values were linearly related to level of roughage suggesting no associative effects were present. Rice hull addition to grain diets also caused no associative effects. However, feeds which have high cell wall contents and low lignin values and are digested slowly will suffer drastically impaired digestibilities at high levels of grain. Forages which fall in this category are corn silage and cereal byproducts such as corn bran, brewers grains and distillers grains. As rate of passage from the rumen increases, fiber digestion is reduced. Compilation of 12 feedlot studies with corn silage above yielded a significant quadratic effect ($P<.05$) which provides support for this concept.

Most of the associative effect supposedly occurs in the rumen. However, reduced starch digestion could also occur in the intestine. Altered starch digestion at intermediate levels of roughage is more apt to be the result of intake, rate of passage and particle size reduction effects. Reduced cell wall digestion is likely caused by reductions in the rate of and time for digestion in the rumen.

Elevated soluble carbohydrate levels reduce the rate of fiber digestion in the rumen (El-Shazly et al., 1961; Terry et al., 1969; Johnson et al., 1976). Soluble carbohydrates may inhibit cellulose digestion by a) providing a more readily available energy source, b) competition for certain nutrients, c) lowering of rumen pH or d) end-product inhibition of cellulose digestion. Cellulolytic bacteria may

be stimulated by low levels of simple sugars, but high levels are inhibitory (Barnett and Reid, 1961). These authors suggested that microorganisms select the more readily available energy source and discriminate against cellulose. Barley addition to in vitro fermenters did not alter cellulose digestion if the pH remained near 6.6 (Stewart, 1977). In contrast, elevated glucose levels impaired cellulose digestion (Terry et al., 1969) when pH was allowed to change. A summary of in vitro digestion of 15 different forages (Smith et al., 1972) indicated that cell wall digestion rates are more highly correlated with soluble dry matter pecentage (r=.72) than with lignin percentage (R=-.47).

Competition of starch and cellulose fermenting microorganisms for nitrogen sources also contributes to reduced fiber digestion (El-Shazly et al., 1961). Since starch fermentation occurs rapidly, soluble nitrogen in the rumen may be depleted at the time the slower cellulose digesting microorganisms normally work. To test of this concept, Burroughs et al., (1950) added starch and casein to good and poor quality forages. Starch addition inhibited cellulose digestion with his poor roughage but had little effect when added to alfalfa. Addition of casein improved dry matter digestion of the poor quality forage. Starch addition to a cellulose medium caused a shift in type of cellulolytic bacteria present. Other nutrients such as calcium, phosphorus, sulfur, branch chain volatile fatty acids or vitamins also may limit cellulose digestion, but direct evidence in vivo is lacking.

Addition of dietary fat inhibits cellulose digestion (Barnett and Reid, 1961; Stewart, 1977). This effect may be on Bacteriodes succinogenes specifically (Bryant et al., 1959). Fat addition decreased

cotton thread disappearance but did not alter filter paper degradation. Cotton thread disappearance depends on Bacteriodes succinogenes whereas filter paper digestion occurs with several cellulolytic species. Calcium addition will override the inhibition of cellulose digestion by fat (Bryant et al., 1959). Similarly, addition of alfalfa ash stimulates cellulose digestion in diets supplemented with fat (Barnett and Reid, 1961). Whether the oil concentration in high concentrate diets is sufficient to inhibit cellulose digestion is uncertain, however, grains generally contain more fat than forages. Grain byproducts are higher in fat than whole grain which may relate to the low cellulose digestibilities in those diets.

Rapid fermentation of soluble carbohydrate yields acid endproducts of fermentation which reduce rumen pH. Cellulolytic microorganisms are pH sensitive and inactive at low pH (Terry et al., 1969; Stewart, 1977; Slyter, 1981). In contrast, El-Shazly et al. (1961) suggested that rumen pH influences cellulose digestion very little compared with ammonia deficiency. Optimal cellulose digestion occurs at pH 6.8 and is severely reduced below pH 6.0. Numbers of cellulolytic bacteria are reduced and cellulolytic protozoa disappear at low pH. Hemicellulose digestion is closely associated with cellulose disappearance (Hungate, 1966). Whether outflow rate and low pH alter in vivo digestion of cellulose and hemicellulose remains uncertain. It is unlikely that specific endproducts of starch digestion such as VFA would inhibit cellulose degradation. However, under certain conditions, formate inhibits cellulose digestion (El-Shazly et al., 1961).

Methane production is reduced when intake levels are high and when diets are highly digestible (Blaxter, 1961). Reduced urinary nitrogen

losses and reduced methane production with high concentrate diets can account for some of their advantage in ME values (Blaxter and Wainman, 1964), but how these factors relate to the associative effect is uncertain.

In summary, associative effects can be visualized as the combined changes in level of feed intake, rate of passage and rate of digestion when two or more feeds are fed together (Figure 4). The level of feed intake and associative effects dictate the extent of digestion which along with level of feed intake determines performance. Under ad libutum feeding conditions, the associative effect would be a level of intake by roughage level interaction. In digestibility studies, level of intake must be controlled to determine associative effects. The associative effect with a mixture of feedstuffs would be the deviation in digestibility from the predicted level based on the digestibility of the individual feedstuffs.

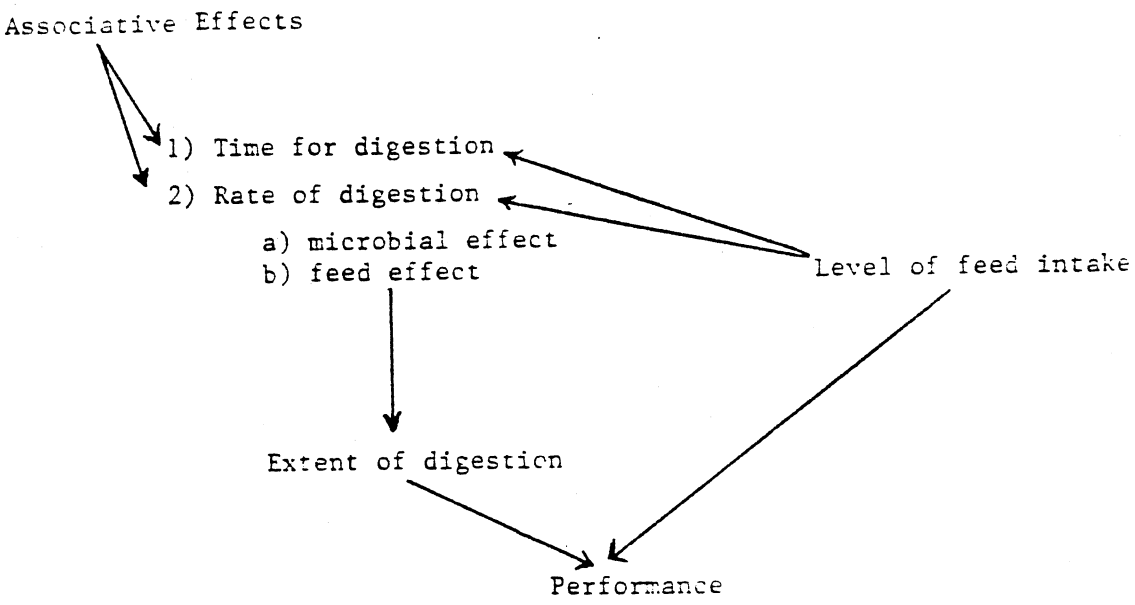


Figure 4. Influence of Associative Effects and Feed Intake on Digestion and Performance.

CHAPTER III

EFFECTS OF ALFALFA ADDITION ON DIGESTIBILITY OF WHOLE SHELLED CORN AND STEAM FLAKED CORN DIETS

S. R. Rust, F. N. Owens and D. R. Gill

Summary

Two trials were conducted to evaluate the influence of level of alfalfa on digestibility of whole shelled and steam flaked corn. In trial 1, sixteen Hereford and Angus steers (394 kg) were employed to evaluate the effects of five levels of alfalfa (0, 5, 15, 40, and 92 percent) on digestibility of a whole corn diet. Steers were fed once daily and had free access to feed.

Dry matter intake increased until the diet contained 15 percent alfalfa and declined thereafter ($P < .01$). Organic matter digestibility decreased as alfalfa was added to the diet ($P < .05$). Starch digestion was not significantly changed by alfalfa addition. Rumen pH and acetate concentrations increased as level of alfalfa increased ($P < .01$). DMD values for the 5 and 15 percent alfalfa level diets were lower than would be predicted from digestibilities of alfalfa and whole shelled corn fed alone. In a second study three alfalfa levels (5,15,and 40 percent) were fed with whole shelled or steam flaked corn to 12 steers (394 kg). No roughage level by corn processing

interactions ($P < .10$) on intake or digestion measurements were detected suggesting that alfalfa had similar effects with both corn processing methods. Rumen propionate proportion was unchanged as alfalfa was increased to 15 percent with steam flaked corn, but the proportion was reduced with a similar level of alfalfa addition to a whole shelled corn diet ($P < .01$).

Digestibility of organic matter ($P < .05$) and starch ($P < .01$) was greater with SFC than WSC diets. Digestibility of neutral detergent fiber, which was derived primarily from the alfalfa hay, was lower with SFC than WSC ($P < .10$). Ruminal ammonia and acetate concentrations were lower for the SFC diet ($P < .05$), while propionate concentration was greater ($P < .01$) with SFC than WSC diets.

Alterations in organic matter digestibility in these trials appeared largely attributable to level of roughage and dry matter intake. After correction for intake differences, no associative effects were apparent. Starch digestion varied drastically between animals with no effect of roughage level. Nitrogen digestibility also differed among animals.

Introduction

An "associative effect" is a condition in which mixed diets produce lower digestibilities or performance than that expected from the proportional mixture of the individual components fed separately. Though associative effects are widely reported (Forbes,1931 and 1933; Kriss 1943; Blaxter and Wainman, 1964; Vance, 1972; Byers, 1975; Joanning, 1981 and Teeter, 1981), their magnitude varies widely.

Explanations for the deviation from linear effects on digestibility or performance have been attributed by various workers to the experimental designs (Garrett, 1979) or improperly balanced diets (Moe, 1980). Although intake of nutrients usually differ between single feeds and mixed diets, the optimum combination of nutrients is difficult to identify. Soluble nitrogen intake may be important, since low intakes reduce the rate and extent of ruminal digestion (El Shazly, 1961). Ruminal pH may be involved as well, since maintenance of a constant ruminal pH alleviated reductions in fiber digestion when grain was added (Terry et al., 1969; Stewart, 1977). The dietary component which is most altered in digestibility also may vary depending upon source of roughage in the diet. With corn silage diets, starch digestion was impaired (Joanning et al., 1981), while fiber digestion has been reduced with hay diets (Van Soest, 1973).The magnitude of the associative effect may vary with roughage source, as starch digestibility was 3 percent greater ($P < .05$) with 40 percent CSH than with 40 percent alfalfa added to a whole corn diet (Teeter, 1981). The effect of level of feed intake on digestibility is often ignored in associative effect trials. For dairy cattle, the NRC (1980) reduces values of organic matter digestibility and TDN by four percent for each multiple of intake above maintenance. Since adding roughage to a high grain diet may increase intake until ruminal bulk fill limitations are reached, an "associative effect" on feed intake is often observed which may alter digestibility.

If ruminal pH or ammonia are involved, reduced digestion is probably occurring in the rumen. Diets containing grains which are

highly processed should depress these factors to a greater degree and exhibit larger nonlinear effects on fiber digestion than more slowly degraded forms of grain. Conversely, if starch digestion is reduced, lower availability of starch from coarse grains should emphasize associative effects of roughage.

Two trials were designed to evaluate the effects of roughage level (chopped alfalfa hay) on digestibility with two different corn processing methods (whole shelled and steam flaked corn) fed under feedlot conditions.

Experimental Procedure

Trial 1

Sixteen steers (394 kg) of Hereford and Angus breeding were randomly assigned to one of five roughage levels (0, 5, 15, 40 and 92 percent). Steers were switched to different roughage levels every two weeks such that every animal received three of the five roughage levels. The diet contained whole shelled corn, alfalfa and a protein-mineral supplement (table 1). Chemical composition of the feedstuffs is shown in table 2. The alfalfa was from a second cutting and was chopped in a hammermill with the screen removed to an average particle size of 4 cm. Diets were formulated to provide a minimum of 13 percent crude protein and adequate minerals and vitamins (table 3). Chromic oxide was added to the pelleted supplement as an indigestibility marker. The steers had ad libitum access to feed with

fresh feed added once daily. Feed refusals were weighed daily and visually monitored for sorting.

In each 14 day period, adaptation lasted nine days and fecal grab samples were collected the following five days. Steers were aroused at 0600 each collection day and fecal samples obtained immediately after defecation. Fecal pH and dry matter were determined at collection time. A weighed aliquot from each daily sample was frozen together with previous days' samples from the same period to form a five-day composite sample. Rumen samples were taken at 1300 the last day of each period via stomach tube. Rumen pH was monitored immediately and the sample frozen for later analysis.

Frozen composited fecal samples were thawed at room temperature and manually mixed. Nitrogen determinations were conducted on the wet sample by the Kjeldahl procedure (AOAC, 1975). The remainder of the composite sample was dried at 55 C in a forced air oven. Dry matter and ash were determined using standard procedures (AOAC, 1975). Neutral detergent and acid detergent fiber were separated by the Van Soest procedures (Goering and Van Soest, 1970). Starch content of feed and fecal samples were determined by the Macrae and Armstrong (1968) procedure. Ammonia analysis was performed on the rumen samples utilizing the Chaney-Marbach procedure (1962).

Volatile fatty acid concentrations in ruminal fluid were determined with a gas chromatograph. Blood plasma samples were analyzed for urea (Chaney and Marbach, 1962) and glucose concentrations (Sigma, 1980).

The data were statistically analyzed using the Linear Regression Package of SAS (Barr and Goodnight, 1981) program as a completely randomized design with removal of animal and period effects. Treatment differences between means were identified using the Least Significant Difference (LSD) analysis.

Trial 2

Twelve Hereford-Angus steers (394 kg) were fed three levels of alfalfa (5, 15 and 40 percent) with either whole shelled or steam flaked corn (table 1). The whole shelled and steam flaked corn were obtained from the same batch of corn grain from Hitch Feedyards, Guymon, OK, transported to Stillwater, OK, and stored frozen until fed. Chemical composition of the corn and alfalfa is shown in table 2. Animals were housed, fed and sampled as in Trial 1. Level of roughage was rotated within corn type for steers in this study, so the data were analyzed as a split plot design with corn type as the main plot and roughage level as the subplot treatment (Steel and Torrie, 1960). Stall within corn processing method mean square was used as the error term to test corn effects. Statistical analysis was conducted using the Linear Regression Package of the SAS system (Barr and Goodnight, 1981). Treatment means were compared using LSD analysis.

Results and Discussion

Trial 1.

Dry matter and organic matter intake tended to increase as alfalfa hay was added up to a level of 15 percent but decreased ($P < .01$) thereafter (table 4). Intake of digestible organic matter decreased ($P < .01$) as more alfalfa was added to the diet due to a decrease in digestibility of the total diet ($P < .01$). Reduced dry matter digestibility with roughage addition to the diet is expected (Galyean et al., 1975; Rust, 1978) due to lower digestibility of the roughage than the grain portion of the diet. Alfalfa addition to these whole shelled corn diets did not reduce digestibility of starch. Some workers (Harvey et al., 1968; Haskins et al., 1969; Vance et al., 1972; Lake, 1977) have suggested that with higher roughage levels, corn must be processed for satisfactory utilization. A feedlot trial in Oklahoma (Gill et al., 1980) demonstrated that with whole shelled corn diets, gain and efficiency were optimum with 5 percent corn silage while with high moisture corn or steam flaked corn, 14 percent corn silage was optimum. Metabolic problems may be more prevalent when less than 12 percent roughage is fed with processed grain diets (Matsushima, 1979). With whole shelled corn diets, less fiber may be needed due to a slower rate of ruminal digestion and possibly increased saliva production during eating and rumination.

Starch digestion was not altered in this trial as level of alfalfa increased. This disagrees with results of earlier studies with alfalfa (Wheeler et al., 1975; Teeter, 1981). Addition of corn silage (Joanning et al., 1981) or rice hulls (White et al., 1972) to grain diets also reduced starch digestion, but cottonseed hull addition to whole corn diets had little effect on starch digestion (Cole, 1975).

Comparisons indicate that the effect of roughage level on starch digestibility may depend upon the type and maturity of the forage being fed.

Nitrogen digestibility remained similar across roughage levels. Altering the concentrate:roughage ratio should change the amount of ruminally degradable protein. The lower gastro-intestinal tract probably compensated, resulting in similar apparent nitrogen digestibilities. Another possible explanation involves the amount of endogenous nitrogen lost. Such secretion may be sufficiently large to mask the effect of roughage on true digestibility of nitrogen.

Digestibility of the various fiber fractions (ADF, NDF and hemicellulose, determined by difference) were not significantly altered as alfalfa was added to the diet. However, with the all corn diet, fiber digestibility tended to be greater than with alfalfa supplemented diets. This indicated that the cell wall fraction in whole corn was probably more accessible to digestion than cell wall material from alfalfa. Addition of different levels of cottonseed hulls to the whole corn diets produced similar trends in cellulose digestibility in another trial (Cole, 1975). Calculation of alfalfa digestibility by the difference technique indicated that digestibility of alfalfa increased as more alfalfa was added to the diet. Results reported by Zinn and Owens (1983) indicate that ruminal ADF digestion approached zero when little roughage was fed and feed intake was high. This agrees with the trend in alfalfa digestibility in this trial though the magnitude in this trial was less, probably due to compensatory digestion of fiber in the cecum and large intestine.

Two explanations for the lower digestibility of fiber in this trial are 1) calculation of digestibility by difference assumes that digestion of fiber from corn is constant across roughage levels and places sampling and analytical error entirely on the alfalfa and 2) the low digestibility for alfalfa at the 5 percent level may be associated with ruminal conditions which renders fiber indigestible. A low ruminal ammonia concentration or high acidity may limit fiber digestion at low roughage levels. Other studies (Blaxter and Wainman, 1964; Cole, 1975) have shown that when roughage comprises less than 10 percent of the diet, fiber digestion is reduced. A plentiful supply of rapidly fermentable substrate will lower both ruminal pH and ammonia concentration to reduce the rate of fiber digestion in the rumen.

Expected dry matter digestibilities, calculated from digestibilities at the 0 and 92 percent levels, were 3 to 6 percent greater than observed values (table 4). This suggests that the classical negative associative effect was detected in this trial. But feed intake tended to be greatest at the 5 and 15 percent alfalfa levels, points where digestibility was depressed. Adjustment of digestibility of level of feed intake could easily explain the digestibility depression observed in this study.

Effects of alfalfa level on fecal parameters are shown in table 5. Fecal dry matter and fecal starch percentages decreased ($P < .01$) as alfalfa was added to the diet. Decreased dry matter content of feces may be due to entrapment of water in excreted fiber. Adding pectin or fiber to a diet for rats similarly decreased the dry matter content of feces (Nyman and Asp, 1982).

Both NDF and ADF percentages in feces increased ($P < .01$) as alfalfa was added to the diet. Fiber tended to dilute the starch and decrease the percentage of starch in feces. The hemicellulose percentage changed little with roughage level. Fecal nitrogen percent decreased ($P < .05$) as fiber was added to the diet. Lower fecal nitrogen values may be the result of fibrous bulk diluting endogenous nitrogen.

Ruminal ammonia concentrations were highest for the 40 percent alfalfa diet and lower for diets containing either more or less alfalfa ($P < .05$) as shown in table 6. The low concentration with the higher alfalfa diet may be a consequence of ammonia washout with liquid from the rumen or due to greater ammonia absorption at the higher pH. At the lower alfalfa levels, more ammonia would be used for synthesis of microbial N, while rumen pH values increased as alfalfa was added to the diet ($P < .01$). Results are similar to observations reported by Van Soest (1982). Acetate levels increased and propionate levels decreased as alfalfa was added to the diet ($P < .01$). Similar results have been reported by Cole (1975) with addition of cottonseed hulls to whole corn diets. The molar proportion of propionate is lower than literature values from feeding studies using whole corn (Gill et al., 1977) though in digestibility studies, Galyean (1975) and Cole (1975) reported similar levels. With greater feed intake, as in feedlot studies , a higher molar proportion of propionate would be expected. Isobutyrate proportion increased as alfalfa was added to the diet ($P < .10$). Isobutyrate, formed from decarboxylation of valine (Van Soest, 1982), reflects higher valine degradation due to the higher protein level with more alfalfa hay in the diet. Caproate levels were higher for the low

roughage diets ($P < .10$), but butyrate, valerate and isovalerate levels were unaltered as alfalfa was added to these whole corn diets.

Trial 2

In this trial, three levels of alfalfa hay were fed with corn in either the whole shelled or the steamed flaked form. Interactions between roughage level and corn processing method on intake and digestibility (table 7) were not significant ($P > .10$). Organic matter digestibility of both corn types was reduced similarly. Midpoint roughage levels produced digestibilities below those predicted values for the intermediate alfalfa levels with either corn type, but again feed intake was greater at the 15 percent roughage level. The effect of level of feed intake on fiber digestion could account for a large share of the reduced organic matter digestion.

Alfalfa digestibility at the lower roughage levels with steam flaked corn was lower than the corresponding values with whole shelled corn diets.

Hemicellulose digestibility tended to increase as alfalfa was added to the diet. This effect matches results of Reynolds et al. (1979). They concluded a large portion of the reduced cell wall digestibility with high grain diets could be attributed to the hemicellulose fraction. Fecal starch values were greater ($P < .01$) for the 5 and 15 percent alfalfa diets with the whole shelled corn diet than the other treatments (table 8). Whole kernels of corn were visible in feces from steers fed the whole corn diets. Fecal hemicellulose values

were significantly greater ($P < .05$) with the low roughage levels in the SFC diets than the other treatments.

Proportion of acetate increased ($P < .05$) and propionate decreased ($P < .01$) as alfalfa was added to either corn diet (table 9). The proportion of propionate remained high with 15 percent alfalfa in the diet with SFC but decreased with WSC ($P < .01$). A negative relationship ($r = -.42$; $P < .05$) was observed between acetate or propionate proportions and hemicellulose digestibility. Reynolds et al. (1979) infused acetate intraruminally with three levels of hay and concluded that the only fraction to decline in digestibility was hemicellulose. The ratio of acetate to propionate increased ($P < .10$) as alfalfa was added to the diet. Valerate levels were reduced ($P < .10$) for the 15 percent alfalfa level with WSC and 40 percent alfalfa with SFC. The reason for this pattern is uncertain; however, nitrogen digestibility followed a similar pattern.

The influence of corn processing method on intake and digestibility averaged across the three roughage levels is shown in table 10. Feed intake was similar with the two corn processing methods,but digestibility of dry matter ($P < .05$), organic matter ($P < .05$) and starch ($P < .01$) were greater with SFC than WSC.Processing of corn grain has been shown to increase digestibility in several studies (McCullough, 1973; McKnight et al., 1973; Galyean et al., 1976; Moe and Tyrrell, 1977; Rust, 1978). Neutral detergent fiber digestibility was 14.3 percent lower ($P < .10$) and hemicellulose digestibility 30.9 percent lower with the SFC diets than WSC diets. Since pH was similar, reduced cell wall digestibility may be due to lower rumen ammonia concentrations or altered rumen VFA concentrations.

Rumen ammonia concentrations (table 11) were higher than 5 mg/dl,the suggested minimum for microbial protein synthesis (Satter and Slyter, 1974). However, with a rapid digested corn source such as SFC, ammonia or pH may have been reduced sufficiently to limit fiber digestion shortly after a meal. Acetate levels were lower ($P < .05$) and propionate levels greater ($P < .01$) for SFC than WSC diets.Higher propionate levels may have inhibited NDF digestibility, but any cause and effect relationship remains uncertain. ADF digestion tended to be greater (10 percent) with WSC than SFC diets (table 10) in agreement with results with WSC and ground corn reported by White et al. (1972). Nitrogen digestibility was similar with both corn types, but isobutyrate and isovalerate proportions were lower ($P < .05$) with SFC than WSC diets. Heating of the corn protein during steam flaking the corn should reduce its hydrolysis in the rumen.

The influence of corn processing method on fecal parameters is shown in table 12. Fecal dry matter ($P < .01$) starch ($P < .01$) and organic matter ($P < .10$) were greater for the WSC diet while fecal nitrogen, NDF and hemicellulose percentages were greater ($P < .01$) for the SFC diets.Fecal ADF concentration was greater for the SFC diets ($P < .05$). The above data suggest that postruminal fiber digestion may have been limited by pH with the SFC diet. The small amounts of corn reaching the large intestine with the SFC diet may be rapidly fermenting, lowering the pH and inhibiting fiber digestion. In contrast, whole corn reaching the large intestine should be relatively inert and yield conditions more favorable to fiber digestion.

The relationship between roughage, feed intake and ruminal parameters and digestibilities of feed components were examined using single and multiple regression coefficients (table 13). A large increase in a regression coefficient due to addition of a variable to the model would identify which variables are related to digestibility. Period, probably related to environmental conditions, had an affect on digestibility of nitrogen, ADF, NDF and hemicellulose. Addition of animal effects increased the regression coefficients substantially for all digestibility estimates, thereby supporting the importance of removing animal and period effects from treatment effects. The majority of the variation in starch digestion was attributable to differences between animals. Relative importance of various physiological factors which differ between animals remains to be defined.

Roughage level and dry matter intake had large effects on organic matter digestion. Including rumen pH in the model decreased the variation about the regression line for DMD and nitrogen digestion.

The residual variation in fiber digestion could be related largely to dry matter intake and roughage level after the fixed variables were removed from the model.

In summary, digestion of organic matter was a function of intake level and roughage level while starch digestibility was largely associated with differences in the ability of individual animals to digest starch. Animals differed in nitrogen and NDF digestion also. ADF and hemicellulose digestibility appeared to be influenced by animal and roughage level effects.

TABLE 1. DIET COMPOSITION FOR TRIALS 1 and 2

	Alfalfa level (%)				
	0	5	15	40	92
Corn[b], (IFN[a] 4-02931)	92.0	87.0	77.0	52.0	0
Alfalfa, (IFN[a] 1-00-059)	0.0	5.0	15.0	40.0	92.0
Supplement	8.0	8.0	8.0	8.0	8.0

[a]International feed number

[b]Trial 1--whole shelled corn; trial 2--whole shelled or steam flaked corn

TABLE 2. ANALYSIS OF DIETARY INGREDIENTS

	SFC[a]	WSC[a]	ALFALFA
Dry matter (%)	80.8	84.5	89.4
Crude protein[b]	9.8	9.7	18.7
Starch[b]	64.6	65.0	5.4
Ash[b]	1.4	1.5	8.9
ADF[b]	5.5	5.7	36.7
NDF[b]	17.2	17.4	82.4
Hemicellulose[b]	11.7	11.7	45.7

[a]SFC = steam flaked corn; WSC - whole shelled corn.

[b]Percent of dry matter.

[c]NDF -ADF

TABLE 3. SUPPLEMENT COMPOSITION FOR TRIALS 1 AND 2

	%
Ground corn, (IFN-4-02-931)	15.2
Alfalfa dehy, (IFN-1-00-023)	4.9
Soybean meal, (IFN-5-04-604)	39.3
Urea	8.8
Cane molasses (IFN-4-04-696)	3.0
Limestone, (IFN-6-02-632)	10.9
Dicalcium phosphate, (IFN-6-01-080)	2.6
Sodium sulfate	1.8
Potassium chloride	1.5
Salt	6.3
Trace mineral mix	3.2
Chromic oxide	2.5
Vitamin A and D	+

TABLE 4. ROUGHAGE EFFECTS ON DIGESTIBILITY OF WHOLE SHELLED CORN DIETS

Item	Roughage level (%)					
	0	5	15	40	92	SD[a]
Number of observations/mean	4	10	6	6	4	
Intake (kg/day)						
Dry matter	7.2[bc]	7.5[b]	7.6[b]	6.5[cd]	5.8[d]	0.8
Organic matter	6.9[bc]	7.2[b]	7.2[b]	6.1[cd]	5.2[d]	0.8
Digestible organic matter	5.6[b]	5.7[b]	5.5[bc]	4.3[cd]	3.4[d]	0.8
Digestibility (%)						
Dry matter						
Observed	80.8[e]	77.3[e]	74.9[ef]	68.6[fg]	62.9[g]	6.6
Predicted[h]		79.8 (3.1)	77.9 (3.9)	73.0 (5.75)		
Organic matter	81.7[e]	78.7[ef]	76.2[ef]	71.0[fg]	65.8[g]	6.4
Starch	91.1	91.9	89.4	91.9	89.5	4.1
Nitrogen	71.6	68.8	71.7	70.0	72.9	7.6
ADF	62.5	49.0	53.0	46.1	55.8	14.4
NDF	57.0	39.7	45.8	40.3	53.3	17.0
Hemicellulose	47.2	25.2	30.6	31.6	42.8	23.1
Alfalfa	--	10.8	41.5	50.1	56.4	

[a] Standard deviation

[bcd] Means in a row with different superscripts differ ($P < .01$)

[efg] Means in a row with different superscripts differ ($P < .05$)

[h] Predicted dry matter digestibility of mixed diets from digestibility of 0 on 92% alfalfa diets. Values in parentheses are percent difference from observed values.

[i] Digestibility of alfalfa calculated by difference.

TABLE 5. ROUGHAGE EFFECTS ON FECAL PARAMETERS

Item	Roughage level (%) 0	5	15	40	92	SD[a]
No. of observations/ mean	4	10	6	6	4	
Fecal dry matter (%)	29.4[b]	27.4[bc]	25.6[c]	21.3[d]	19.5[d]	1.9
Fecal characteristics (% of fecal DM)						
Organic matter	91.9[b]	90.2[b]	90.0[b]	86.8[c]	83.3[d]	1.5
Starch	26.9[b]	20.3[b]	21.2[b]	10.1[c]	1.7[d]	5.5
Nitrogen	3.1[f]	3.0[f]	2.6[fg]	2.6[g]	2.3[g]	0.4
ADF	12.1[b]	18.5[c]	22.1[c]	34.0[d]	32.9[e]	2.4
NDF	28.4[b]	35.8[c]	27.5[c]	49.4[d]	57.5[e]	3.3
Hemicellulose	16.4	17.3	15.4	14.4	13.6	2.6
pH	5.9[b]	6.1[b]	6.2[b]	6.7[c]	7.4[d]	0.3

[a]Standard deviation

[bcde]Means in a row with different superscripts differ ($P < .01$)

[fg]Means in a row with different superscripts differ ($P < .05$)

TABLE 6. ROUGHAGE EFFECTS ON RUMINAL PARAMETERS

	Roughage Level (%)					
	0	5	15	40	92	SD[a]
No. of Observations/mean	4	10	6	6	4	
Rumen characteristics						
Ammonia (mg/dl)	12.9^{gc}	15.4^{gc}	20.5^{ghcd}	31.0^{hd}	13.5^{ge}	8.2
pH	5.6^{c}	5.8^{c}	5.9^{cd}	6.3^{d}	7.1^{e}	0.4
Volatile Fatty Acids						
Total (mmoles/ml)	74.9$_{cd}$	117.7$_{c}$	77.5$_{de}$	81.2$_{ef}$	88.2$_{f}$	62.5
Acetate[b]	54.3^{c}	50.9^{c}	57.7^{cd}	64.1^{d}	69.1^{d}	4.0
Propionate[b]	31.6^{i}	33.8^{ij}	27.2^{ij}	19.9^{ij}	16.9^{j}	5.9
Isobutyrate[b]	0	0.5	0.8	0.9	1.3	0.6
Butyrate[b]	9.8	9.6	10.4	10.3	8.0	3.5
Isovalerate[b]	1.8	2.6	2.3	2.5	2.6	0.7
Valerate[b]	1.7$_{i}$	2.1$_{ij}$	1.5$_{k}$	2.0$_{jk}$	2.0$_{k}$	0.5
Caproate[b]	0.7^{i}	0.4^{ij}	0.1^{k}	0.3^{jk}	0.2^{k}	0.3
C_2/C_3						

[a] Standard deviation

[b] Moles/100 moles

[cdef] Means in a row with different superscripts differ ($P < .01$)

[gh] Means in a row with different superscripts differ ($P < .05$)

[ijk] Means in a row with different superscripts differ ($P < .10$)

TABLE 7. ROUGHAGE LEVELS EFFECTS ON DIGESTIBILITY OF STEAMFLAKED AND WHOLE CORN DIETS (TRIAL II)

	WSC[a]			SFC[a]			
Roughage level (%)	5	15	40	5	15	40	SD[b]
Intake (kg/day)							
Dry matter	7.4	7.6	6.5	7.2	7.5	7.0	0.9
Organic matter	7.1	7.2	6.1	7.0	7.1	6.6	0.8
Digestible organic matter	5.6	5.5	4.3	5.8	5.6	4.8	0.7
Digestibility (%)							
Dry matter	77.4	74.9	68.8	81.6	77.0	70.9	4.5
Organic matter	78.8	76.2	71.0	83.2	78.7	73.2	4.3
Starch	91.8	89.4	91.9	98.5	97.4	96.1	2.9
Nitrogen	70.2	71.7	70.0	69.4	69.2	67.7	4.1
ADF	49.4	53.0	46.2	48.0	40.9	44.4	9.2
NDF	39.4	45.8	40.3	35.6	31.5	40.5	10.1
Hemicellulose	22.9	30.6	31.6	18.3	8.7	30.0	13.8
Alfalfa[c]	10.8	41.5	50.1	0.9	27.1	48.6	

[a] WSC - Whole shelled corn; SFC - Steam flaked corn

[b] Standard deviation; 6 observations/mean

[c] Alfalfa digestibility predicted by difference technique
WSC - 80.8% digestibility for corn; SFC - 85.8% digestibility for corn.

TABLE 8. ROUGHAGE LEVEL EFFECTS ON FECAL PARAMETERS OF WHOLE SHELLED AND STEAM FLAKED CORN DIETS

	WSC[a]			SFC[a]			
Roughage level (%)	5	15	40	5	15	40	SD[b]
Fecal:							
Dry matter (%)[c]	27.7	25.6	21.3	24.0	22.1	19.2	1.3
Organic matter[c]	89.9[e]	90.0[e]	86.8[d]	87.6[d]	88.1[d]	86.1[d]	1.1
Starch[c]	21.0[e]	21.2[e]	10.1[d]	5.0[d]	5.6[d]	4.8[d]	4.0
Nitrogen[c]	2.87	2.64	2.58	3.59	3.08	3.0	0.3
ADF[c]	18.9	22.1	34.0	22.1	27.2	37.0	2.2
NDF[c]	35.8[f]	37.5[f]	49.4[f]	49.4[g]	51.8[g]	53.9[f]	4.1
Hemicellulose[c]	17.0[f]	15.4[f]	14.4[f]	24.9[g]	22.6[g]	16.9[f]	2.6
pH	6.2	6.2	6.7	5.9	6.0	6.6	0.2

[a]WSC - Whole shelled corn; SFC - Steam-flaked corn.

[b]Standard deviation; 6 observations/mean.

[c]Percentage of fecal dry matter.

[de]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .05$).

TABLE 9. ROUGHAGE LEVEL EFFECTS ON RUMEN PARAMETERS OF WHOLE SHELLED AND STEAM FLAKED CORN DIETS

	WSC[a]			SFC[a]			
Roughage level (%)	5	15	40	5	15	40	SD[b]
Rumen							
Ammonia (mg/dl)	10.1	20.5	31.0	6.3	6.8	17.9	7.2
pH	5.8	5.9	6.3	5.8	5.8	6.3	0.2
Volatile fatty acid							
Total (mmoles/ml)	145.8_{f}	77.5_{g}	81.2_{h}	76.5_{f}	92.0_{f}	84.8_{gh}	54.7
Acetate[c]	47.6_{e}	57.7_{d}	64.1_{d}	47.7_{e}	45.7_{e}	62.4_{d}	5.1
Propionate[c]	38.5	27.2	19.9	20.1	41.9	22.1	5.2
Isobutyrate[c]	0.4	0.8	0.9	0.3	0.0	0.5	0.5
Butyrate[c]	8.6	10.4	10.3	7.7	8.7	11.5	3.8
Isovalerate[c]	2.1_{k}	2.3_{ij}	2.5_{jk}	1.6_{ijk}	1.5_{jk}	1.8_{i}	0.7
Valerate[c]	2.3_{k}	1.5_{ij}	2.0_{jk}	1.8_{ijk}	1.9_{jk}	1.3_{i}	0.5
Caproate[c]	0.5_{i}	0.1_{j}	0.3_{k}	0.7_{i}	0.4_{i}	0.3_{k}	0.4
C_2/C_3	1.3^{i}	2.3^{j}	3.3^{k}	1.2^{i}	1.1^{i}	3.2^{k}	0.6

[a] WSC - Whole shelled corn; SFC - Steam-flaked corn

[b] Standard deviation; 6 observations/mean

[c] Moles/100 moles

[de] Means in a row with different superscripts differ ($P < .01$).

[fgh] Means in a row with different superscripts differ ($P < .05$).

[ijk] Means in a row with different superscripts differ ($P < .10$).

TABLE 10. CORN PROCESSING EFFECTS ON DIGESTIBILITY

Item	Corn processing		
	WSC[a]	SFC[a]	SD[b]
Intake (kg/day)			
Dry matter	7.2	7.2	2.4
Organic matter	6.8	6.8	2.3
Digestible organic matter	5.1	5.4	1.7
Digestibility (%)			
Dry matter	73.7[e]	76.5[f]	3.3
Organic matter	75.3[e]	78.4[f]	3.3
Starch	91.1[c]	97.3[d]	4.7
Nitrogen	70.6	68.8	3.7
ADF	49.5[h]	44.6[g]	9.4
NDF	41.9[h]	35.9[g]	9.7
Hemicellulose	28.2	19.5	18.0
Alfalfa[i]	57.1	54.8	

[a] WSC - Whole shelled corn; SFC - Steam-flaked corn.

[b] Standard deviation; 18 observations/mean.

[cd] Means in a row with different superscripts differ ($P < .01$).

[ef] Means in a row with different superscripts differ ($P < .05$).

[gh] Means in a row with different superscripts differ ($P < .10$).

[i] Alfalfa digestibility predicted by the difference technique. Assume 80.8 and 85.8% DMD for whole shelled and steam-flaked corn respectively.

TABLE 11. CORN PROCESSING EFFECTS ON RUMINAL PARAMETERS

Item	Corn processing		
	WSC[a]	SFC[a]	SD[b]
Rumen:			
Ammonia (mg/dl)	20.5[g]	10.3[f]	10.2
pH	6.0	6.0	0.5
Volatile Fatty Acid			
Total (mmoles/ml)	101.5	84.4	50.7
Acetate[c]	56.5[g]	52.0[f]	5.2
Propionate[c]	28.5[d]	34.7[e]	4.9
Isobutyrate[c]	0.7[g]	0.3[f]	0.5
Butyrate[c]	9.8	9.3	3.15
Isovalerate[c]	2.3[g]	1.6[f]	0.8
Valerate[c]	1.9	1.7	0.6
Caproate[c]	0.3	0.5	0.6
C_2/C_3	2.3[i]	1.8[h]	0.6

[a] WSC - Whole shelled corn; SFC - Steam-flaked corn.

[b] Standard deviation; 18 observations/mean.

[c] Moles/100 moles.

[de] Means in a row with different superscripts differ ($P < .01$).

[fg] Means in a row with different superscripts differ ($P < .05$).

[hi] Means in a row with different superscripts differ ($P < .10$).

TABLE 12. CORN PROCESSING EFFECTS ON FECAL PARAMETERS

Item	Corn processing		
	WSC[a]	SFC[a]	SD[b]
Fecal:			
Dry matter (%)	24.9[e]	21.8[d]	2.4
Organic matter[c]	88.9[i]	87.3[h]	2.6
Starch[c]	17.4[e]	5.2[d]	7.2
Nitrogen[c]	2.7[d]	3.2[e]	0.3
ADF[c]	25.0[f]	28.8[g]	3.5
NDF[c]	40.4[d]	50.9[e]	6.4
Hemicellulose[c]	15.7[d]	21.4[e]	3.9
pH	6.4	6.2	0.4

[a]WSC = Whole shelled corn; SFC = Steam-flaked corn.

[b]Standard deviation; 18 observations/mean.

[c]Expressed as a percentage of fecal dry matter.

[de]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .05$).

[hi]Means in a row with different superscripts differ ($P < .10$).

TABLE 13. REGRESSION COEFFICIENTS OF DIETARY AND RUMINAL FACTORS ON DIGESTIBILITY

	Digestibility					
	Organic Matter	Starch	Nitrogen	ADF	NDF	Hemicellulose
Period[a]	.02	.11[f]	.43[d]	.34[d]	.45[d]	.35[d]
Period Animal[a]	.11	.57[f]	.52	.50	.63[e]	.63[e]
Variables in model						
DMI	.43[c]	.58[e]	.59[f]	.60[f]	.75[d]	.67[e]
Roughage	.87[c]	.64[e]	.61[f]	.70[e]	.77[d]	.74[e]
Roughage; Roughage^{2}[b]	.87[c]	.67[e]	.62[f]	.70[e]	.77[d]	.77[e]
Roughage; DMI	.88[c]	.66[e]	.61[f]	.70[e]	.78[d]	.74[e]
Roughage; DMI; Rumen pH	.93[c]	.67[f]	.67[f]	.76[e]	.78[e]	.74[e]
Roughage; DMI; Roughage^{2}	.88[c]	.70[e]	.62	.70[e]	.78[e]	.77[e]
Roughage; Roughage^{2}, Rumen pH	.89[c]	.68[f]	.66[f]	.74[e]	.79[e]	.76[e]
Roughage; Roughage^{2}; Rumen pH; Rumen NH_3	.89[c]	.68	.67	.75[e]	.81[e]	.78[e]
Roughage; Roughage^{2}, Rumen pH; Rumen NH_3; DMI	.93[c]	.70	.68[c]	.77[e]	.81[e]	.79[f]

[a] Variables fixed in the model as class variables for determination of other regression coefficients.

[b] Roughage^{2} = quadratic effect for roughage

[c] Significance level ($P < .0001$)

[d] Significance level ($P < .01$)

[e] Significance level ($P < .05$)

[f] Significance level ($P < .10$)

CHAPTER IV

EFFECTS OF ROUGHAGE SOURCE, ROUGHAGE LEVEL AND INTAKE LEVEL ON DIGESTIBILITY OF FEEDLOT DIETS

S. R. Rust, F. N. Owens and D. R. Gill

Summary

Twenty-four Hereford-Angus steers (365 kg) were fed six roughage sources (cottonseed hulls, prairie hay, alfalfa hay, sorghum silage, and two varieties of corn silage with whole shelled corn to evaluate two roughage levels (10 and 50 percent) at two levels of feed intake (1 and 2 percent of body weight). With the low roughage diet and higher intake level, digestibilities of OM, starch, nitrogen and ADF were similar with all roughage sources except that neutral detergent fiber and hemicellulose digestibility were lower with alfalfa in the diet. With 50 percent roughage in the diet fed at 2 percent of body weight, organic matter ($P < .10$), starch ($P < .01$) and ADF ($P < .15$) digestibilities were influenced by the type of roughage. With high concentrate diets, the digestibility of the forage appeared to be less critical than the effect of forage on digestibility of the grain (starch) where a 13 percent range was apparent. With higher roughage diets, digestibility of the roughage became more critical though roughage sources continued to have different effects on grain (starch) digestibility.

Elevated feed intake decreased digestibilities of OM, starch, nitrogen, hemicellulose ($P < .01$) and neutral detergent fiber ($P < .10$). Acid detergent fiber digestion was similar at both intakes. As intake increased, ruminal volatile fatty acid concentrations increased, but the proportion of acetate decreased ($P < .05$). Averaged across roughage sources, increasing the roughage levels from 10 percent to 50 percent decreased organic matter digestibility 5.3 percent ($P < .01$) but increased digestibility of NDF ($P < .03$), due primarily to increased ($P < .01$) digestibility of ADF. Ruminal pH, acetate and butyrate proportions increased with added roughage while the propionate proportion decreased ($P < .01$). Starch digestibility increased slightly with intake level and roughage level.

Introduction

Forage is added to grain diets to prevent acidosis, liver abscesses and laminitis. Roughage added to grain diets at lower levels will not reduce gains provided intake can increase to compensate for the reduced net energy content of the diet (Matsushima, 1979; Owens and Gill, 1980; Gill et al., 1981). Generally, intake will not compensate for reduced energy density when more than 15 percent to 30 percent roughage is added to a concentrate diet. This value may change depending on the type of forage fed.

Selection of a roughage to feed has been based on 1) availability, 2) digestibility, and 3) cost of the roughage. Possible interactions between grain and roughage have not been quantitated. Associative effects of roughage with grain have been reported by many workers

(Forbes et al., 1931; Forbes, 1933; Kriss et al., 1943; Blaxter and Wainman, 1964; Vance et al., 1972; Byers et al., 1975 Joanning et al., 1981; Teeter, 1981). An "associative effect" is defined as the nonlinear response in digestibility. Validity of the concept of an associative effect has been questioned by some workers. Certainly, in some trials, associative effects may be a result of improperly balanced diets (Moe, 1980) or artifacts of an experimental design (Garrett, 1979). Since intake of a mixture of feeds may exceed that of individual feeds, greater intake may contribute to the "associative effects". As intake increases, nutrient digestibility of most feed components declines (Reid et al., 1980).

Based on physical and chemical differences between roughages, animal responses to different roughages and grain diets may differ. Review of the literature provides support for this concept. Corn silage and alfalfa addition to corn diets reduced digestibility (Vance et al., 1972; Byers, 1975; Joanning et al., 1981), while cottonseed hulls increased digestibility of whole shelled corn (Teeter, 1981).

The objective of this study was to evaluate the effects of six different roughage sources on digestibility of a corn-based diet. Two intake levels and two roughage levels were fed to subdivide the intake from the roughage level effects. Since most of the fiber in the diet was from the roughage and most of the starch in the diet came from grain, the influence of intake level and roughage level on roughage and grain digestion was subdivided on this basis.

Experimental Procedure

Twenty-four Hereford and Angus steers (365 kg) were utilized in six 4 x 4 latin square designs. Six roughage sources (table 1) commonly used in feedlot diets were selected. Each roughage source was assigned to one latin square. A 2 x 2 factorial arrangement of treatments was used within each 4 x 4 latin square. These were dry matter intake levels (1 and 2 percent of body weight) and percentage of roughage in the diet (10 to 50 percent). Each of the four periods lasted 21 days consisting of 16 days for adaptation and five days for collection of fecal grab samples. Ruminal and blood samples were obtained the last day of each period.

Steers were fed at 0900 and 1600 each day with orts weighed once daily. Steers were individually housed in pens with concrete slatted floors. The diet consisted of whole shelled corn, roughage and supplement (table 2). Chemical composition of the roughages and corn is shown in table 1. Supplements (table 3) were designed to avoid high protein levels and were thoroughly mixed with other diet ingredients at feeding time. Chromic oxide incorporated into the supplement was used as an indigestible marker to estimate digestibility.

Fecal grab samples were collected between 0600 and 0800 each collection morning. The pH was measured immediately after collection. A portion of the fecal collection was frozen for later analysis. Rumen samples, collected via stomach tube, and blood samples, obtained by jugular venipuncture were collected the last day of each period.

Dry matter, ash and nitrogen were determined using AOAC (1975) procedures. Starch analysis was determined with the Macrae and

Armstrong (1968) procedure. The Van Soest procedure (USDA, 1970) was used to estimate acid detergent fiber (ADF) and neutral detergent fiber (NDF). Hemicellulose was calculated as the difference between NDF and ADF. To aid the filtration of NDF, fecal samples were autoclaved and subjected to a amylo-glucosidase digestion prior to extraction with NDF solution.This pretreatment prevented the starch from gelatinizing on the gooch crucibles to inhibit filtration. Pepsin insoluble nitrogen was determined by pepsin digestion in .1N HCl followed by macro-Kjeldahl nitrogen determination on the filtrate (USDA, 1970). Pepsin insoluble nitrogen was used as a second indigestibility marker for comparison with digestibility estimated with chromic oxide. Fecal and ruminal pH values were determined with a pH meter equipped with a combination electrode. Rumen ammonia values were determined with the Chaney-Marbach procedure (1962). Ruminal volatile fatty acid concentrations were determined gas chromatographically (Sharp, 1977). Blood glucose values were estimated using a glucose oxidase kit[1]. For plasma urea determination, plasma samples were incubated with urease prior to ammonia analysis with the Chaney-Marbach (1962) reagents.

Statistical analysis was performed using the General Linear Models Procedure of the SAS system (Barr and Goodnight, 1981). Data from each square were pooled by the procedures of Steel and Torrie (1960). The

[1] Worthington Diagnostics, Grandview Business Center, San Francisco, CA. 94080.

analysis of variance table is shown in table 4. Treatment means were compared using the Least Significance Difference technique.

Results and Discussion

Digestibilities of diets containing 10 percent roughage from each of the 6 different forages and fed at 2 percent of body weight are shown in table 5. Digestibility estimates for organic matter, starch, nitrogen and ADF were not significantly ($P < .10$) different. If the organic matter of the concentrate in the diet is 80 percent digestible (NRC, 1980) then a 72 percent OMD would be expected if the roughage digestibility was zero. Since some of the digestibilities were below 72 percent, certain roughages had adversely influenced digestion of the whole shelled corn in the diet. With high concentrate diets, effects of roughage on the total diet may be of greater concern than digestibility of the forage. Forages which are available and palatable rather than highly digestible may offer economic advantages in high grain diets if the purpose of the forage is to simulate rumination and aid ruminal mixing.

Calculated organic matter digestibilities based on the NRC (1980) values for dairy cattle for the six diets also are shown in table 5. Total digestible nutrient (TDN) values were considered to be equal to organic matter digestibility to calculate theoretical OMD values. Alfalfa and two of the silage supplemented diets had digestibilities considerably below values expected. With all three of these diets, starch digestibility was below 80 percent. Digestibility of neutral detergent fiber ($P < .01$) and hemicellulose ($P < .10$) were significantly lower for the diet supplemented with alfalfa than with other roughages.

This may be to differences in the chemical composition and chemical bonding between cellulose, hemicellulose and lignin.

The effects of different roughage sources on fecal parameters in high concentrate diets fed at high intakes are shown in table 6.Fecal pH was lower ($P < .05$) for CSH and PH supplemented diets. Fecal ADF was greater ($P < .01$) for the CSH diet and tended to be greater for the PH diet as well. Fecal starch values were slightly lower with the CSH and PH diets as compared with the other diets. One possible explanation for these trends may be that more extensive digestion of starch in the cecum and large intestine yields a lower fecal starch and pH. This change could inhibit cellulose digestion and increase fecal ADF. Fecal dry matter, organic matter, nitrogen, NDF and hemicellulose values were similar for all diets. Ruminal pH values were not significantly different for the six diets (table 7). Rumen ammonia concentration was lowest for the CSH diet and greatest for the grain variety of corn silage ($P < .01$). Isovalerate levels paralleled ($P < .05$) rumen ammonia levels. Ruminal proportions of acetate, propionate, butyrate, isobutyrate, valerate, caproate and total VFA levels were similar for all diets.

Effects of the different roughages on blood parameters is shown in table 8. Blood glucose values were slightly lower ($P < .10$) for the CSH supplemented diets than the AH or FCS diets. Blood urea nitrogen levels were similar for all diets. Insulin levels were significantly lower ($P < .10$) for the CSH, PH, AH and SS diets than the GCS diet. A linear relationship between insulin level and blood glucose was not

seen with this level of roughage.

The effects of roughage source on digestibility appear more critical with higher roughage diets. Organic matter digestibility was greater ($P < .10$) with the corn silage diets than the other roughages in a 50 percent roughage diet fed at 2 percent of body weight (table 9).

Observed OMD values were similar to calculated TDN (NRC, 1980) values for the PH, SS and FCS diets. Observed OMD values were greater than TDN values for CSH and GCS but lower than TDN values for the AH diet. The difference between predicted and determined values emphasizes three points. First, feedstuff vary. Book values are estimated on average TDN values. Secondly, roughage sources may behave differently with corn fed whole than when fed processed. Book values for TDN of grain were calculated for processed grain. Finally, the physical and chemical properties of a roughage may influence digestion of other feedstuffs.

Starch digestibility with the 50 percent roughage diets was lowest with the AH and greatest with the CSH diet ($P < .06$). Cellulose digestibility tended to be lower with the AH, SS and CSH diets ($P < .15$) while nitrogen, NDF and hemicellulose digestibilities were similar for all diets.

Fecal dry matter was significantly lower with FCS diet than the GCS, PH and CSH diets ($P < .01$). Fecal organic matter values were lower for the silage diets ($P < .01$). Fecal starch values were lower with the CSH diet. This finding agrees with trends reported by Teeter (1981). Fecal nitrogen values were significantly lower for the PH, SS and GCS

diets than the CSH supplemented diet ($P < .10$) Fecal ADF and NDF values were significantly higher for the CSH than the other diets ($P < .01$). Since CSH has the lowest digestible energy value of the roughage sources used in this study, one would expect more fiber in feces with CSH. Fecal hemicellulose values were significantly greater for the PH diet than the CSH diet ($P < .01$). Fecal pH values were higher with the silage diets ($P < .10$). Fecal pH values increased as fecal ash values increased; however, the relationship between fecal pH and fecal ADF was negative ($r = -.16$). This observation questions the suggestion that fecal pH depends on buffering by indigestible fiber or minerals bound to indigestible fiber. The relationship between fecal pH and fecal starch also was poor ($r = -44$) at this roughage level.

Effects of the various roughage sources fed at the high intake and roughage level on ruminal parameters is shown in table 11. Ruminal pH and ammonia values were similar with the various roughage supplemented diets. Relative proportions of acetate, propionate, butyrate, isovalerate and caproate were similar among all diets. Isobutyrate levels tended to be lower for the SS and FCS diets than the AH diet ($P < .15$). Since isobutyrate is an end product of valine metabolism (Van Soest, 1982) higher isobutyrate levels with the alfalfa supplemented diet may be due to the high protein content of this diet. Valerate levels were greater for the AH diet than the other roughage diets ($P < .10$); although valerate is formed by the condensation of acetyl CoA and propionyl CoA (Van Soest, 1982), the reason for greater valerate levels with alfalfa diets has no apparent explanation.

Blood glucose, blood urea and insulin levels were statistically similar for all roughages supplemented at 50 percent of the diet dry matter (table 12).

Selection of a roughage to supplement whole corn diets used for growing cattle needs to consider the influence of forage on grain digestibility as well as digestibility of the roughage. Based on expected digestibilities, the cottonseed hull diet was 18 percent more digestible than expected, while the alfalfa diet was 7 percent less digestible than expected .Prairie hay, sorghum and corn silages were near expected values (+ 1 to +5 percent). Forage quality and type is more critical in diets containing high levels of roughage than in feedlot type diets. Positive and negative effects may be less when the grain in the diet has been more extensively processed than the whole grain in this study. With steamed rolled barley, associative effects of alfalfa were not detected (Garrett, 1979) while with cracked corn-corn silage diets, associative effects reduced digestibility in two trials (Byers, 1975; Joanning et al ., 1981). Selection of a forage should include the influence of the forage on digestion of the entire diet as well as forage digestibility, palatability, availability, protein content, physical characteristics and cost.

The effects of intake and roughage level were pooled across roughage sources to generate more statistical power for evaluation of their influence on metabolic parameters. The effects of level of intake on digestibility are shown in table 13. Organic matter digestibility was significantly reduced ($P < .01$) as intake was increased from 1 to 2 percent of body weight (1.2 and 1.9 multiples of

maintenance respectively). This corresponds with a 9 percent reduction in OMD for each multiple of maintenance increase in intake. A similar reduction in OMD of 8 percent per multiple of maintenance was reported by Haaland et al.(1980). Other researchers have reported OMD depressions ranging from 2.9 to 8.2 percent for each multiple of maintenance increase in intake (Brown, 1966; ARC, 1980; NRC, 1980). Digestibilities of starch, ($P < .01$) nitrogen ($P < .01$) and NDF ($P < .10$) all were significantly reduced as intake increased while acid-detergent fiber digestibility was virtually unchanged as intake increased. Increasing the level of feed intake increases the rate at which solids leave the rumen and pass through the total tract (Sutton, 1979; Teeter, 1981) but some undigested processed grains may leave the rumen faster than long roughages (Balch, 1950). Since much of the ADF is associated with the coarse and fibrous roughage fraction, it may be to large to leave the rumen. Alternatively, it may be associated with the pad floating in the rumen and retained in the rumen so that increasing the level of intake would have little influence on the time which ADF has in the rumen to be digested. Digestibility of organic was reduced ($P < .01$) as roughage level in the diet was increased (table 14). Similar results have been reported by other researchers (Cole et al., 1976; Reynolds et al., 1979; Price et al., 1980; Vinet et al., 1980). Roughages have lower digestibility values than grain, so the resulting diet has lower digestibility. Neutral-detergent fiber ($P < .03$)and acid-detergent fiber ($P < .01$) digestibilities were increased as roughage was added to the diet while starch digestibility was not statistically altered. Starch digestibility tended to increase with added roughage. This

disagrees with results reported by Byers (1975) and Joanning et al. (1981). Differences in roughage sources and grain processing may explain the lack of agreement between trials. Nitrogen digestion was similar with both roughage levels.

No significant interactions were detected ($P < .10$) between level of intake and level of roughage on digestibility of organic matter, starch, nitrogen, ADF and NDF (table 15). However hemicellulose digestibility increased as roughage was added at the lower level of intake but decreased with added roughage at the higher level of intake ($P < .14$). Hemicellulose is less rigidly bound to the cell wall structure (Pigden and Heany, 1968; Wood, 1970) than cellulose. This may allow hemicellulose to associate with the cell wall fraction which is more readily degraded into smaller particle sizes which would be flushed from the rumen as intake increased. At the lower level of intake, roughage addition increased hemicellulose digestibility and ruminal pH. This relationship suggests that hemicellulose digestion may be pH sensitive. Results from this study and others (Van Soest, 1973; Reynolds et al., 1979) suggest that hemicellulose digestibility is sensitive to time spent in the rumen and ruminal pH. Cellulose is associated with the fiber mass which leaves the rumen more slowly and would by less susceptible to fluctuations in ruminal pH and feed intake.

Intake and roughage effects on digestibility expressed as percentage unit changes are shown in table 16. As intake increased, the digestibility of all parameters listed decreased, but the magnitude of the decrease was much smaller for ADF digestibility. Several

researchers have attributed the majority of the reduction in dry matter digestibility with increased intake to altered cellulose and hemicellulose digestion (Rodrique and Allen, 1960; Leaver et al., 1969; Robertson and Van Soest, 1972; Tyrrell and Moe, 1975; Van Soest, 1980) whereas other workers have indicated that reducedstarch digestibility is the major cause (Wheeler et al., 1975; Joanning et al., 1981). Results from this study would indicate that on a percentage basis , the hemicellulose digestibility is reduced to a greater extent as intake increases; however, on a weight basis, reduced starch digestion would account for more of the reduced dry matter digestion since starch was present at 2 to 3 times the concentration of cell walls in these diets. Few authors have discussed the reduction in protein digestibility with increased feed intake. In this study, protein digestibility was reduced at a magnitude similar to other nutrients, but the contribution of protein to the total depression in digestibility is small due to the small proportion present. The effects of roughage addition were most pronounced on digestibility of ADF. The associative effect can be calculated as the difference between the sum and the component effect of level of intake and level of fiber. Differences between determined and observed values at the 50 percent roughage level and high intake level are one type of associative effect. The associative effect was small for organic matter, starch and nitrogen but tended to be larger for the cell wall fractions. These were determined using the effects of intake and roughage level to predict digestibility at the high roughage level and high intake level.

The effects of intake and roughage levels on digestibility and the resultant associative effects may vary with roughage source (table 17). Positive associative effects on organic matter digestion were detected with the corn silages and cottonseed hull diets while negative associative effects were observed with prairie and alfalfa hays and sorghum silage. The effects of intake and roughage level within each of these six roughage sources is shown in tables 2-7 in the Appendix.

The effects of intake and roughage levels on fecal parameters are shown in table 18. Fecal organic matter and starch content increased ($P < .01$) as intake level increased. Fecal ADF and NDF decreased as intake level increased ($P < .01$ and $P < .05$ respectively). Fecal pH was lower at the higher feed intake ($P < .01$). If a greater amount of fermentable material reached the large intestine, it could ferment and lower pH of the feces. Increasing feed intake did not alter fecal dry matter, nitrogen or hemicellulose content. Increasing the roughage level from 10 to 50 percent, lowered fecal dry matter, organic matter, starch and nitrogen ($P < .01$). The indigestible fiber from the higher roughage diets diluted the starch and nitrogen in feces. Fecal fiber fractions (ADF and NDF) were increased ($P < .01$) as roughage level increased. Fecal pH values were higher for the higher roughage diet ($P < .01$). Fecal pH was more closely associated with fecal chromium concentrations ($r = .64$; $P < .0001$) than the other fecal parameters (table 19). Hemicellulose content of the feces was not significantly altered with roughage added to the diet (table 18).

The overall effects of intake level and roughage level on ruminal parameters are shown in table 20. Ruminal pH values were increased with the higher roughage diet ($P < .05$) in agreement with results of Cole (1975). Rumen pH increased from 6.15 to 6.37 as cottonseed hulls increased from 0 to 14 percent of the diet. Ruminal acetate proportions decreased ($P < .05$) as intake level was doubled but increased as roughage was added to the diet ($P < .01$).Propionate proportions were reduced with the 50 percent alfalfa diet ($P < .01$) while butyrate proportions increased ($P < .10$). Acetate to propionate ratio decreased with the higher intake level ($P < .10$) but increased as roughage was added to the diet ($P < .01$). Isovalerate levels decreased at the higher roughage diets ($P < .01$). This may reflect the lower protein content of the diet as lower protein roughage replaced corn in the diet. Total volatile fatty acid concentration increased at the higher intake level ($P < .05$).

Similar results (Rumsey et al., 1970) have been reported with hay and concentrate diets. As intake was increased from .5 to 2.0 percent of body weight, total volatile fatty acid concentration ($P < .01$) and propionate proportion ($P < .05$) increased while acetate proportion ($P < .05$) and rumen pH ($P < .01$) decreased. Rumen ammonia, isobutyrate, valerate and caproate levels were not significantly altered by increasing either intake level or roughage in the diet.

Blood glucose levels were not altered by intake or roughage level ($P < .10$). Adding alfalfa to a level of 70 percent in a corn-alfalfa diet tended to lower plasma glucose levels (Judson et al., 1968). Blood urea nitrogen levels were increased as roughage was added to the diet

($P < .01$) while plasma insulin levels were not significantly altered by intake or roughage level.

Some preliminary studies at Oklahoma State University indicated pepsin insoluble nitrogen may serve as an internal feed marker for digestibility determinations (Zinn R. A., 1980, personal communication). To evaluate the feasibility of using pepsin insoluble nitrogen (PIN) as a digestibility marker, digestibility values calculated from PIN were compared with those estimated from chromic oxide. Digestibility values predicted from pepsin insoluble nitrogen were generally greater than those from chromic oxide (table 22). Standard errors were equal to or smaller for the digestibility values predicted from PIN than chromic oxide. It is difficult to tell which procedure is more accurate, although the PIN estimates appear more precise. Further work needs to be conducted comparing these digestibility markers in total fecal collection studies.

TABLE 1. FEEDSTUFFS

Source	Abbreviation	IFN[a]	Analysis (%) DM	Crude Protein	Starch	ADF	NDF	Hemicellulose
Corn silage[b]								
Forage variety	FCS	3-08-153	32.8	7.6	23.2	30.0	38.5	8.5
Grain variety	GCS	3-08-153	33.8	8.4	21.1	31.3	38.3	7.0
Sorghum silage[b]	SS	3-07-962	27.6	7.7	18.5	37.3	41.6	4.3
Alfalfa hay[b]	AH	1-00-059	90.6	18.2	2.0	40.1	52.7	12.6
Prairie hay	PH	1-07-957	91.2	5.9	3.8	46.2	66.8	20.6
Cottonseed hulls[b]	CSH	1-01-599	88.5	7.5	3.9	64.2	66.2	2.0
Whole shelled corn	WSC	4-02-931	88.5	10.0	73.8	2.4	8.6	6.2

[a]International feed number.

[b]Mineral analysis is shown in Table 1 in the Appendix.

TABLE 2. DIET COMPOSITION[a]

Item	IFN[b]	Roughage Level (%) 10	50
Whole shelled corn	4-02-931	82.0	42.0
Roughage		10.0	50.0
Supplement		8.0	8.0

[a]Percent of ration dry matter.

[b]International feed number.

TABLE 3. SUPPLEMENT COMPOSITION

Item[c]	IFN[d]	Diets[b] CSH & PH	Silages	AH
Soybean meal	5-04-604	72.3	45.3	--
Ground corn	4-02-931	5.1	4.9	50.4
Dicalcium phosphate	6-01-080	10.7	13.1	13.1
Calcium Carbonate	6-02-632	2.7	15.1	15.1
Potassium Chloride	6-03-756	--	5.6	5.6
Salt		1.6	3.1	3.1
Urea		3.8	7.5	7.5
Sodium sulfate		2.4	2.4	2.4
Trace mineral mix		0.2	0.3	0.3
Chromic oxide		1.3	2.5	2.5

[a]Ingredients expressed as a percentage of dry matter.

[b]Supplement composition for diets with roughages containing low, medium and high amounts of protein.

[c]Vitamins A and D were added to supply NRC requirements.

[d]International feed number.

TABLE 4. POOLED ANALYSIS OF VARIANCE TABLE

Source of Variation	df
Total	95
Roughage	5
Intake level	1
Roughage level	1
Roughage level * intake level	1
Period	3
Pen	18
Error	66

TABLE 5. EFFECTS OF ROUGHAGE SOURCE ON NUTRIENT DIGESTIBILITY WITH 10% ADDED ROUGHAGE (INTAKE EQUALS 2% OF BODY WEIGHT)

Item	Roughage Source[a]						SEM[b]
	CSH	PH	AH	SS	GCS	FCS	
Digestibility (%)							
Organic matter							
Determined	73.8	77.1	65.2	69.6	67.8	74.1	5.3
Calculated[c]	74.4	75.5	74.5	74.4	75.8	75.8	--
Starch	90.8	89.2	77.4	79.7	77.4	84.8	5.9
Nitrogen	62.3	66.1	51.6	63.8	55.5	68.3	5.8
ADF	27.1[e]	37.2[e]	25.0[d]	34.2[e]	44.8[e]	47.0[e]	7.1
NDF	48.1[g]	47.6[g]	19.4[f]	42.7[g]	40.6[g]	54.8[g]	10.25[h]
Hemicellulose	56.0	53.6	19.4	41.0	40.0	56.2	15.10[h]

[a]Roughage source abbreviations identified in experimental procedure.

[b]Standard error of the mean.

[c]Calculated from TDN of ingredients listed in NRC for Dairy Cattle (1980).

[de]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .10$).

[h]Value is a standard deviation because of unequal treatment means (CSH-2; PH-3;AH-4;SS-3;GCS-3; FCS-3).

TABLE 6. ROUGHAGE SOURCE EFFECTS ON FECAL CHARACTERISTICS WITH 10% ADDED ROUGHAGE (INTAKE EQUAL TO 2% OF BODY WEIGHT)

	Roughage source[a]						
	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Fecal:							
pH	5.7[f]	5.8[f]	5.9[fg]	5.9[fg]	6.1[g]	6.1[g]	0.1
Dry matter (%)[c]	28.2	26.0	29.0	28.9	31.4	28.7	2.0
Organic matter[c]	93.3	89.2	918	88.7	88.3	88.5	1.2
Starch[c]	20.6	26.6	35.2	36.7	37.4	34.2	6.5
Nitrogen[c]	2.8[e]	2.8[de]	2.8[d]	2.4[d]	2.6[d]	2.4[d]	0.2
ADF[c]	24.7	18.2	14.3	12.7	10.5	11.2	2.3[h]
NDF[c]	37.9	33.5	31.9	28.4	27.1	24.3	8.1[h]
Hemicellulose[c]	14.3	16.5	17.4	16.3	15.1	12.9	3.4[h]

[a] Roughage source abbreviations are identified in experimental procedure.

[b] Stardard error of the mean.

[c] Percentage of fecal dry matter.

[de] Means in a row with different superscripts differ ($P < .01$).

[fg] Means in a row with different superscripts differ ($P < .05$).

[h] Values are standard deviations because of unequal observations/mean.

TABLE 7. EFFECT OF ROUGHAGE SOURCE ON RUMINAL PARAMETERS WITH 10% ADDED ROUGHAGE (INTAKE AT 2% OF BODY WEIGHT)

	Roughage Source[a]						
Item	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Rumen:							
pH[c]	6.0_{f}	6.2_{fg}	6.2_{fgh}	5.9_{gh}	5.9_{h}	5.8_{fgh}	0.3
Ammonia (ng/dl)	5.0^{f}	8.8^{fg}	10.0^{fgh}	16.7^{gh}	15.1^{h}	10.7^{fgh}	2.8
Volatile fatty acid (moles/ 100 moles)							
Acetate	59.7	57.0	56.2	57.3	55.9	59.5	4.3
Propionate	28.6	30.6	23.0	28.3	21.3	21.9	4.5
Butyrate	7.7	9.0	12.2	8.8	12.4	13.6	1.9
Isobutyrate	0.2	0.2	1.0	0.5	1.8	0.7	0.5
Valerate	1.6_{d}	1.4_{d}	3.6_{de}	1.6_{d}	3.4_{e}	1.7	1.0
Isovalerate	1.9^{d}	1.8^{d}	3.7^{de}	2.5^{d}	5.0^{e}	2.4	0.7
Caproate	0.3	0	0.3	1.1	0.2	0.2	0.3
Total (m moles/ml)	81.3	79.4	69.1	110.6	71.8	102.5	12.3

[a] Roughage source abbreviations are identified in experimental procedure.

[b] Standard error of the mean.

[c] One value missing per mean (3 observations/mean).

[de] Means in a row with different superscripts differ ($P < .05$).

[fgh] Means in a row with different superscripts differ ($P < .01$).

TABLE 8. EFFECT OF ROUGHAGE SOURCE ON BLOOD PARAMETERS WITH 10% ADDED ROUGHAGE (INTAKE EQUALS 2% OF BODY WEIGHT)

	Roughage Source[a]						
	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Blood:							
Glucose (mg/100 ml)	61.0[c]	70.8[cd]	88.8[e]	75.3[cde]	71.9[cd]	79.0[de]	6.1
Urea-N (mg/100 ml)	5.1	5.0	4.5	5.8	6.3	3.9	0.9
Insulin (ng/ml)	0.6[c]	0.4[c]	0.5[c]	0.6[c]	1.6[d]	1.0[cd]	0.3

[a]Roughage source abbreviations are identified in experimental procedure.

[b]Standard error of the mean.

[cde]Means in a row with different superscripts differ ($P < .10$).

TABLE 9. EFFECT OF ROUGHAGE SOURCE ON NUTRIENT DIGESTIBILITY WITH 50% ADDED ROUGHAGE (INTAKE EQUALS 2% OF BODY WEIGHT)

	Roughage Source[a]						
	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Digestibility (%)							
Organic matter							
Determined	68.0^{fgh}	65.9^{fg}	61.3^{f}	65.2^{fg}	76.6^{h}	71.6^{gh}	3.5
Calculated[c]	57.7	63.1	65.8	64.4	71.9	71.9	--
Starch	96.3^{e}	78.7^{d}	83.7^{de}	76.7^{d}	90.4^{de}	88.5^{de}	4.5
Nitrogen	54.4$_{i}$	57.0	57.1	60.4	69.7	64.4	5.2
ADF	43.6^{i}	56.3^{j}	40.4^{i}	46.5^{ij}	56.0^{j}	46.5^{ij}	4.7
NDF	44.6	53.3	41.2	49.2	52.0	43.8	5.4
Hemicellulose	49.0	48.2	42.5	42.1	43.5	39.0	9.6

[a]Roughage source abbreviations are identified in experimental procedure.

[b]Standard error of the mean.

[c]Calculated from TDN of ingredients listed in NRC for dairy cattle.

[de]Means in a row with different superscripts differ ($P < .06$).

[fgh]Means in a row with different superscripts differ ($P < .10$).

[ij]Means in a row with different superscripts differ ($P < .15$).

TABLE 10. EFFECTS OF ROUGHAGE SOURCE ON FECAL PARAMETERS WITH 50% ADDED ROUGHAGE (INTAKE EQUALS 2% OF BODY WEIGHT)

	Roughage Source[a]						
Fecal:	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Dry matter (%)	25.5^{k}	23.9^{jk}	20.8^{ij}	22.7^{ijk}	24.1^{k}	20.5^{i}	1.1
Organic matter[c]	93.1^{g}	89.5^{fg}	89.1^{fg}	83.6^{de}	78.3^{d}	85.2^{ef}	1.3
Starch[c]	3.8^{i}	19.5^{jk}	13.0^{ij}	25.1^{k}	14.7^{ijk}	14.5^{ijk}	3.7
Nitrogen[c]	2.6^{n}	2.0^{l}	2.5^{mn}	2.0^{l}	2.1^{lm}	2.2^{lmn}	0.1
ADF[c]	27.7^{e}	30.0^{d}	33.8^{d}	30.0^{d}	27.9^{d}	28.6^{d}	3.4
NDF[c]	70.2^{d}	51.7^{e}	49.4^{de}	42.5^{de}	44.6^{de}	46.1^{de}	3.4
Hemicellulose[c]	12.5^{l}	21.7^{lm}	15.6^{mn}	16.0^{n}	16.7^{n}	17.5^{mn}	1.8
pH	6.0	6.1	6.3	6.4	6.4	6.3	0.1

[a] Roughage source abbreviations are listed in experimental procedure.

[b] Standard error of the mean.

[c] Percent of fecal dry matter.

[defg] Means in a row with different superscripts differ ($P < .01$).

[ijk] Means in a row with different superscripts differ ($P < .05$).

[lmn] Means in a row with different superscripts differ ($P < .10$).

TABLE 11. EFFECT OF ROUGHAGE SOURCE ON RUMEN PARAMETERS WITH 50% ADDED ROUGHAGE (INTAKE EQUALS 2% OF BODY WEIGHT)

	Roughage Source[a]						
	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Ruminal:							
pH[c]	6.1	6.8	6.3	6.4	6.3	6.3	0.2
Ammonia (ng/dl)	9.5	5.6	15.2	13.7	15.2	6.3	3.1
Volatile fatty acid (moles/100 moles)							
Acetate	68.6	66.7	63.4	64.7	63.8	69.6	2.0
Propionate	13.8	17.9	15.5	18.3	17.6	16.3	1.5
Butyrate	13.9_{fg}	12.1_{fgh}	13.5_{h}	12.8_{f}	13.9_{fg}	10.5_{f}	1.0
Isobutyrate	0.5_{d}	0.8_{d}	1.4_{e}	0.2_{d}	1.0_{d}	0.2_{d}	0.3
Valerate	1.1	0.9	2.6	1.5	1.5	0.8	0.4
Isovalerate	1.5	1.5	2.8	1.9	1.9	1.1	0.5
Caproate	0.7	0.3	0.8	0.7	0.4	1.4	0.5
Total VFA (mmoles/ml)	90.5	95.7	81.8	81.3	72.3	105.6	10.2
C_2/C_3	4.3	3.7	3.6	4.1	4.1	5.1	0.5

[a] Roughage source appbreviations are identified in experimental procedures.

[b] Standard error of the mean.

[c] One observation missing per mean (3 observations/mean).

[de] Means in a row with different superscripts differ ($P < .10$).

[fgh] Means in a row with different superscripts differ ($P < .15$).

TABLE 12. EFFECT OF ROUGHAGE SOURCE ON BLOOD PARAMETERS WITH 50% ADDED DIETARY ROUGHAGE (INTAKE EQUAL TO 2% OF BODY WEIGHT)

	Roughage Source[a]						
	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Blood:							
Glucose (mg/%)	86.0	79.2	76.1	70.9	71.8	67.3	9.5
Urea-N (mg/%)	4.5	4.6	6.8	6.4	6.3	5.5	0.9
Insulin (ng/ml)	0.6	0.5	0.8	0.7	0.5	0.6	0.2

[a]Roughage source abbreviations are identified in experimental procedure.

[b]Standard error of the mean.

TABLE 13. EFFECTS OF INTAKE ON DIGESTIBILITY

Item	Intake level[a] 1%	2%	% change	SEM[b]
Digestibility (%):				
Organic matter	76.0[d]	69.7[c]	-8.4	1.0
Starch	91.3[d]	84.5[c]	-7.5	1.0
Nitrogen	67.3[d]	60.9[c]	-9.5	1.4
ADF	43.5	42.0	-3.5	1.7
NDF	49.3[f]	45.0[e]	-8.7	1.8
Hemicellulose	57.5[d]	45.1[c]	-12.4	2.7

[a]Intake expressed as a percent of body weight.

[b]Standard error of the mean.

[c,d]Means in a row with different superscripts differ ($P < .01$).

[e,f]Means in a row with different superscripts differ ($P < .10$).

TABLE 14. EFFECT OF ROUGHAGE LEVEL ON DIGESTIBILITY

Item	Roughage level (%) 10%	50%	%change	SEM[a]
Digestibility (%):				
Organic matter	74.8[c]	70.8[b]	-5.3	1.0
Starch	86.8	89.0	+2.6	1.0
Nitrogen	64.9	63.2	-2.6	1.4
ADF	36.6[b]	49.0[c]	+33.9	1.7
NDF	44.2[d]	50.0[e]	+13.1	1.8
Hemicellulose	50.8	52.3	+3.0	2.7

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

[de]Means in a row with different superscripts differ ($P < .03$).

TABLE 15. ROUGHAGE-INTAKE LEVEL INTERACTION EFFECTS ON DIGESTIBILITY

	Intake level (% of body weight)				
	1		2		
Roughage level (%)	10	50	10	50	SEM[a]
Digestibility (%):					
Organic matter	78.4	71.3	73.6	68.1	1.4
Starch	90.3	92.3	83.2	85.7	1.4
Nitrogen	68.6	66.0	61.3	60.5	1.9
ADF	37.3	49.8	35.9	48.2	2.4
NDF	45.0	53.4	43.2	46.5	2.5
Hemicellulose	53.5[bc]	61.3[d]	47.5[bc]	43.0[b]	3.8

[a]Standard error of the mean.

[bcd]Means in a row with different superscripts differ ($P < .14$).

TABLE 16. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY (% CHANGE)

	Change due to:		
	Intake Level	Roughage Level	Associative[a] Effect (%)
Digestibility:			
Organic matter	-8.4	-5.3	+.6
Starch	-7.5	+2.6	-.2
Nitrogen	-9.5	-2.6	+.3
ADF	-3.5	+33.9	-.8
NDF	-8.7	+13.1	-1.0
Hemicellulose	-12.4	+3.0	-11.3

[a]Percentage difference between observed and predicted values for high intake and high roughage level diet.

TABLE 17. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY AND ASSOCIATIVE EFFECTS WITH VARIOUS ROUGHAGE SOURCES

Roughage Source[a]:	CSH			PH			AH			SS			GCS			FCS		
	I[b]	R[b]	A[c]	I	R	A	I	R	A	I	R	A	I	R	A	I	R	A
Digestibility change:																		
Organic mater	-10.9	-17.5	+14.8	- 6.2	-11.7	- 2.3	- 7.3	- .1	- 5.8	- 5.0	+ 3.7	- 9.9	-14.6	+ 1.0	+11.7	-10.2	-10.2	+ 8.9
Starch	- 7.0	+ .1	+ 5.9	- 4.8	+ .2	-12.0	- 8.3	+10.7	- 3.2	- 5.0	+ 7.5	-10.9	-12.6	+ 2.9	+11.2	- 8.7	- 6.8	+12.8
Nitrogen	- 7.5	-18.7	+ 8.9	- 3.5	- 6.2	- 7.7	-14.7	+15.8	- 6.6	- 5.4	- 1.9	- 3.5	-23.7	- 2.9	+30.5	- 8.4	- 6.2	- 1.2
ADF	+12.8	+75.6	- 3.7	-15.9	+22.7	+19.2	-27.8	+25.7	+19.4	+30.6	+86.8	-18.5	- 3.2	+21.5	+ 2.4	- 2.6	+ 5.4	- 1.1
NDF	+26.8	+32.6	-26.7	+ 7.2	+19.7	-23.6	-51.4	+19.0	+78.1	+57.4	+28.2	-35.3	-25.9	+ 1.3	+26.5	+ 9.6	+ 8.0	-20.0
Hemicellulose	+ 1.4	+11.1	-21.2	+20.6	+32.6	-51.8	-60.6	+12.0	+55.9	+ 2.0	+48.8	-44.9	-34.7	-11.9	+23.2	+ 9.6	+ 6.4	-34.8

[a] Roughage source abbreviations are identified in experimental procedure.

[b] I = Intake effect; R = Roughage effect.

[c] A = Associative effect. Percentage difference between observed and predicted values for high intake and high roughage level diets.

TABLE 18. INTAKE AND ROUGHAGE LEVEL EFFECTS ON FECAL PARAMETERS

	Intake level[a]		Roughage level (%)		
	1	2	10	50	SEM[b]
Fecal:					
Dry matter (%)	26.0	25.8	27.7[d]	24.1[c]	0.4
Organic[g] matter	84.9[c]	88.2[d]	88.5[d]	84.7[c]	0.5
Starch[g]	16.5[c]	23.5[d]	27.1[d]	12.8[c]	1.1
Nitrogen[g]	2.5	2.4	2.7[d]	2.2[c]	1.1
ADF[g]	29.1[d]	25.0[c]	17.6[c]	36.5[d]	9.7
NDF[g]	43.9[f]	41.1[e]	33.1[c]	51.1[d]	1.1
Hemicellulose[g]	14.3	15.5	15.1	14.6	1.0
pH	6.3[d]	6.1[c]	6.0[c]	6.4[d]	0.1

[a]Intake expressed as a percent of body weight.

[b]Standard error of the mean.

[cd]Means under intake or roughage level subheadings with different superscripts differ ($P < .01$).

[ef]Means under intake and roughage level subheadings with different superscripts differ ($P < .07$).

[g]Percentage of fecal dry matter.

TABLE 19. PARTIAL CORRELATION COEFFICIENT BETWEEN FECAL pH AND OTHER FECAL PARAMETERS

	Fecal				
	Ash	ADF	NDF	Starch	Chromium
Fecal pH	.35	.32	.29	.38	.64
	($P < .03$)	($P < .05$)	($P < .08$)	($P < .02$)	($P < .0001$)

TABLE 20. EFFECTS OF INTAKE AND ROUGHAGE LEVEL ON RUMEN PARAMETERS

	Intake[a]		Roughage level(%)		
	1	2	10	50	SEM[b]
Ruminal:					
pH[i]	6.4	6.2	6.1[e]	6.5[f]	.07
Ammonia (ng/dl)	12.1	11.0	10.6	12.5	0.8
Volatile fatty acid (moles/100 moles)					
Acetate	65.0[f]	61.9[e]	60.3[c]	66.6[d]	0.8
Propionate	18.5	21.1	23.0[d]	16.6[c]	0.8
Butyrate	11.5	11.7	10.9[g]	12.3[h]	0.4
Isobutyrate	0.8	0.7	0.8	0.7	0.1
Valerate	1.5	1.8	1.8[d]	1.5[c]	0.2
Isovalerate	2.4	2.3	2.8[d]	1.9[c]	0.2
Caproate	0.2[e]	0.5[f]	0.3	0.4	0.1
Total VFA (mmoles/ml)	78.4[h]	86.8[g]	83.7[c]	81.5[d]	3.2
C_2/C_3	3.7	3.4	3.0	4.2	0.1

[a] Intake expressed as a percent of body weight.
[b] Standard error of the mean.
[cd] Means in a row under a specific heading with different superscripts differ ($P < .01$).
[ef] Means in a row under a specific heading with different superscripts differ ($P < .05$).
[gh] Means in a row under a specific heading with different superscripts differ ($P < .10$).
[i] Rumen pH values for period 2 were omitted. 36 observations/mean.

TABLE 21. EFFECTS OF INTAKE AND ROUGHAGE LEVEL ON BLOOD PARAMETERS

	Intake level[a]		Roughage level (%)		
	1	2	10	50	SEM[b]
Blood:					
Glucose(mg/100ml)	71.96	74.40	73.52	72.80	2.14
Urea-N(mg/100ml)	5.58	5.15	5.26[c]	5.73[d]	0.2
Insulin (ng/ml)	0.59	0.69	0.68	0.60	0.05

[a]Intake expressed in percent of body weight.

[b]Standard error of the mean.

[c]Means under a subheading in a row with different superscripts differ ($P < .10$).

TABLE 22. COMPARISON OF CHROMIC OXIDE AND PEPSIN INSOLUBLE NITROGEN AS INDIGESTIBLE MARKERS

	Roughage source[a]						
Digestibility (%):	CSH	PH	AH	SS	GCS	FCS	SEM[b]
Organic matter							
C	73.2^{cd}	74.4^{d}	66.8^{c}	71.0^{cd}	76.0^{d}	75.6^{d}	1.7
P	76.2^{de}	79.3^{c}	69.7^{c}	71.9^{cd}	78.3^{e}	74.7^{cde}	1.6
Starch							
C	95.6^{d}	88.9^{cd}	84.8^{c}	82.6^{c}	87.3^{c}	88.1^{c}	1.8
P	96.4^{e}	90.8^{de}	86.4^{cd}	83.8^{c}	88.7^{cd}	88.7^{cd}	1.8
Nitrogen							
C	59.9_{f}	63.9_{h}	59.8_{f}	64.5_{fg}	67.1_{gh}	69.3_{fgh}	2.4
P	64.1^{f}	71.0^{h}	64.2^{f}	65.0^{fg}	70.5^{gh}	67.4^{fgh}	2.0
ADF							
C	34.2^{c}	48.0^{de}	35.9^{c}	39.0^{cd}	50.8^{e}	48.8^{de}	2.9
P	45.4^{ed}	57.9^{e}	42.2^{c}	38.3^{c}	53.9^{de}	42.5^{c}	3.0

[a]Roughage source abbreviations are identified in experimental procedures.

[b]Standard error of the mean.

[cde]Means in a row with different superscripts differ ($P < .01$)

[fgh]Means in a row with different superscripts differ ($P < .05$).

CHAPTER V

EFFECT OF LIMESTONE AND ROUGHAGE LEVEL ON DIGESTIBILITY BY STEERS

S. R. Rust and F. N. Owens

Summary

Twenty-two Hereford steers (242 kg) were fed two levels of roughage (10 and 50 percent) with two limestone levels (.7 and 2.0 percent) within each roughage level. Organic matter, nitrogen, ADF, NDF and hemicellulose digestibilities increased with added limestone. Ruminal pH increased with the higher limestone level which may have contributed to the increased fiber digestion. Starch digestion was not altered by level of limestone. Rumen ammonia ($P < .01$) and blood urea ($P < .05$) levels were increased with the 2 percent limestone diet. Feeding the 50 percent alfalfa diet resulted in lower organic matter digestion but increased ADF digestibility ($P < .01$) and slightly increased starch digestibility. Blood urea levels were increased with the higher roughage diet.

Introduction

Limestone is the most popular supplemental calcium source in cattle diets. Calcium requirements for growing cattle are 15-22 grams/day. However, this requirement supposedly could increase when

less soluble forms of limestone are used. Limestone varies in both the time required to neutralize a given amount of acid and the total amount of acid neutralized (Wheeler et al., 1981). Addition of limestone to a high concentrate diet shifted site of starch and organic matter digestion from the small intestine to the rumen (Zinn and Owens, 1980). A recent review (Owens and Zinn, 1983) indicated no consistent trend toward benefits in cattle performance. Additional limestone may increase rumen pH (Galyean, et al., 1981) which should increase fiber digestion (Slyter, 1981). Ruminal starch digestion may be increased as limestone is added to the diet (Zinn and Owens, 1980). Additionally high limestone levels may have a stabilizing effect on the rumen during diet adaptation (Owens and Zinn, 1983). Generally, studies which have reported an increase in cattle performance with added limestone also show increased feed intake (Zinn et al., 1982). The benefits of additional limestone may be due to several reasons such as a) neutralization of acid in the rumen or total tract, b) increased fiber or starch digestion in the rumen or intestines,c) increased rate of ruminal fermentation, or d) increased intake during periods of diet changes or metabolic problems.

To evaluate the effects of limestone on fiber and starch digestion, a study was designed with two roughage levels and two limestone levels. Digestibility and ruminal effects were monitored.

Experimental Procedure

Twenty-two Hereford steers (242 kg) were utilized in a split plot designed with two alfalfa levels (10 and 50 percent) as the main plot and limestone level (.7 and 2 percent) as the subplot treatment. A crossover design was used in the subplot with 21 day periods. Steers were fed twice per day (0800 and 1700) with orts recorded daily. The diets consisted of whole shelled corn, alfalfa and supplement (table 1). The pelleted supplements were balanced to provide adequate amounts of vitamins and minerals (table 2). Chromic oxide was added to the supplement as an indigestible marker. Limestone replaced corn in the supplement. Diets were restricted to 2.5 percent of body weight. Animals were housed in individual pens with concrete slatted floors.

Each 21 day period consisted of a sixteen days for adaptation followed by 5 days of fecal collection.Fecal grab samples were collected between 0600 and 0800. Fecal dry matter and pH were determined as soon as possible after collection. A portion of each sample was retained to composite. Rumen samples were collected via stomach tube the last day of each period. Blood samples were collected by jugular venipuncture on day 21.

Fecal composite samples were mixed and subsampled for laboratory analysis. Dry matter and ash concentrations were determined for feed and feces (AOAC, 1975). Total nitrogen determinations were conducted on non-dried feed and feces using macro-Kjeldahl procedure (AOAC, 1975). Starch content of feed and feces was determined by the procedures of Macrae and Armstrong (1968). Estimates of neutral detergent fiber (NDF), acid detergent fiber and hemicellulose were determined by the Van Soest procedures (Goering and Van Soest, 1970).

Samples were autoclaved and subjected to amyloglucosidase digestion prior to NDF determination to prevent gelling on the filter. Rumen and fecal pH values were monitored with a combination electrode. Ruminal ammonia levels were estimated by the Chaney-Marbach procedure (1962). Ruminal volatile fatty acid concentrations were determined by the procedure of Sharp (1977). Blood glucose levels were estimated with a glucose oxidase enzyme kit from Worthington Diagnostics[2]. Blood urea nitrogen levels were determined by urease digestion followed by ammonia analysis (Chaney and Marbach, 1962).

Statistical analysis was conducted using the General Linear Models subroutine of the SAS system (Barr and Goodnight, 1981). Roughage level effects were tested using the animal within roughage level mean square as the error term. Treatment differences were detected using the protected Least Significant Difference (Steel and Torrie, 1960) procedure. Partial correlation coefficients also were determined with the SAS programs.

Results and Discussion

Interactions between roughage level and limestone level were not significant ($P < .10$) in this study. Therefore, the main effects of roughage level and limestone level will be presented and discussed. Feeding the 2 percent limestone level increased organic matter, nitrogen, ADF

[1] Sigma Chemical, St. Louis, MO

[2] Worthington Diagnostics, San Francisco, CA.

and NDF digestibility ($P < .01$; table 3). Similar effects on digestibility were reported by Varner and Woods (1972b) with limestone addition to a 30 percent corn cob-rolled corn diet. In this study, increased starch, NDF and protein digestibilities accounted for 17, 62 and 14 percent respectively of the increased OMD with added limestone. Hemicellulose digestion was increased at the 2 percent limestone level ($P < .05$). Total tract starch digestion was not significantly influenced by limestone level in this study. Limestone addition to a high concentrate diet may shift site of starch disappearance to the rumen (Zinn and Owens, 1980) These authors further suggested that increased ruminal fermentation may limit feed consumption. Several researchers have reported decreased feed intake and performance with high levels of dietary calcium (Varner and Woods, 1972a; Dew and Thomas, 1982; Zinn et al., 1982). A paradox seems to be developing in that high levels of calcium stimulate OMD with restricted diets but may reduce intake and performance of cattle allowed feed free choice. The reason for this discrepancy is uncertain. Additional limestone increased fiber digestion with only a small, nonsignificant effect on starch digestion.

Fecal organic matter content was lower ($P < .01$) with the high limestone diet (table 4), probably due to an increase amount of limestone in feces diluting the carbonaceous material. Elevated limestone levels increased fecal pH ($P < .01$). Fecal dry matter , starch, nitrogen, ADF, NDF and hemicellulose were similar ($P < .10$) with both limestone levels.

Ruminal ammonia values tended to increase ($P < .10$) with the 2 percent limestone diet (table 5). This is most likely the result of

increased ruminal protein digestion. The acetate to propionate ratio was significantly reduced ($P < .05$) with added limestone. No significant differences were detected for any of the volatile fatty acid proportions. In contrast, Varner and Woods (1972b) indicated that acetate proportions increased and propionate decreased with added limestone. However, Nicholson et al. (1963) found a mixed buffer containing 33 percent limestone reduced acetate proportions. Varner and Woods (1972b) also indicated that added calcium reduced lactate levels and protozoal numbers.

Blood urea levels were significantly reduced ($P < .05$) with the 2 percent limestone diet (table 6). This appears to contradict the increase in protein digestibility observed with added limestone. Blood glucose levels were not altered by level of limestone in the diet.

Organic matter digestibility decreased ($P < .01$) as alfalfa replaced corn in the diet (table 7) while acid detergent fiber digestibility significantly increased ($P < .01$). These results agree with those reported by Cole (1975). Starch, nitrogen, NDF and hemicellulose digestibilities were similar at both roughage levels.

Effects of roughage level on fecal parameters are shown in table 8. Dry matter , organic matter, starch and nitrogen content of feces was reduced ($P < .01$) with the 50 percent alfalfa diet. These components were diluted by indigestible fiber from the added alfalfa. Fecal NDF ($P < .01$), ADF ($P < .01$) and hemicellulose ($P < .05$) contents increased as alfalfa was added to the diet. Fecal pH was greater with the high alfalfa diet and was correlated with fecal nitrogen ($r = .54$; $P < .02$), fecal starch ($r = -.56$; $P < .02$) and fecal ash ($r = .42$; $P < .08$). In this study fecal acidity appears to have originated from

postruminal starch fermentation as suggested by the partial correlation coefficients between fecal pH and fecal starch and nitrogen. More fecal starch would suggest more fermentable substrate was presented to the large intestine which would allow more fermentation and acid production thereby lowering fecal pH.

Ruminal pH was increased ($P < .01$) with added alfalfa (table 9). Acetate proportion and the acetate to propionate ratios increased as roughage was added to the diet ($P < .01$), while propionate and valerate ($P < .01$), isovalerate ($P < .10$) and caproate levels ($P < .05$) all decreased. Butyrate and isobutyrate proportions and total VFA levels were similar for the 10 and 50 percent alfalfa diets.

Blood plasma urea nitrogen was increased ($P < .01$) with the higher alfalfa diet (table 10). The high alfalfa diet contained more crude protein which may account for the greater blood plasma urea levels. Plasma glucose levels were similar for steers fed both diets.

High levels of calcium in this study altered ruminal pH. This change probably increased hemicellulose, cellulose and organic matter digestibilities. Limestone addition may have suppressed some of the inhibitory effects of added starch on cellulose digestion discussed by Varner and Woods (1972b).These authors postulated that suppression involves rumen metabolites. Nitrogen and hemicellulose digestion also were increased by added limestone and it seems possible that the ruminal pH increase may be responsible. The ruminal effect of limestone may include direct or indirect effects on pH, lactate, VFA concentrations, available calcium or nitrogen, rate of passage,

rumination, osmolarity or prevention of acidosis and bloat. It seems unlikely that any single parameter is responsible for the various benefits or detriments of supplemental limestone which has been reported. Responses to limestone addition may differ with various ruminal or postruminal as well as dietary factors, plus the feeding regime and environment.

TABLE 1. RATION INGREDIENTS AND COMPOSITION

Ingredient	IFN[a]	Roughage level (% of DM) 10	50
Whole shelled corn	4-02-931	82	42
Alfalfa	1-00-059	10	50
Supplement		8	8

	Composition (% of dry matter)			
Crude protein		12.4	13.6	
Starch		58.5	31.6	
ADF		6.7	24.6	
Calcium	-	+	-	+
determined	.40	.70	.76	1.06
calculated	.43	.88	.92	1.37

[a]International feed number

TABLE 2. SUPPLEMENT COMPOSITION [a]

Ingredient	IFN [b]	Limestone level (% of DM) 0.7	2.0
Dry rolled corn	4-02-931	67.7	51.0
Urea		6.0	6.0
Potassium chloride		10.3	10.3
Limestone	6-02-632	9.1	25.8
Dicalcium phosphate	6-01-080	2.2	2.2
Salt		2.5	2.5
Chromic oxide		2.0	2.0
Trace mineral		.3	.3
Vitamin A		+	+

[a] Percent of dry matter

[b] International feed number

TABLE 3. INFLUENCE OF LIMESTONE ON DIET DIGESTIBILITY

	Limestone level (%)		
	0.7	2.0	SEM[a]
Digestibility (%):			
Organic matter	68.8[b]	74.0[c]	0.60
Starch	90.3	92.3	1.12
Nitrogen	62.1[b]	67.6[c]	0.85
ADF	27.9[b]	35.6[c]	1.85
NDF	35.0[b]	46.6[c]	2.80
Hemicellulose	41.8[d]	56.0[e]	4.96

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

[de]Means in a row with different superscripts differ ($P < .05$).

TABLE 4. INFLUENCE OF LIMESTONE ON FECAL PARAMETERS

	Limestone level (%)		
	0.7	2.0	SEM[a]
Fecal:			
Dry matter (%)	21.7	22.5	0.41
Organic matter[b]	91.1[d]	88.4[c]	0.16
Starch[b]	13.8	12.6	1.58
Nitrogen[b]	2.5	2.5	0.06
ADF[b]	33.2	33.6	0.67
NDF[b]	54.9	52.2	1.30
Hemicellulose[b]	21.7	18.2	1.82
pH	6.12[c]	6.37[d]	0.04

[a]Standard error of the mean.

[b]Percentage of fecal dry matter.

[cd]Means in a row with different superscripts differ ($P < .01$).

TABLE 5. EFFECTS OF LIMESTONE ON RUMINAL PARAMETERS

	Limestone (%)		
	0.7	2.0	SEM[a]
Ruminal:			
pH	6.6	6.6	0.05
Ammonia (ng/dl)	2.3[d]	3.3[e]	0.39
Volatile fatty acid (moles/ 100 moles)			
Acetate	60.3	58.8	0.80
Propionate	23.2	25.1	1.11
Butyrate	10.1	10.2	0.47
Isobutyrate	1.1	1.0	0.10
Valerate	2.2	2.2	0.14
Isovalerate	2.4	2.3	0.13
Caproate	0.7	0.5	0.11
Total VFA (mmoles/ml)	85.1	86.3	3.4
C_2/C_3	3.1[c]	2.6[b]	0.15

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .05$).

[de]Means in a row with different superscripts differ ($P < .10$).

TABLE 6. EFFECTS OF LIMESTONE ADDITION ON BLOOD GLUCOSE AND UREA VALUES

	Limestone level (%)		
	0.7	2.0	SEM[a]
Blood:			
Glucose (mg/100 ml)	69.6	67.3	5.16
Urea-N (mg/100 ml)	11.4[c]	9.8[b]	0.38

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .05$).

TABLE 7. INFLUENCE OF ROUGHAGE LEVEL ON DIGESTIBILITY

	Roughage Level (%)		
	10	50	SEM[a]
Digestibility (%):			
Organic matter	74.9[c]	68.4[b]	1.42
Starch	90.1	92.3	1.48
Nitrogen	63.9	65.7	1.22
NDF	37.7	43.4	2.92
ADF	19.7[b]	41.9[c]	2.43
Hemicellulose	52.0	46.3	3.37

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

TABLE 8. INFLUENCE OF ROUGHAGE LEVEL ON FECAL PARAMETERS

	Roughage level (%)		
	10	50	SEM[a]
Fecal:			
Dry matter (%)	24.4[d]	20.2[c]	.46
Organic matter[b]	90.8[d]	88.9[c]	.26
Starch[b]	20.5[d]	7.1[c]	1.56
Nitrogen[b]	2.8[d]	2.2[c]	.06
NDF[b]	40.1[c]	64.3[d]	1.07
ADF[b]	21.8[c]	43.0[d]	.65
Hemicellulose[b]	18.5[e]	21.2[f]	.79
pH	5.9[c]	6.6[d]	.06

[a] Standard error of the mean.

[b] Percent of fecal dry matter.

[cd] Means in a row with different superscripts differ ($P < .01$).

[ef] Means in a row with different superscripts differ ($P < .05$).

TABLE 9. EFFECTS OF ROUGHAGE LEVEL ON RUMINAL PARAMETERS

	Roughage level (%)		
	10	50	SEM[a]
Ruminal:			
pH	6.3[b]	6.8[c]	.10
Ammonia (ng/dl)	3.0	2.7	.36
Volatile fatty acid (moles/100 moles)			
Acetate	51.1[b]	66.6[c]	1.19
Propionate	30.7[c]	18.6[b]	1.58
Butyrate	10.5	9.8	0.63
Isobutyrate	1.0	1.0	0.11
Valerate	3.1[c]	1.4[b]	0.29
Isovalerate	2.7[g]	2.0[f]	0.25
Caproate	0.9[e]	0.4[d]	0.12
Total VFA (mmoles/ml)	89.8	82.2	4.11
C_2/C_3	1.9[b]	3.7[c]	0.17

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

[de]Means in a row with different superscripts differ ($P < .10$).

TABLE 10. EFFECTS OF ROUGHAGE LEVEL ON BLOOD PARAMETERS

	Roughage level (%)		
	10	50	SEM[a]
Blood:			
Glucose (mg/100 ml)	66.2	70.3	4.48
Urea-N (mg/100 ml)	7.3[b]	13.4[c]	0.55

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

CHAPTER VI

EFFECTS OF PROTEIN LEVEL, PROTEIN SOURCE AND ROUGHAGE LEVEL ON DIGESTIBILITY OF WHOLE SHELLED CORN DIETS

S. R. Rust and F. N. Owens

Summary

To evaluate the effects of protein level and source on digestibility, fifteen Hereford steers (345 kg) were fed one of three roughage levels (10, 50 or 70 percent), with protein at 9 percent of diet dry matter (basal diet) or 11.8 percent supplied by either urea or corn gluten meal. Dry matter intake was limited to 2 percent of body weight. Organic matter and starch digestion were not influenced by protein level or source in this study. Ruminal ammonia, blood urea and nitrogen digestibility were increased by addition of either nitrogen source ($P < .01$). Neutral detergent fiber digestibility was lower ($P < .05$) when corn gluten meal was added.

Organic matter ($P < .01$), nitrogen ($P < .05$) and hemicellulose ($P < .05$) digestibilities decreased as roughage was added to the diet, but acid detergent fiber digestibility increased as roughage was added ($P < .01$). Ruminal pH, acetate proportion and acetate to propionate ratio

were increased with the higher roughage diets but valerate and isovalerate proportions decreased ($P < .05$).

Corn gluten meal addition to the low roughage diet decreased NDF ($P < .01$) and hemicellulose ($P < .06$) digestibility. Data suggest the form of nitrogen available to the rumen microorganisms from corn gluten meal may limit fiber digestion.

Introduction

Nitrogen requirements for feedlot cattle can be subdivided into requirements for microbial growth and animal growth. Ruminal microorganisms generally do not respond to ammonia concentrations above 5 mg NH_3/100 ml of rumen fluid (Satter and Slyter, 1974). Certain species of rumen microorganisms utilize amino acids and peptides (Allison, 1982); but the specific requirements have not been determined. Although ruminal protozoa engulf entire protein particles, protozoa do not appear to efficiently utilize this protein. Large intestinal and cecal microorganisms supposedly have nitrogen needs similar to ruminal organisms. Nitrogen required by the animal is absorbed from the small intestine primarily as amino acids. The postruminal nonammonia nitrogen supply is derived from microbes leaving the rumen and dietary protein which escapes ruminal digestion.Several models for predicting protein requirements estimate the degree of ruminal escape of dietary protein. Bypass values for protein sources depend on intake and energy level of the diet (Owens and Zinn, 1982). Limited evidence supports the concept that performance will be

increased when bypass of dietary protein is increased Species showing response include lactating cows, wool-growing sheep, young rapidly growing sheep and calves limit fed with high roughage diets. Formaldehyde treatment of protein increases its ruminal escape (Miller, 1972; Faichney and White, 1977). Treatment of soybean meal with formaldehyde increased daily gains by 7 percent with lambs fed an 85 percent concentrate diet (Nimrick, 1972). Conversely, addition of protein with a low bypass value to a low quality forage diet may increase digestibility (Oldham, 1980). Feeding studies from Oklahoma (Martin et al., 1980; Zinn et al., 1980) indicate soybean meal provides better performance with high moisture corn while urea yields better performance with whole shelled or steamed flaked corn. Performance responses of cattle have been similar with supplementation of either soybean meal or cottonseed meal.

This study was designed to compare effects of a high bypass protein (corn gluten meal) or urea, on digestibility of a whole shelled corn diet with three levels of roughage.

Experimental

Fifteen Hereford steers (345 kg) were randomly assigned to one of three roughage levels (10, 50 or 70 percent). Steers were maintained on a roughage level for the total trial and fed one of three protein treatments during three 21-day periods. Protein treatments included no supplemental protein or control (9.0 percent CP), addition of 4.68 percent corn gluten meal or 1.0 percent urea.

The composition of diets is shown in table 1. Alfalfa and prairie hays were chopped and mixed in a ratio of 2:1 so as to provide a crude protein content similar to the protein content of whole shelled corn such that addition of roughage would not alter the dietary crude protein content. The pelleted supplement was providing diets with a minimum of .55 percent calcium, .35 percent phosphorus and .7 percent potassium (table 2). The protein content of each of the nine diets is shown in table 2. Chromic oxide was added to the supplement to serve as an indigestible marker for digestibility calculations.

Steers were housed in individual pens with concrete slatted floors. Diets were offered twice daily with orts recorded daily. Intake was limited to 2 percent of body weight. Twenty-one day periods were divided into 16 days for adaptation to the diet with fecal grab samples collected for the last five days. Fecal samples were collected between 0600 and 0800 each day. Immediately after collection, pH was determined. Two hundred grams of wet feces were saved daily and frozen for later analysis. Ruminal fluid samples were obtained via stomach tube the last day of each period. Ruminal fluid samples were monitored for pH and frozen. Blood samples were collected from the jugular vein the last day of each period, centrifuged to obtain plasma, and plasma frozen for later analysis.Feed and fecal samples were analyzed for dry matter and ash (AOAC, 1975). Nitrogen was determined by macro-Kjeldahl procedure (AOAC, 1975) on the undried feed and fecal samples. Starch content was determined by the procedures of Macrae and Armstrong (1968). Fiber content was estimated using the Van Soest procedures (USDA, 1970) for the NDF and ADF. To prevent filtration problems

during NDF analysis with samples high in starch, samples were autoclaved for 90 min and subjected to amyloglucosidase[1] digestion for 24 hours prior to NDF determination. The supernatant fluid was used for starch analysis and the filtrate was used for NDF estimation. Rumen samples were analyzed for volatile fatty acid content by the gas chromatographic procedures. Ruminal ammonia concentrations were estimated by the Chaney- Marback (1962) procedure. Rumen and fecal pH values were determined with a Digi-sense-hand-held pH meter and a combination electrode. Plasma urea-N values were estimated by incubating with a urease solution followed by the Chaney-Marbach (1962) procedure for ammonia analysis. Blood glucose values were determined with a Statzyme kit[2].

Statistical analysis was conducted using the General Linear Models subroutine of the SAS system (Barr and Goodnight, 1981) separating roughage level, animal within roughage level, period and protein level by roughage level effects. Treatment means were compared using the Least Squares Difference procedure (Steel and Torrie, 1960). The effect of roughage level was tested using the pen within roughage level mean square.

Results and Discussion

Main effects of protein level and source and fiber level will be

[1] Sigma Chemical, St. Louis, Mo.

[2] Worthington Diagnostics, San Francisco, CA 94080

discussed first followed by interactions of this factor. Elevating protein content of the diet from 9.0 to 11.8 percent did not increase digestibility of organic matter or starch (table 3). These results indicate that 9 percent crude protein was sufficient to sustain organic matter digestibility with this diet. Results do not mean that the protein requirement for a 345 kg growing calf is 9 percent. Maximum growth was not a response criteria and intake was limited to 2 percent of body weight. Orskov (1982) indicated that intake responses to added protein are greater than digestibility responses with growing lambs. Nitrogen digestibility was increased ($P < .01$) when either corn gluten meal or urea was added to the diet. Similar nitrogen digestibility responses to added protein have been reported by other researchers (Preston et al., 1965; Kay et al., 1968; Orskov and Fraser, 1969; Rust, 1978). Dilution of metabolic fecal nitrogen may explain the increased protein digestibility at higher protein intakes.

Nitrogen digestibility was similar for the corn gluten meal and urea supplemented diets. Digestibility of NDF was significantly reduced ($P < .05$) with the corn gluten meal diet as compared to the control or urea diets. Although ADF digestibility was not significantly lower with the corn gluten supplement, decreased ADF digestibility accounted for all the depression in NDF digestion with corn gluten meal. Corn gluten meal is relatively insoluble (Broderick, 1980) which indicates that some of this protein is associated with the NDF fraction. Another possible explanation for the reduced NDF digestibility may involve a reduced ruminal disappearance as available nitrogen may have been lacking. The latter explanation seems more

feasible as NDF from supplement contributes less than 5 percent of the total NDF content. Hemicellulose digestibility tended to increase with the urea supplementation.

Composition of feces was largely unchanged with protein supplementation (table 4). NDF percentage of fecal dry matter was greater for steers fed the corn gluten meal supplemented diet than steers fed the urea or basal diet ($P < .05$). Hemicellulose content of feces was greater ($P < .06$) from steers fed the corn gluten meal than steers fed the urea diet.

Ruminal ammonia levels were increased ($P < .01$) by the addition of protein to the diet (table 5). If the corn gluten meal were less degraded to ammonia, the concentration of ammonia in ruminal fluid should be lower with the corn gluten meal than the urea diet. Ammonia levels may have been similar with the two protein sources for three reasons. First, the corn gluten may have been degraded in the rumen. Secondly, rumen samples were collected 4 hours after feeding. This may be after ammonia concentrations peak with urea feeding (Mizwicki et al., 1980). At four hours, the ammonia release curve for urea diets is declining while with more slowly degraded protein, ammonia concentration would be increasing. Thirdly, ammonia absorption across the rumen wall and urea recycling may be sufficient to mask ammonia release differences. Since both were higher than the negative control, this explanation is tenuous.

Ruminal pH and VFA concentrations did not differ significantly among treatments. Addition of protein to the basal diet tended to increase blood glucose concentrations (table 6). This may result from

increased gluconeogenesis from amino acids absorbed from the small intestine. Blood urea levels were increased as protein was added to the diet ($P < .01$) but still below the value (10 mg/100 ml) suggested by Preston et al. (1965) as an index of protein adequacy. Differences between the corn gluten meal and urea supplemented diets proved nonsignificant.

Organic matter digestibility (OMD) decreased ($P < .01$) as roughage was added to the diet (table 7). Digestibility of organic matter with the 10 percent roughage level is lower than anticipated. The prediction for OMD of the 10 percent roughage diet, based on values for the 50 to 70 percent roughage diets is 78 percent. The predicted value is more in line with results from similar diets in other trials. The reason for low OMD with 10 percent roughage is uncertain.Nitrogen digestibility decreased as roughage was added to the diet ($P < .05$). With the higher roughage diets, more nitrogen may be bound to the fiber rendering it indigestible or metabolic fecal nitrogen may have increased with fiber addition to the diet. Digestibility of the ADF fraction was significantly greater for the higher roughage diets ($P < .01$) while hemicellulose digestibility decreased as roughage was added to the diet ($P < .05$).These results contradict previously reported results reviewed by Van Soest (1982). He concluded that cellulose and hemicellulose digestion were closely related and were influenced similarly by dietary treatments. With the 70 percent roughage diet, 66 percent of the cellulose and 80 percent of the hemicellulose were provided by the roughage. Digestion of starch and NDF were unaltered by roughage addition.

Dry matter, organic matter and starch content of feces decreased ($P < .01$) as roughage was added to the diet (table 8). Fecal ADF and NDF fractions increased at the higher roughage levels ($P < .01$). Hemicellulose content of feces also increased with the higher roughage diet ($P < .05$), while nitrogen content of feces decreased ($P < .05$). Fecal pH values were increased as roughage was added to the diet ($P < .01$). This may reflect the buffering capacity of fibrous portions of the feces or reduced productions of acid in the cecum and colon with the higher roughage diets.

Ruminal pH and acetate proportions increased ($P < .01$) as roughage was added to the diet (table 9). Similar results have been reported in a review by Van Soest (1982). Acetate to propionate ratio also was higher for the higher roughage diets ($P < .05$). Isovalerate and valerate levels were lower for the 50 and 70 percent roughage diets ($P < .05$). Other VFA levels did not differ significantly with roughage level. Rumen ammonia levels were not significantly changed when roughage was added to the diet. Blood glucose and urea-nitrogen levels were similar at the 10, 50 and 70 percent roughage diets (table 10).

Protein treatment by roughage level interactions are presented in table 11. Significant interactions were seen for NDF and hemicellulose digestibility ($P < .01$) and rumen ammonia levels ($P < .06$). Only with the lowest fiber level was NDF digestibility markedly reduced with the corn gluten meal supplementation. Ruminal ammonia concentrations also were greatest with this particular combination. One would have expected a low degradation rate for corn gluten meal and thus a low ruminal ammonia level. A low ruminal ammonia could reduce fiber

digestion El Shazly, 1961), but in this study, the lowest NDF digestion occurred with the diet which had the highest rumen ammonia level. This discrepancy might be the result of a limited supply of recycled nitrogen over the feeding period or some type of inhibition of fiber digestion in the rumen or postruminally with corn gluten meal addition to the 10 percent roughage diet. Hemicellulose digestion was significantly reduced ($P < .06$) with the low roughage, corn gluten meal supplemented diet. One explanation for this effect relates to ruminal protozoa. Protozoa are suggested to be the primary digesters of hemicellulose in the rumen (Van Soest, 1982). The form of nitrogen available in the rumen (amino acids, peptides or soluble protein) with protein coming primarily from corn grain and corn gluten meal may have limited ciliate protozoal activity and limited hemicellulose digestion.

Partial correlation coefficients for digestibility estimates and ruminal parameters are presented in table 8 of the Appendix.

TABLE 1. DIET INGREDIENTS AND COMPOSITION

Ingredients	IFN[a]	Roughage level (% of DM) 10	50	70
Alfalfa	1-00-059	3.3	16.7	23.3
Prairie hay	1-07-956	6.7	33.3	46.7
Whole shelled corn	4-02-931	82	42	22
Supplement		8.0	8.0	8.0
Composition (% of DM)[b]				
Dry matter		88.60	89.54	90.04
Starch		65.76	36.97	21.96
Nitrogen		1.78	1.78	1.78
ADF		7.18	24.90	33.69
NDF		18.33	39.26	49.62
Hemicellulose		11.15	14.36	15.93
Ash		3.86	4.83	6.25

[a]International feed number.

[b]Each diet formulated to contain .55% calcium, .35% phosphorus and .7% potassium.

TABLE 2. SUPPLEMENT INGREDIENTS[a]

Item	IFN[c]	Roughage level (%) 10 C	10 G	10 U	50 C	50 G	50 U	70 C	70 G	70 U
Protein treatment[b]										
Ground corn	4-02-931	66.4	8.4	53.9	79.5	21.4	67.0	80.4	23.1	67.9
Corn gluten meal	5-02-900	---	58.5	----	----	58.5	----	----	58.5	----
Urea		---	----	12.5	----	----	12.5	----	----	12.5
Dicalcium phosphate	6-01-080	3.3	2.1	3.3	9.4	8.3	9.4	12.0	10.9	12.0
Calcium carbonate	6-02-632	15.5	16.1	15.5	1.9	2.6	1.9	----	----	----
Potassium chloride		7.3	7.3	7.3	1.6	1.6	1.6	----	----	----
Crude protein content of total diet		9.1	11.5	11.8	8.6	11.0	11.3	9.0	11.4	11.7

[a]Other ingredients include: Salt (3.1%); Chromic oxide (2.5%); Sodium sulfate (1.6%); trace mineral mix (0.3%); Vitamin A (1000 IU/animal day); Vitamin D (275 IU/animal/day. Used 3/16" pellet.

[b]Protein treatment: C = control; G = corn gluten meal; U = urea.

[c]International feed number.

TABLE 3. EFFECT OF PROTEIN TREATMENT ON DIGESTIBILITY

	Treatment			
	Control	Corn Gluten[a]	Urea[a]	SEM[b]
Digestibility (%):				
Organic matter	65.8	65.8	64.9	.69
Starch	87.8	88.4	88.7	.74
Nitrogen	43.8[c]	57.2[d]	54.7[d]	5.42
ADF	45.7	37.9	38.7	2.21
NDF	47.6[f]	41.9[e]	45.6[ef]	1.55
Hemicellulose	44.4	44.3	49.3	2.42

[a]Represents type of protein source used in supplement.

[b]Standard error of the mean.

[cd]Means in a row with different superscripts differ ($P < .01$).

[ef]Means in a row with different superscripts differ ($P < .05$).

TABLE 4. EFFECT OF PROTEIN TREATMENT ON FECAL PARAMETERS

	Treatment			
	Control	Corn Gluten Meal[a]	Urea[a]	SEM[b]
Fecal parameter:				
Dry matter (%)	22.9	23.7	23.0	.46
Organic matter[c]	88.7	89.0	89.1	.37
Starch[c]	14.7	14.2	15.4	1.32
Nitrogen[c]	2.3	2.3	2.4	.89
ADF[c]	30.5	33.8	33.1	.85
NDF[c]	51.6[d]	55.8[e]	51.8[d]	1.07
Hemicellulose[c]	21.1[fg]	22.0[g]	18.8[f]	1.01
pH	6.3	6.4	6.3	.03

[a]Represents type of protein source used in supplement.

[b]Standard error of the mean.

[c]Percent of fecal dry matter.

[de]Means in a row with different superscripts differ ($P < .05$).

[fg]Means in a row with different superscripts differ ($P < .06$).

TABLE 5. EFFECT OF PROTEIN TREATMENT ON RUMINAL PARAMETERS

	Treatment			
	Control	Corn gluten meal[a]	Urea[a]	SEM[b]
Ruminal:				
pH	6.6	6.6	6.7	.06
Ammonia (ng/dl)	2.20[c]	5.07[d]	4.77[d]	.58
Volatile fatty acid		(moles/100moles)		
Acetate	69.3	67.7	68.0	.69
Propionate	19.3	20.1	20.3	.74
Butyrate	8.3	9.1	8.9	.55
Isobutyrate	1.3	1.7	1.3	.16
Valerate	0.2	0.2	0.1	.12
Isovalerate	1.4	1.2	1.4	.27
Caproate	0.1	0	0	.05
C_2/C_3	3.7	3.5	3.5	.15

[a]Represents protein source used in the supplement.

[b]Standard error of the mean.

[cd]Means in a row with different superscripts differ ($P < .01$).

TABLE 6. EFFECT OF PROTEIN TREATMENT ON BLOOD PARAMETERS

	Treatment			
	Control	Corn gluten meal[a]	Urea[a]	SEM[b]
Blood (mg/100 mls):				
Glucose	42.4	53.2	50.9	4.56
Urea - N	3.8[c]	6.5[d]	7.3[d]	.41

[a]Represents protein source used in supplement.

[b]Standard error of the mean.

[cd]Means in a row with different superscripts differ ($P < .01$).

TABLE 7. EFFECT OF ROUGHAGE LEVEL ON DIGESTIBILITY

	Roughage level (% of DM)			
	10	50	70	SEM[a]
Digestibility (%):				
Organic Matter	71.7[c]	66.5[cb]	59.5[b]	1.94
Starch	86.9	86.8	90.8	1.80
Nitrogen	57.3[f]	52.3[ef]	47.2[e]	2.66
ADF	24.5[b]	50.6[c]	46.1[c]	3.82
NDF	43.9	47.4	44.0	2.73
Hemicellulose	57.7[f]	42.0[ef]	39.6[e]	3.91

[a]Standard error of the mean.

[bcd]Means in a row with different superscripts differ ($P < .01$).

[ef]Means in a row with different superscripts differ ($P < .05$).

TABLE 8. EFFECT OF ROUGHAGE LEVEL ON FECAL PARAMETERS

	Roughage level (% of DM)			
	10	50	70	SEM[a]
Fecal:				
Dry matter (%)	26.4[d]	22.0[c]	21.4[c]	.71
Organic matter[b]	91.4[d]	88.3[c]	87.5[c]	.59
Starch[b]	28.4[e]	13.2[d]	4.6[c]	1.62
Nitrogen[b]	2.6[g]	2.3[fg]	2.1[f]	.10
ADF[b]	18.9[c]	34.6[d]	42.0[e]	1.11
NDF[b]	35.3[c]	57.7[d]	64.1[d]	1.88
Hemicellulose[b]	16.4[f]	23.1[g]	22.1[g]	1.57
pH	5.8[c]	6.3[d]	6.8[c]	.06

[a]Standard error of the mean.

[b]Percentage of fecal dry matter.

[cde]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .05$).

TABLE 9. EFFECT OF ROUGHAGE LEVEL ON RUMINAL PARAMETERS

	Roughage level (% of DM)			
	10	50	70	SEM[a]
Ruminal:				
pH	6.31[b]	6.74[c]	6.74[c]	.07
Ammonia (ng/dl)	4.7	3.8	3.6	1.81
Volatile fatty acid (moles/100 moles)				
Acetate	64.6[b]	69.4[c]	70.4[c]	.86
Propionate	20.8	19.3	19.6	.76
Butyrate	10.0	8.8	7.8	.77
Isobutyrate	1.5	1.5	1.3	.20
Valerate	0.6[e]	0[d]	0[d]	.14
Isovalerate	2.4[c]	0.9[b]	0.8[b]	.22
Caproate	0.1	0	0	.05
C_2/C_3				

[a]Standard error of the mean.

[bc]Means in a row with different superscripts differ ($P < .01$).

[de]Means in a row with different superscripts differ ($P < .05$).

TABLE 10. EFFECT OF ROUGHAGE LEVEL ON BLOOD PARAMETERS.

	Roughage level (% of DM)			
	10	50	70	SEM[a]
Blood (mg/100 mls):				
Glucose	42.8	52.8	50.6	7.58
Urea - N	4.9	6.0	6.5	.64

[a]Standard error of the mean.

TABLE 11. EFFECT OF PROTEIN TREATMENT WITHIN A ROUGHAGE LEVEL

	Roughage level (% of DM)									
	10			50			70			
Protein Treatment[a]	C	G	U	C	G	U	C	G	U	SEM[b]
Digestibility (%):										
Organic Matter	71.1	71.3	72.7	67.3	66.0	66.3	60.0	61.0	57.4	1.47
Starch	86.9	87.4	86.4	87.1	85.5	87.8	89.3	91.6	91.3	1.54
Nitrogen	50.7	58.7	62.4	38.4	61.7	56.6	42.5	52.3	46.8	4.16
ADF	30.6	17.1	25.8	56.1	49.1	46.6	49.6	45.8	42.9	3.96
NDF	47.8^{d}	33.5^{c}	50.3^{d}	49.7^{d}	46.9^{d}	45.6^{d}	45.6^{d}	44.7^{d}	41.7^{cd}	2.78
Hemicellulose	58.8^{f}	47.5^{e}	66.7^{f}	38.8^{e}	43.2^{e}	43.9^{e}	37.1^{e}	42.5^{e}	39.2^{e}	4.34
Ruminal:										
pH	6.24	6.25	6.46	6.76	6.71	6.77	6.71	6.80	6.74	.11
Ammonia (ng/dl)	3.18^{efg}	7.56^{i}	3.38^{efgh}	2.14^{ef}	4.30^{gh}	4.89^{gh}	1.46^{e}	3.67^{efgh}	5.82^{hi}	1.04

[a] C - control; G - corn gluten meal; U - urea.

[b] Standard error of the mean.

[cd] Means in a row with different superscripts differ (P .01).

[efghi] Means in a row with different superscripts differ (P .06).

CHAPTER VII

EFFECTS OF INTAKE LEVEL AND ROUGHAGE SOURCE ON THE RATE OF PASSAGE AND SITE OF DIGESTION IN FINISHING SWINE

S. R. Rust, F. N. Owens, C. V. Maxwell and D. Griffin

Summary

To evaluate the influence intake level and addition of various roughage on rate of passage and site of digestion, seven Yorkshire barrows (82 kg) were fitted with duodenal and ileal T-cannulas.Treatments included a low intake level (2 percent of body weight), a high intake level (3 percent of body weight) or alfalfa hay, cottonseed hulls or corn silage replacing 30 percent of the diet at the high intake level. Increasing level of intake had little influence on digestibility of organic matter, starch, nitrogen or ADF and rate of passage. Averaged across roughage sources, roughage addition reduced organic matter and nitrogen digestibility ($P < .01$) and increased rate of passage through the GI tract ($P < .05$). The type of roughage had varying effects on digestion and rate of passage. Alfalfa addition tended to reduce total tract starch digestion ($P < .15$). Addition of alfalfa and corn silage to the diet shifted organic matter and starch digestion from the stomach to the small intestine whereas the cottonseed hull diet shifted organic matter digestion toward the

stomach with little effect on the site of starch digestion. This data suggests cottonseed hulls act as an nontypical source of roughage. The cottonseed hull and corn silage diets tended to slow passage through the small intestine ($P < .17$).

Introduction

Extent of digestion is dependent on rate of and time for digestion. These factors in turn are altered by level of intake, rate of passage and nutrient balance of the diet. Although the effects of nutrient balance, rate of digestion and rate of passage have been researched, the effects of different roughage sources on rate of passage and extent of digestion have received little attention. The physiochemical properties of fiber dictate what type of bacterial fermentation occurs (Bryant, 1974) while the physical properties of fiber determine the time spent in the gut (Heller, et al., 1980). Generally, dry matter digestion decreases as rate of passage through the gastrointestinal tract increases in ruminant animals, however, level of intake has little effect on digestion with nonruminants (Reid, et al., 1980). Similarly, Hungate (1966) suggests VFA production in the cecum and large intestine will increase as additional dietary roughage slows the rate of digesta passage. Digestibility of fibrous feed fractions is the chemical entity most likely to be influence by rate of passage. Large particles pass through the gastrointestinal tract much slower than smaller particles (Ruminant: Balch and Campling, 1965; Thompson and Lanning, 1972; Nonruminants: Swenson,

1977). However, a separation of digesta by size and density may occur in areas of storage and mixing such as the rumen, stomach or cecum. In addition, certain sphincter-like orifices may prevent passage of large particles.

This study was designed to evaluate the influence of level of feed intake and added roughage from various sources on rate of passage through various segments of the gastrointestinal tract and site of digestion in finishing pigs.

Experimental Procedure

Seven Yorkshire barrows (82 kg) were fitted with T-canulas in the duodenum and terminal ileum. The duodenal canula was placed ten centimeters posterior to the pyloric sphincter and ileal canula was positioned twenty centimeters anterior to the ileo-cecal junction. Surgical procedures were conducted by a resident veterinarian at Oklahoma State University. Canulas were made from tygon tubing molded and glued with cyclohexanone.

The five dietary treatments included 1) basal diet, 2) 30 percent alfalfa (AH), 3) 30 percent cottonseed hulls (CSH), 4) 30 percent corn silage (CS) fed at three percent of body weight and 5) basal diet fed at two percent of body weight. The basal diet fed at two percent of body weight provided an equal amount of grain intake as the 30 percent roughage diets. The cottonseed hulls and alfalfa were ground through a Wiley mill equipped with a two millimeter screen prior to feeding while corn silage was fed unground due to difficulties of grinding.

Pigs were fed at 0830 and 1630 every day with orts recorded daily. Water was added to all diets to reduce sorting and spillage. The basal diet was a pig grower diet (16 percent CP) formulated to provide adequate amino acids, vitamins and minerals for growing pigs (table 1). Chromic oxide was added to the diet as an indigestible marker for digestibility measurement. Pigs were fed each diet for ten days with fecal grab samples collected the final three days (table 2). On day nine, duodenal and ileal samples were collected. Immediately after collection, pH of the sample was measured and the sample was frozen. Between days ten and thirteen, rate of passage was estimated. Time required for digesta to traverse the total tract and cecum and large intestine were determined by placing ten grams of ferric oxide in the feed or five grams in the ileum and recording time of appearance of red color in the feces. Small intestinal transit time was measured by adding phenol red indicator to the duodenal canula and recording the time of first appearance of red digesta at the ileal cannula. To test the procedure, small pieces of plastic tubing (142 mm diameter; 2, 5 and ten mm lengths) were placed in the duodenal cannula simultaneously with phenol red. Eighty-five percent of the plastic tubing particles appeared at the ileal cannula simultaneously with the phenol red indicator. This observation indicated that there was little difference in transit time for liquids and solids in the small intestine. Hence, only the dye marker was used in later measurements.

During the trial, pigs were in metabolism stalls with grated flooring. Animals were washed daily and the room temperature was

maintained between 10 and 18 C. Midway through the trial, intakes (grams per day) were adjusted upward since the pigs had gained 40 kg.

Fecal, duodenal and ileal samples were analyzed for dry matter and ash (AOAC, 1975). Starch content of the samples were determined using the procedure of Macrae and Armstrong (1968). Acid detergent fiber was analyzed by the Van Soest procedure (USDA, 1970). Nitrogen determination on feed and feces was conducted by the macro-Kjeldahl procedure (AOAC, 1975).

Water holding capacity of several plant fibers materials were measured by submersing 20 grams of plant material in 250 ml of water for 24 hours. Water was removed and excess water expelled by hand pressure. The squeezed plant residue was dried at 65 C to calculate water holding capacity. Capacity was expressed as grams of water retained per gram of dry matter.

Statistical analysis was performed using the General Linear Models program of the SAS system (Barr and Goodnight, 1981). Differences in treatment means were detected with an LSD test (Steel and Torrie, 1960). The data were analyzed as a completely randomized design with the only variable in the model being treatment. Pigs which consumed less than 85 percent of feed offered were deleted from the analysis. Number of pigs per mean are shown in each data table. Three pigs were removed from the trial as two pigs died and one pig developed leg problems.

Results and Discussion

Increasing intake of of the basal feed from two to three percent of body weight did not alter digestibility of dry matter, organic matter, starch, nitrogen or ADF (table 3). This corroborates the results of DeGoey and Ewan (1975) who fed a corn-soybean meal diet at two, three, four and five percent of body weight to 20 kg pigs. McDonald et al. (1973) also found no effect of intake level on digestibility of high concentrate diets by pigs.

Fiber addition reduced ($P < .01$) the digestibility of dry matter, organic matter and nitrogen (table 3). Reduced protein digestion may be the result of a greater amount of the dietary protein being bound to indigestible cell walls or to an increased excretion of endogenous nitrogen. Total tract starch digestion tended to be lower for the alfalfa-supplemented diet ($P < .15$). Digestion of ADF was similar and low for all treatments. Calculation of forage digestion by the difference technique (Schneider and Flatt, 1975) indicates that only ten to 15 percent of the forage organic matter was digested with the alfalfa or corn silage supplemented diets while cottonseed hulls were indigestible.

The influence of intake level and roughage source on site of digestion of organic matter (OMD) is shown in table 4. Increasing intake from two to three percent of body weight tended to increase OMD in the stomach; however, this effect was not significant. Proportion of organic matter digested in the small intestine was similar for all treatments. The cottonseed hull supplemented diet tended to shift OMD to the stomach whereas the other roughage diets tended to reduce OM disappearance in the stomach. The values for proportion of OMD in the

stomach plus small intestine are similar to OMD values published by Keys and De Barthe (1974). The proportion of organic matter digested in the cecum and large intestine was slightly greater for the alfalfa and corn silage supplemented diets than the basal diet. However, cottonseed hull addition tended to reduce the percentage of organic matter digestion occurring post-ileally. Increased feed consumption did not appear to alter extent of cecal and large intestinal digestion.

Starch digestion with the alfalfa supplemented diet was restricted to the small intestine (table 5), while small amounts of starch disappeared from the stomach with the control and cottonseed hull diets. This contrasts with results of Keys and DeBarthe (1974) in which more than 50 percent of the starch disappeared before reaching the duodenum. Intake levels in this study were three percent of body weight versus one and one-half percent of body weight in their study. Addition of fiber or greater intake may reduce residence time in the stomach, thereby reducing OM disappearance in the stomach. Small intestinal starch digestibility was high for all diets. Pigs receiving the alfalfa and corn silage supplemented diets had greater starch disappearance in the small intestine than pigs fed the control or cottonseed hull supplemented diets. Increasing level of intake did shift a small amount of starch to the cecum and large intestine for digestion (2.1 versus 6.5 percent). Starch digestion in the cecum plus colon were similar for the basal, cottonseed hull and corn silage diets.

Elevated feed consumption tended to move food through the entire tract faster, but no significant differences were detected (table 6). Several researchers have indicated a tendency for faster propulsion of

digestion as intake levels increase (total tract [nonruminants] Castle and Castle, 1957; Seerley et al., 1962; Parker and Clawson, 1967; large intestine (ruminant): Grovum and Williams, 1973). Averaged across fiber sources, addition of fiber to the basal diet reduced the time required for the fed marker to appear in the feces ($P < .05$). Passage rate through the small intestine tended to be slower for the cottonseed hull and corn silage supplemented diets ($P < .17$) while passage rates were similar with the alfalfa and the control diet. Passage rate through the cecum and large intestine was greater for the roughage-supplemented diets as compared to the basal diet consumed at an equivalent intake level ($P < .10$). The difference in the estimated large intestinal transit time between measured values and those obtained by subtraction may be the result of the method of measurement and the defecation pattern. Pigs defecated primarily at the time of feeding which reduced the accuracy of the measurements.

In this study, decreasing rate of passage through the small intestine with added fiber did not increase enzymatic digestion of starch. But addition of alfalfa to a corn diet appeared to interfere with starch digestion in the stomach and large intestine resulting in a slightly lower total tract digestibility for starch ($P < .15$). The stomach and large intestine are sites where fermentation occurs in nonruminants. This suggests alfalfa addition to the diet inhibited starch fermentaion in these organs. The mechanism whereby this inhibition is occuring is uncertain to this author. Addition of alfalfa or corn silage to the concentrate diet reduced digestibility of organic matter and starch in the stomach and increased OMD in the cecum

and large intestine. However, addition of cottonseed hulls to the concentrate diet did not alter site of starch digestion but tended to shift OMD from the large intestine to the stomach. No relationship between rate of passage and total tract digestibility was detected in this study. Castle and Castle (1957) monitored digestibility and rate of passage in hogs and concluded that the relationship is not necessarily one of cause and effect.

Addition of roughage to the concentrate diet decreased fecal dry matter and nitrogen content ($P < .01$) but increased fecal organic matter and ADF content ($P < .01$) as compared to the basal diet.

Organic matter content of feces was highest for the cottonseed hull diet, followed by the alfalfa diet while the corn silage diet had the least organic matter ($P < .01$). ADF content of feces was higher for the cottonseed hull supplemented diet than the corn silage diet ($P < .01$). Corn silage contained approximately 28 percent of its dry matter weight as corn kernels which may explain this lower fecal ADF value. Nitrogen content of feces was lower for pigs fed the cottonseed hull diet than for pigs fed the other forages ($P < .01$). Since large intestimal OMD was lower for this diet, the lower fecal nitrogen values may result from a lower amount of microbial nitrogen. Fecal starch values were not significantly changed by dietary treatments. Increasing feed consumption did not appear to alter fecal parameters ($P < .10$).

Duodenal and ileal pH values were similar for all treatments (table 7). Addition of roughage to the concentrate diet increased fecal pH ($P < .01$).

The water holding capacity of several fiber sources is shown in table 8. The amount of water a roughage will bind may influence rate of passage and cell wall susceptibility to degradation. Reducing particle size increases water holding capacity for roughages such as prairie hay, sorghum sudangrass hay and wheat straw whereas particle size reduction has only as minor impact on water holding capacity of alfalfa hay or cotton seed hulls. In general, ground vegetative portions of plants have greater water holding capacity than byproducts from grain processing. The lower water binding capacity of CSH than alfalfa explains the lower fecal dry matter values observed with the CSH diet.

TABLE 1. DIET INGREDIENTS (% OF DM)

Ingredient	IFN[a]	%
Ground corn	4-02-931	75.2
Soybean meal	5-04-604	21.2
Dicalcium phosphate	6-01-080	1.5
Limestone	6-02-632	0.8
Salt		0.5
Vitamin-trace mineral mix[b]		0.5
Chromic oxide		0.2
CTC - 50[c]		

[a]International feed number.

[b]Supplied 4,000,000 IU vitamin A, 300,000 IU vitamin D, 4g riboflavin, 20g pantothenic acid, 30g niacin, 800g choline chloride, 15 mg vitamin B_{12}, 10,000 IU vitamin E, 2g menadione, 200 mg iodine, 90g iron, 20g manganese, 10g copper, 90g zinc and 100 mg selenium per ton of feed.

[c]Contains 50 grams of chlorotetracycline per pound of premix.

TABLE 2. COLLECTION SCHEDULE

Day 1 - 7	Adaptation to diet in the duodenum
Day 8	0800 Feces collection
Day 9	0800 Feces collection
	0930 Duodenal and ileal fluid collection
Day 10	0800 Feces collection
	0800 Add ferric oxide to diet
Day 12	0930 Place ferric oxide in ileal cannula
Day 13	0930 Place phenol red in duodenal cannula

TABLE 3. EFFECTS OF INTAKE AND ROUGHAGE SOURCE ON TOTAL TRACT DIGESTIBILITY

	Intake		Roughage Source[b]			
	Low	High	AH	CSH	CS	SD[c]
Digestibility (%):						
Dry matter	86.0[g]	84.7[g]	71.3[f]	52.4[e]	74.5[f]	5.6
Organic matter	88.9[g]	87.7[g]	73.3[f]	54.1[e]	78.4[f]	5.2
Starch	99.6[c]	98.8[c]	95.8[h]	98.3[c]	98.1[c]	2.1
Nitrogen	85.9[f]	84.4[f]	72.7[e]	64.4[e]	74.6[e]	6.1
ADF	10.2	6.8	15.8	0.6	9.9	13.6
Forage[d]	--	--	10.9	-6.9	15.2	--
No. of observations/mean	5	7	4	4	7	

[a]Low = 2 % of body weight; High = 3% of body weight.

[b]AH = alfalfa hay; CSH = cottonseed hulls; CS = corn silage.

[c]Standard deviation.

[d]Calculated by difference.

[efg]Means in a row with different superscripts differ (P .01).

[hi]Means in a row with different superscripts differ (P .15).

TABLE 4. EFFECT OF INTAKE LEVEL AND ROUGHAGE SOURCE ON PROPORTION OF ORGANIC MATTER DIGESTION THAT OCCURS IN VARIOUS SEGMENTS OF THE GI TRACT

	Intake[a]		Roughage Source[b]			
	Low	High	AH	CSH	CS	SD[c]
Site of digestion						
Total tract	88.9[h]	87.7[h]	73.3[g]	54.1[f]	78.4[g]	5.2
Stomach and Small Intestine[de]	69.7 (4)	74.7 (6)	66.3 (3)	84.5 (4)	66.3 (4)	30.7
Stomach[d]	5.0 (4)	10.4 (4)	0.0 (2)	19.1 (3)	2.1 (4)	9.8
Small intestine[de]	64.7 (4)	64.3 (4)	66.3 (2)	65.4 (3)	64.2 (4)	--
Large intestine						
Observed[d]	25.7	25.1	32.7	11.5	32.4	35.3
Calculated[de]	30.3	25.3	33.7	15.5	33.7	--
Digestibility in large intestine (%)	53.0	52.2	35.1	20.4	30.2	29.2
No. of observations/ mean	5	7	4	4	7	

[a] Low = 2% of body weight; High = 3% of body weight.
[b] AH = alfalfa hay; CSH = cottonseed hulls; CS = corn silage.
[c] Standard deviation.
[d] Expressed as a percentage of total tract digestion.
[e] Calculated by difference. Values in parenthesis equals number of observations per mean.
[fgh] Means in a row with different superscripts differ (P .01).

TABLE 5. EFFECT OF INTAKE LEVEL AND ROUGHAGE SOURCE ON PROPORTION OF TOTAL STARCH DIGESTION THAT OCCURS IN VARIOUS SEGMENTS OF THE GI TRACT

	Intake[a]		Roughage source			
	Low	High	AH	CSH	CS	SD[c]
Site of digestion						
Total tract	99.6[g]	98.8[g]	95.8[f]	98.3[g]	98.1[g]	2.1
Stomach and small intestine[d]	95.5	93.3	100.0	96.9	99.0	6.7
Stomach[d]	12.2 (4)	9.4 (4)	0.0 (2)	7.8 (3)	0.4 (4)	11.9
Small intestine[de]	82.9 (4)	82.8 (4)	95.9 (2)	87.5 (3)	96.7 (4)	--
Large intestine						
Observed[d]	2.1	6.5	-.1	3.1	2.2	6.6
Calculated[de]	4.5	6.7	0	3.1	1.0	--
Digestibility in large intestine	36.9	61.8	23.1	44.9	24.2	41.0
No. of observations/ mean	5	7	4	4	7	

[a] Low = 2% of body weight; High = 3% of body weight.
[b] AH alfalfa hay; CSH cottonseed hulls; CS corn silage
[c] Standard deviation
[d] Expressed as a percentage of total tract digestion
[e] Calculated by difference
[fg] Means in a row with different superscripts differ

TABLE 6. EFFECT OF INTAKE LEVEL AND ROUGHAGE SOURCE ON INTESTINAL TRANSIT TIME

	Treatment					
	Intake[a]		Roughage source[a]			
	Low	High	AH	CSH	CS	SD[c]
Transit time (minutes)						
Total tract	2078[e]	1890[e]	1327[d]	1432[d]	1429[d]	376.4
Small intestine	141[j]	157[j]	144[j]	225[k]	235[k]	77.4
Large intestine						
Measured	1905[hi]	2089[i]	1356[g]	1466[gh]	1451[gh]	447.1
Difference	1937[f]	1733[ef]	1183[d]	1335[de]	1194[d]	342.9
No. of observations/ mean	5	7	4	4	7	

[a]Low = 2 % of body weight; High = 3% of body weight.

[b]AH = alfalfa hay; CSH = cottonseed hulls; CS = corn silage.

[def]Means in a row with different superscripts differ (P .05).

[ghi]Means in a row with different superscripts differ (P .10).

[jk]Means in a row with different superscripts differ (P .17).

TABLE 7. EFFECT OF INTAKE LEVEL AND ROUGHAGE SOURCE ON FECAL AND INTESTINAL PARAMETERS

	Intake[a]		Roughage source[a]			
	Low	High	AH	CSH	CS	SD[c]
Fecal						
Dry matter (%)[d]	34.1^{f}	29.7^{f}	22.3^{e}	32.8^{f}	19.9^{e}	3.7
Organic matter[d]	74.8^{e}	75.6^{e}	87.4^{g}	91.7^{h}	77.7^{f}	1.2
Starch[d]	1.3	3.6	4.6	1.2	3.3	3.8
ADF[d]	11.6^{e}	13.4^{e}	41.6^{fg}	50.5^{g}	39.2^{f}	7.4
Nitrogen[d]	3.1^{g}	3.1^{g}	2.6^{f}	1.7^{e}	2.5^{f}	0.2
pH						
duodenum	5.1	4.5	4.1	4.4	4.0	0.7
ileum	6.85^{e}	7.09^{e}	7.04^{f}	7.22^{f}	7.08^{f}	0.5
feces	6.08^{e}	6.09^{e}	6.63^{f}	6.62^{f}	6.56^{f}	0.3
No. of observations/ mean	5	7	4	4	7	

[a] [b] Low = 2% of body weight; High = 3% of body weight.

[b] [c] AH = alfalfa hay; CSH = cottonseed hulls; CS = corn silage.

[c] Standard deviation.

[d] Expressed as a percentage of fecal dry matter.

[efgh] Means in a row with different superscripts differ ($P < .01$).

TALBE 8. WATER HOLDING CAPACITY OF SOME COMMON SOURCES OF FIBER

Fiber source	IFN[a]	Water holding capacity ($^{g}H_2O$/gDM) Chopped	Ground
Alfalfa hay	1-00-063	5.71[b]	5.56
Cottonseed hulls	1-01-599	3.96	3.97
Prairie hay	1-07-957	3.82[c]	5.62
Sorghum sudan-grass hay	1-04-480	4.83[c]	7.72
Wheat straw	1-05-175	6.60[d]	7.91
Rice hulls		3.09	
Corn bran		4.45	
Beet pulp	4-00-669		
Corn cobs	1-02-782	4.55	
Solka floc		4.18	

[a]International feed number.

[b]Particle size-4cm; lot of fines

[c]Stems intact; particle size--7-8cm

[d]Stems were cracked in half; particle size 5-6cm

CHAPTER VIII

EFFECT OF ORAL OR ABOMASAL GLUCOSE ADDITION ON ENERGETIC EFFICIENCY OF WETHERS

S. R. Rust, F. N. Owens and L. E. Walters

Summary

Nineteen crossbred wethers (21 kg) were fed or abomasally infused with glucose for 165 days to evaluate energetic efficiency of ruminal versus intestinal digestion. A third group was fed the basal diet without glucose added. Carcass composition was determined by separating physically fat from lean in each carcass. Four lambs were slaughtered at the start of the trial to calculate efficiency of protein and fat gain of fed or infused animals.

Lambs receiving the glucose treatments tended to gain faster than the control treatment. Diet digestibility was not alterted by glucose treatment. Consumption of 180 grams of glucose decreased ruminal butyrate and tended to increase the proportion of propionate. Lambs infused with glucose tended to have faster rates of carcass gain and a higher dressing percentage ($P < .08$). But carcasses, intestines and omentum from abomasally infused lambs contained more fat both in the carcass and in the intestines plus omentum than lambs receiving glucose orally. Efficiency of converting added glucose calories to carcass

calories was almost twice as great (16.7 vs. 8.6 percent) with abomasal glucose infusion than feeding of glucose.

Introduction

Four avenues exist for starch disappearance from the digestive tract of the ruminant animal. These are 1) bacterial fermentation in the rumen; 2) engulfment by rumen protozoa and delivered to the small intestine; 3) enzymatic digestion in the small intestine, and 4) fermentation by bacteria in the cecum and large intestine. Studies by Karr et al. (1966) indicated that substantial quantities of starch are presented to the small intestine for digestion with high consumption of grain diets. Fermentation in the rumen results in energy losses (i.e., methane, five to ten percent and heat production, 10 to 20 percent) and volatile fatty acids are used less efficiently at the tissue level for growth (50-75 percent) and maintenance (89-96 percent) than glucose (Mayes and Orskov, 1974; Baldwin et al., 1980). Theoretically, the above inefficiencies of ruminal starch digestion can be obliterated by shifting the site of digestion to the small intestine. Based on energy balance equations, amylase digestion of starch to glucose should be 20 percent more efficient than ruminal fermentation of starch to volatile fatty acids (Nicholson and Sutton, 1969). But such an energetic advantage of enzymatic starch digestion over ruminal fermentation has not been tested in a long term feeding study. This experiment with growing lambs was conducted to compare relative energetic efficiencies and effects on growth and carcass composition of providing the

end-product of starch digestion--glucose--for bacterial fermentation in the rumen or for absorption from the small intestine.

Experimental Procedure

Twenty-one crossbred (21 kg) wether lambs were utilized in a randomized block design to examine the effects of site of glucose administration on growth and carcass composition. Thirteen of the lambs were equipped with abomasal cannulas. Cannulas were placed along the lesser curvature of the abomasum about 15 centimeters cranial to the pyloric sphincter. Cannulas were constructed from tygon tubing (95 mm in diameter). After three weeks of recouperation, lambs were assigned to one of three treatments: 1) basal diet or control, 2) basal diet plus 180 grams of glucose per day mixed with the diet, or 3) basal diet plus 180 grams of glucose infused into the abomasum. Lambs were allowed free access to feed for ten days after treatment assignments so that lambs could be assigned to one of three intake groups. The amount of feed fed each day to each lamb within a group was equal to the amount consumed by the lamb within the group consuming the least the previous day. Lambs were fed at 0830 and 1630 daily. Orts were weighed every morning. The basal diet contained 75 percent concentrate and 25 percent roughage (table 1) and the nutrient composition is shown in table 2. The trial continued for 165 days.

Lambs were housed in individual metabolism crates with separate feeders and waterers. The infusion apparatus consisted of a reservoir, a peristaltic pump and tygon tubing for delivery of glucose solution to

each lamb. The flow rate of the pump was adjusted such that 180 ml of dextrose solution was delivered in about 20 hours. Two peristaltic pumps were employed throughout the trial, a Brinkman MP-GE (Brinkman Mfg. Co., Des Plaines, Il.) and a Technicon. Reservoirs were maintained at 4 C to prevent fermentation. Fresh dextrose solution was prepared and added to the reservoirs daily and enough hydrochloric acid was added tothe glucose reservoir to lower the pH below 3. Dextrose (corn sugar) was obtained from Clinton Corn Processing Company, Clinton, Ia. Small check valves were inserted in the tygon delivery tubes just prior to the abomasal cannulas to prevent backflow into the tygon tubing. Seven lambs were infused with glucose, [illegible] lambs received glucose added to the diet and four lambs served as controls. Of the two lambs which were removed from the study, one died from urinary calculi and the other developed cannula problems.

Weight gain, nitrogen balance and digestibility were determined three times during the trial. Total feces and urine were collected for five days at the end of each period. Urine was acidified with HCl to lower pH below 4.0. Ten percent of the feces and one percent of the urine was frozen for later analysis. Rumen samples were collected each period via stomach tube and blood samples were obtained by jugular venipuncture.

Digestibilities of organic matter, starch, nitrogen, ADF and ash were determined. Dry matter, nitrogen and ash were analyzed by standard procedures (AOAC, 1975). Starch analysis was determined by the procedure of Macrae and Armstrong (1968). Acid detergent fiber was estimated by the procedure of Van Soest (USDA, 1970). Rumen and fecal

pH were determined with a combination electrode. Ten grams of feces was blended with 50 mls of water before a pH value was determined. Rumen ammonia was measured by the colorimetric procedure of Chaney and Marbach (1962). Rumen volatile fatty acid analysis was conducted by the procedures of Sharp (1977). Blood glucose was determined with a kit purchased from Sigma Chemical, St. Louis, Mo. Blood urea was estimated by the modified Chaney and Marbach (1962) procedure.

Data were analyzed using the General Linear Models of the SAS subroutine (Barr and Goodnight, 1981). Variables in the analysis of variance were intake level, glucose treatment and the intake level by treatment interaction. Differences in treatment means were detected using the Least Significant Difference (LSD) test (Steel and Torrie, 1960).

Results and Discussion

Lambs which received the glucose by either method tended to gain faster ($P < .20$) than control animals (table 3). Feed required per unit of gain was slightly lower for the lambs receiving additional glucose. Rate of gain of lambs was lower than reported in many other studies (Johnson and Clemens, 1972; Wyatt et al., 1973; Ackerson et al., 1974); however, these lambs were housed in metabolism stalls instead of individual pens and pair feeding restricted intake. Lambs at higher feed intake level gained weight 33.7 percent more rapidly ($P < .05$) than lambs at the lower intake level (table 4). Feed required per unit of gain was similar across intake groups.

Digestibilities of organic matter, starch, nitrogen and ADF within each period were similar across method of glucose administration (table 5). Therefore, pooled digestibility estimates were analyzed. Starch digestibility was greater than 99 percent in this study. ADF digestibility with the orally supplemented glucose was slightly less than the other treatments. This may indicate that soluble carbohydrate inhibited cellulose digestion as suggested by Stewart (1977). Little et al. (1966) reported similar effects of oral or abomasal infusion of glucose on dry matter and energy digestibility. Ash digestibility tended to increase as glucose was added to the diet or infused into the abomasum ($P < .10$). Since ash content of the added corn sugar was only four percent, absorption of minerals in the basal diet must have increased. Although the reason for this increase is uncertain, mineral absorption paralleled apparent digestibility of carbohydrates as had been noted previously in a corn processing trial (Rust and Owens, 1978). In both studies, more fermentable carbohydrate may have been digested in the large intestine, a major site of mineral absorption. Nitrogen retention per day was slightly greater for the lambs receiving supplemental glucose. Percentage of nitrogen consumed which was retained was similar for lambs receiving supplemental glucose and lambs fed the basal diets.

Level of intake did not significantly influence digestibility estimates (table 6); however, all intake levels fed were less than four percent of body weight. Feeder lambs generally consume feed amounts equal to four to five percent of their body weight and gain 200 to 450 grams in body weight per day. The intermediate intake level lambs

retained a significantly higher percentage of their dietary nitrogen than lambs at the low or high intake levels and grams nitrogen retained daily also tended to be greater ($P < .12$) for this intermediate intake group. The reason for the higher nitrogen retention with the intermediate intake level is unknown.

The effects of glucose treatment on fecal parameters is shown in table 7. Fecal dry matter was significantly reduced for the infused glucose treatment as compared to the basal diet. The level of glucose infused was determined initially by assessing the maximum amount which could be infused without causing diarrhea. Therefore, wetter feces with infused glucose is expected. Fecal organic matter and starch are both greater for the lambs on the glucose treatments than the control lambs ($P < .05$). Lambs receiving the glucose infusion had more fecal starch than lambs receiving glucose in the diet though the level was still very low. Possibly, some of the infused glucose was incorporated in microbial polysaccharide in the small or large intestine. The lower fecal pH ($P < .05$) for the lambs receiving glucose infusion supports this idea. This suggests that the absorptive capacity of the small intestine was exceeded with infusion. These results support the concept that of limited glucose absorptive capacity by the small intestine as advanced by Little et al. (1966) and Mayes and Orskov (1974). Fecal nitrogen and ADF content were not significantly altered by glucose treatment. The effects of intake level on fecal characteristics are shown in table 8. Fecal dry matter, organic matter, starch, nitrogen and ADF were similar across intake levels though fecal pH tended to decline as intake increased ($P < .05$).

Elevated consumption may have passed more fermentable substrate to the lower gut thereby reducing fecal pH (Grovum and Williams, 1973).

Supplemental glucose decreased ($P < .05$) rumen ammonia values and surprisingly increased ruman pH (table 9). Three possibilities may explain the low ammonia values with the oral glucose treatment. First, dextrose, or VFAs formed from dextrose, has a strong osmatic effect which may have stimulated liquid movement from the blood into the rumen which may lower ammonia levels. Secondly, added glucose may have increased microbial protein synthesis in the rumen which would lower ammonia levels. Overall ruminal digestion may have been retarded with the oral glucose treatment as the higher pH levels which would indicate. Finally, the lower ammonia values may reflect increased microbial uptake due to the increased fermentation from the soluble glucose levels. The higher ruminal pH values do not support this premise. The lower ruminal acidity with the infused glucose treatment also may have reduced urea recycling to the rumen. Fermentation of the sugar in the lower gut may have decreased the amount of nitrogen available to recycle though blood urea levels were not altered as will be presented later.

Butyrate ($P < .10$) and isobutyrate ($P < .05$) proportions were lower with lambs receiving the oral glucose treatment than lambs on the basal diet (table 7). Likewise, the valerate proportion was greater ($P < .05$) and the isovalerate proportion less ($P < .01$) with the added dietary glucose. Alteration of the proportion of volatile fatty acids mentioned above provide further support for the concept of reduced or retarded protein degradability in the the rumen with glucose infusion.

Acetate, propionate, and caproate proportions and total VFA levels were similar for lambs receiving all three treatments.

Rumen pH values tended to be lower ($P < .10$) with the medium intake level (table 10). The reason for this difference is uncertain. Caproate levels tended to be greater for the infused glucose treatment than the oral treatment ($P < .10$). The other volatile fatty acid proportions were unaffected by level of intake. No significant differences were detected in blood plasma glucose or urea concentrations with different treatments or intake levels (table 11). Although plasma glucose concentration tended to be greater with infused glucose, similar results have been reported by Little et al. (1965) with abomasal glucose infusion of lambs.

Lambs receiving the infused glucose had higher ($P < .08$) dressing percentage values than lambs on the other two treatments (table 12). Lambs receiving infused glucose also had heavier carcasses than lambs fed the control diet ($P < .06$). The higher dressing percent for the lambs on the infusion treatment suggests that carcasses contained more fat which is supported by lean and fat separation data (72.1 vs 71.0 or 70.3 percent fat in carcass) and the kidney, heart and pelvic fat which tended to be higher with infused glucose treatment than the other treatments ($P < .17$). Lambs receiving the oral glucose treatment had slightly leaner carcasses than lambs fed only the basal diet.

The effects of intake level on carcass characteristics are shown in table 13. Slaughter weight and carcass weight increased as intake level increased ($P < .01$). Dressing percent also tended to increase as feed intake increased. But lambs consuming the intermediate intake

level had less lean and more fat than the lambs on the other two intake levels ($P < .01$). Kidney, heart and pelvic fat contents were similar for lambs on all three intake levels.

Rates of deposition of protein and fat in the carcass are shown in tables 14 and 15. Values in these tables have been adjusted for initial carcass composition and, therefore, should represent the increased deposition per day averaged across the trial. Protein deposition per day (grams or kcal) tended to increase with either glucose treatment (table 14). Eighty-eight percent of the daily nitrogen retention occurred in the carcass. Wool growth would account for a large portion of the remaining 12 percent. Grams of fat deposition were significantly greater for lambs receiving infused glucose ($P < .08$). Total calorie gain per day tended to be greater for both glucose treatments as compared to the basal treatment ($P < .12$). Total carcass weight and caloric gain was greater for lambs receiving glucose infusion than lambs receiving only the basal diet ($P < .05$). After subtracting the caloric deposition of the lambs on the basal diet alone, lambs receiving dextrose infused into the abomasum utilized the added glucose calories (686 kcal/day) twice as efficiently (8.9 vs 4.6 percent) for carcass caloric gain than lambs fed the glucose. Infused glucose was utilized 93 percent more efficiently than oral glucose treatment for caloric deposition in the carcass. Including caloric gain in the intestines together with the carcass into efficiency calculations gave infusion of glucose a 115 percent advantage (11.7 vs 5.4 percent) in efficiency of added glucose over oral glucose. The results of this study confirm previously reported results (Blaxter, 1962; Black, 1971) that

post-ruminal digestion of starch is energetically more beneficial than ruminal fermentation; however, the magnitude was much larger in this study (115 vs 30-36 percent). Fat accounted for most (87 percent) of the increased caloric gain for both glucose treatments.

Total protein deposition in the carcass was similar for the three treatments. Protein deposition per day was increased ($P < .05$) at the highest intake level (table 15). Fat (calorie and weight) deposition increased as feed intake increased ($P < .01$). Total weight and calorie gain per day increased as lambs ate more food ($P < .01$) and carcass weight gain increased linearly with feed intake ($r^2 = .9998$). As intake increased, protein as a percent of total weight deposited was 9.1, 7.4 and 11.5 percent for the low, medium and high intake levels, respectively. Contrary to these results, Byers (1982) indicated protein gain as a percent of total gain decreased as energy intake increased.

The effect of treatments on post-ruminal gut composition is shown in table 16. Intestinal fat deposition differences were apparent visually at slaughter. Intestinal protein weight ($P < .05$), fat weight ($P < .01$) and total weight ($P < .01$) were greater for the infused than the oral treatments. Glucose infusion into the abomasum thereby appeared to be utilized for fat gain by the intestine and omentum. Weight of intestinal fat for lambs receiving infused glucose was 48 and 27 percent greater for lambs receiving no glucose or glucose orally, respectively. Why absorbed glucose caused fat deposition to occur in the gut instead of in the carcass is uncertain. However, Van Soest (1982) suggested that high levels of intestinal glucose absorption will

lead to deposition of omental fat. Either the ability to transport glucose from the intestine may be limited, thereby providing substrate for fat deposition, or the glucose may have been metabolized to lactate during absorption (Armstrong and Smithard, 1979). Lactate may be a better substrate for lipogenesis than glucose (Prior, 1978). Omental fat was deposited at the rate of 15.3 grams per day. The post-ruminal gut contained 89-91 percent fat.

Protein, fat and total intestinal weight gain tended to increase with level of feed intake (table 17). The intestinal protein, fat and total gain was higher for lambs on the high intake level than on the lower level ($P < .08$). Eighty-nine percent of the increase in gut weight with increased feed intake was attributable to fat.

In conclusion, results of this study indicate that over a long term, increasing the carbohydrate supply to the small intestine of lambs fed a high concentrate diet will increase fat deposition in the intestines to a greater degree than providing a similar amount of additional carbohydrate for ruminal fermentation.

TABLE 1. BASAL DIET COMPOSITION

Item	IFN[a]	%
Dry rolled corn	4-02-931	42.9
Cottonseed hulls	1-01-599	16.4
Alfalfa	1-00-059	7.0
Soybean meal	5-04-604	33.0
Salt		0.2
Limestone	6-02-632	0.3
Ammonium chloride		0.3
Aurofac 50		+
Rumensin 60[b]		+
Vitamin A		+
Vitamin D		+

[a]International feed number

[b]20 grams/ton

TABLE 2. BASAL DIET ANALYSIS[a]

	%
Dry Matter	92.94
Starch	38.53
Nitrogen	2.90
ADF	10.08
Ash	4.32

[a]Dry matter basis.

TABLE 3. EFFECT OF GLUCOSE ADMINISTRATION METHOD ON PERFORMANCE

	Method			
	Control	Oral[a]	Infused[b]	SD[c]
Daily gain (g/day)	91[d]	109[e]	114[e]	18.66
Feed/gain	11.06	10.48	10.40	1.45
No. of lambs/ treatment	4	9	6	

[a]Glucose added to feed.

[b]Glucose infused into abomasum.

[c]Standard Deviation.

[de]Means in a row with different superscripts differ ($P < .20$).

TABLE 4. EFFECT OF INTAKE LEVEL ON PERFORMANCE

Item	Intake level			SD[a]
	Low	Medium	High	
ADG (g/day)	89[e]	106[ef]	119[f]	18.66
Feed/gain	10.63	10.07	10.71	1.45
Feed intake (g/day)	941[b]	1090[e]	1247[d]	55.92
% of body weight	3.0	3.3	3.7	
No. of lambs/intake group	6	4	9	

[a]Standard deviation.

[bcd]Means in a row with different superscripts differ ($P < .01$).

[ef]Means in a row with different superscripts differ ($P < .05$).

TABLE 5. EFFECT OF METHOD OF GLUCOSE ADDITION ON DIGESTIBILITY

	Method			
	Basal	Oral[a]	Infused[b]	SD[c]
Digestibility (%):				
Organic matter	80.9	80.9	82.7	4.38
Starch	99.5	99.5	99.3	0.27
Nitrogen	79.5	79.7	80.3	4.29
ADF	11.8	8.5	12.6	10.00
Ash	61.9[d]	70.9[e]	72.9[e]	7.00
Nitrogen balance				
g/day	10.74	12.00	12.21	3.75
% of intake	59.3	54.3	53.6	18.5
No. of observations/ mean	4	9	6	

[a]Basal diet plus 180 grams of glucose fed per day.

[b]Basal diet plus 180 grams of glucose infused per day.

[c]Standard deviation.

[de]Means in a row with different superscripts differ ($P < .10$).

TABLE 6. EFFECT OF INTAKE ON DIGESTIBILITY

	Intake level			
	Low	Medium	High	SD[a]
Digestibility (%):				
Organic matter	83.4	82.9	79.6	4.38
Starch	99.5	99.5	99.3	0.27
Nitrogen	80.2	81.3	79.0	4.29
ADF	12.4	14.7	7.3	10.00
Ash	73.0	72.4	66.2	7.00
Nitrogen balance				
g/day	10.7[d]	15.6[e]	10.8[d]	3.73
% of intake	60.7[bc]	74.6[c]	42.8[b]	18.52
No. of observations/mean	6	4	9	

[a]Standard deviation.

[bc]Means in a row with different superscripts differ ($P < .05$).

[de]Means in a row with different superscripts differ ($P < .12$).

TABLE 7. EFFECT OF METHOD OF GLUCOSE ADMINISTRATION ON FECAL PARAMETERS

	Method			
	Basal	Oral[a]	Infused[b]	SD[c]
Fecal:				
Dry matter %	50.7[f]	44.9[ef]	38.6[e]	4.56
Organic matter[d]	91.8[g]	93.6[h]	93.5[h]	0.90
Starch[d]	1.0[g]	1.2[h]	2.0[i]	0.59
Nitrogen[d]	2.9	3.0	3.2	.27
ADF[d]	49.0	46.1	43.5	4.02
pH	7.32[h]	7.20[h]	6.67[g]	0.42
No. of observations/ mean	4	9	6	

[a]Basal diet plus 180 grams of glucose fed/day.

[b]Basal diet with 180 grams of glucose infused/day.

[c]Standard deviation.

[d]Percent of fecal dry matter.

[ef]Means in a row with different superscripts differ ($P < .01$).

[ghi]Means in a row with different superscripts differ ($P < .05$).

TABLE 8. EFFECT OF INTAKE ON FECAL PARAMETERS

	Intake level			
	Low	Medium	High	SD[a]
Fecal:				
Dry matter %	45.4	44.2	43.3	4.56
Organic matter[b]	93.2	93.3	93.1	0.90
Starch[b]	1.3	1.4	1.4	.59
Nitrogen[b]	3.2	3.1	2.9	.27
ADF[b]	45.7	44.4	46.7	4.02
pH	7.51[e]	7.17[de]	6.70[d]	.42
No. of observations/mean	6	4	9	

[a]Standard deviation.

[b]Percent of fecal dry matter.

[de]Means in a row with different superscripts differ ($P < .05$).

TABLE 9. EFFECT OF METHOD OF GLUCOSE ADMINISTRATION ON RUMINAL PARAMETERS

	Method			
	Basal	Oral[a]	Infused[b]	SD[c]
Ruminal:				
Ammonia (ng/dl)	18.0[g]	9.8[f]	12.3[f]	3.96
pH	5.98[f]	6.50[g]	6.28[g]	0.22
Volatile fatty acid (moles/100 moles)				
Acetate	61.2	59.3	60.5	3.50
Propionate	19.1	23.6	20.2	4.01
Butyrate	13.8[i]	10.7[h]	13.6[i]	2.38
Isobutyrate	1.3[g]	0.6[f]	1.0[g]	.34
Valerate	1.5[f]	3.4[g]	2.0[fg]	1.05
Isovalerate	2.8[e]	1.8[d]	2.2[de]	0.33
Caproate	0.4	0.6	0.5	.27
Total VFA (mmoles/ml)	117.4	118.1	123.0	24.7
C_2/C_3	3.4	3.5	3.2	1.99
No. of observations/ mean	4	9	6	

[a]Basal diet plus 180 grams of glucose fed per day.

[b]Basal diet plus 180 grams of glucose infused per day.

[c]Standard deviation.

[de]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .05$).

[hi]Means in a row with different superscripts differ ($P < .10$).

TABLE 10. EFFECT OF INTAKE ON RUMINAL PARAMETERS

	Intake			
	Low	Medium	High	SD[a]
Ruminal:				
Ammonia (ng/dl)	11.9	12.0	12.7	3.96
pH	6.42[c]	6.04[b]	6.38[c]	0.22
Volatile fatty acid (moles/100 moles)				
Acetate	60.7	58.2	60.5	3.52
Propionate	19.5	23.2	22.2	4.01
Butyrate	13.3	11.5	12.0	2.38
Isobutyrate	0.9	1.1	0.8	.34
Valerate	2.7	3.4	2.0	1.05
Isovalerate	2.3	2.0	2.2	0.33
Caproate	0.6[bc]	0.8[c]	0.4[b]	.27
Total VFA (mmoles/ml)	123.0	124.7	111.5	24.7
C_2/C_3	4.1	2.7	3.2	1.99
No. of observations/mean	6	4	9	

[a]Standard deviation.

[bc]Means in a row with different superscripts differ ($P < .10$).

TABLE 11. EFFECT OF GLUCOSE ADMINISTRATION METHOD AND INTAKE ON BLOOD PLASMA GLUCOSE AND UREA

	Diet			Intake			
	Basal	Oral[a]	Infused[b]	Low	Medium	High	SD[c]
Blood (mg/100 ml):							
Glucose	82.0	79.9	103.4	79.0	78.0	107.5	26.93
Urea	21.1	18.8	21.0	21.2	18.7	18.9	3.02
No of observations per mean	4	9	6	6	4	9	

[a]Basal diet plus 180 grams of glucose fed per day.

[b]Basal diet plus 180 grams of glucose infused per day.

[c]Standard deviation.

TABLE 12. INFLUENCE OF METHOD OF GLUCOSE ADMINISTRATION ON CARCASS CHARACTERISTICS

	Method			
	Control	Oral[a]	Infused[b]	SD[c]
Characteristic:				
Weight (kg)				
Initial	24.9	24.8	26.1	--
Slaughter	38.4	41.1	43.5	4.80
Carcass[d]	20.4[e]	23.1[ef]	25.6[f]	3.21
KHP (%)	2.35[i]	2.30[i]	3.58[j]	1.23
Dressing percent	58.2[g]	58.5[g]	61.5[h]	2.15
Carcass composition (% of total carcass weight)				
Protein	29.0	29.7	27.9	2.02
Fat	71.0	70.3	72.1	2.02
# of lambs/treatment	4	9	6	

[a] Glucose added to diet.

[b] Glucose infused into abomasum.

[c] Standard deviation.

[d] Cold carcass weight.

[ef] Means in a row with different superscripts differ ($P < .06$).

[gh] Means in a row with different superscripts differ ($P < .08$).

[ij] Means in a row with different superscripts differ ($P < .17$).

TABLE 13. INFLUENCE OF INTAKE LEVEL ON CARCASS CHARACTERISTICS

	Intake Level			
	Low	Medium	High	SD[a]
Characteristic:				
Weight (kg)				
Initial	26.7	25.0	23.9	--
Slaughter	36.9[c]	40.8[d]	44.5[d]	4.80
Carcass[b]	20.4[c]	.1[cd]	25.6[d]	3.21
Dressing percent	58.0	59.0	60.5	2.15
KHP (%)	2.9	2.6	2.7	1.23
Carcass Composition (% of total carcass weight)				
Lean	31.6[d]	25.7[c]	28.7[cd]	2.02
Fat	68.4[c]	74.3[d]	71.3[cd]	2.02
No. of observation per mean	6	4	9	

[a]Standard deviation.

[b]Cold carcass weight.

[cd]Means in a row with different superscripts differ ($P < .01$)

TABLE 14. INFLUENCE OF SITE OF GLUCOSE ADMINISTRATION ON ENERGETIC EFFICIENCY AND GROWTH PARAMETERS OF THE CARCASS AND INTESTINES

	Treatment			
	Control	Oral[a]	Infused[b]	SD[c]
Deposition of:				
Total carcass gain (g/day)	69.5[e]	78.3[ef]	86.7[f]	8.93
(kcal/day)[d]	367.0[e]	398.6[ef]	428.3[f]	47.00
Protein (g/day)	8.3	10.9	11.4	3.21
(kcal/day)	31.6	35.5	40.6	8.49
Fat (g/day)	55.6[g]	60.2[gh]	66.1[h]	7.17
(kcal/day)[d]	335.4[i]	362.2[j]	387.7[j]	40.62
Caloric gain of carcass plus intestine (kcal/day)				
Total	393.8[e]	430.8[ef]	473.9[f]	47.80
Protein	33.6	37.5	43.4	8.65
Fat	360.2[e]	392.4[ef]	430.5[f]	41.53
No. of observations/ mean	4	9	6	

[a][b]Basal diet plus 180 grams of glucose fed per day.
[c]Standard deviation.
[d]Assumed the following kcal/gram for protein = 5.65 and fat = 9.40.
[ef]Means in a row with different superscripts differ ($P < .05$).
[gh]Means in a row with different superscripts differ ($P < .08$).
[ij]Means in a row with different superscripts differ ($P < .12$).

TABLE 15. INFLUENCE OF INTAKE LEVEL ON ENERGETIC EFFICIENCY AND GROWTH PARAMETERS OF THE CARCASS AND INTESTINE

	Intake Level			
	Low	Medium	High	SD[a]
Deposition of:				
Total carcass gain (g/day)	63.2[c]	76.9[cd]	90.6[d]	8.93
(kcal/day)[b]	312.2[c]	425.3[d]	450.1[d]	47.00
Protein (g/day)	8.3[e]	8.1[e]	13.1[f]	3.21
(kcal/day)[b]	30.0[e]	33.0[ef]	42.0[f]	8.49
(% of weight gain)	9.1	7.4	11.5	--
Fat (g/day)	47.6[c]	63.8[d]	69.0[d]	7.17
(kcal/day)[b]	281.4[c]	392.2[d]	407.8[d]	40.93
Caloric gain of carcass plus intestine				
Total (kcal/day)	343.3[c]	458.6[d]	489.1[d]	47.80
Protein, (kcal/day)	31.8[e]	35.4[ef]	44.4[f]	8.65
Fat, (kcal/day)	310.7[c]	423.2[d]	444.3[d]	41.53
No. of observations/mean	6	4	9	

[a] Standard deviation.
[b] Assumed the following kcal/gram for protein = 5.65 and fat = 9.40.
[cd] Means in a row with different superscripts differ ($P < .01$).
[ef] Means in a row with different superscripts differ ($P < .05$).

TABLE 16. EFFECTS OF METHOD OF GLUCOSE ADMINISTRATION ON POSTRUMINAL GUT COMPOSITION

	Treatment			
	Basal	Oral[a]	Infused[b]	SD[c]
Intestinal:				
Protein				
Weight (g)	109[f]	105[f]	138[g]	22.5
Percent	10.4	8.8	9.0	2.0
Fat				
Weight (g)	943[d]	1094[d]	1391[e]	171.09
Percent	89.6	91.2	91.0	2.2
Total Weight (g)	1052[d]	1199[d]	1529[e]	169.06
Omental weight (g)	2410	2774	2364	533.68
No. of observations/ mean	4	9	6	

[a]Basal diet plus 180 grams of glucose fed per day.

[b]Basal diet plus 180 grams of glucose infused per day.

[c]Standard deviation.

[de]Means in a row with different superscripts differ ($P < .01$).

[fg]Means in a row with different superscripts differ ($P < .05$).

TABLE 17. EFFECTS OF INTAKE LEVEL ON POSTRUMINAL GUT COMPOSITION

	Intake Level			
	Low	Medium	High	SD[a]
Intestinal:				
Protein				
Weight (g)	98[b]	124[bc]	126[c]	22.5
Percent	8.7	10.0	9.1	2.0
Fat				
Weight (g)	1027[b]	1133[bc]	1253[c]	171.09
Percent	91.3	90.0	90.9	2.2
Total Weight (g.)	1125[b]	1257[bc]	1379[c]	169.06
Omental weight (g)	2600	2452	2598	533.68
No. of observations per mean	6	4	9	

[a]Standard deviation.

[bc]Means in a row with different superscripts differ ($P < .08$).

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APPENDIX

TABLE 1. MINERAL COMPOSITION OF THE FORAGES UTILIZED IN CHAPTER IV

	Roughage Source				
	CSH	AH	SS	GCS	FCS
Mineral Analysis[a] (%)					
Calcium	0.32	1.75	0.56	1.60	0.51
Phosphorus	0.12	0.20	0.23	0.24	0.20
Magnesium	0.24	0.52	0.29	0.43	0.28
Potassium	1.21	1.14	1.74	1.36	1.70

[a]Mineral analysis was conducted by the Forage and Soil laboratory at Oklahoma State University.

TABLE 2. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH ALFALFA HAY

	Intake-roughage level interaction					Intake[e]		Roughage level (%)		
Intake level	1.2MM	1.2MM	1.6MM	1.6MM	SEM[b]	1.2	1.6	10	50	SEM[b]
Roughage level	10%	50%	10%	50%						
Digestibility: Organic Matter	70.3	65,2	70.3	61.3	2.0	70.3[f]	63.2[e]	67.7	65.8	1.4
Starch	84.5	93.5	77.4	83.7	2.4	89.0[f]	80.6[e]	80.9[e]	88.6[f]	1.7
Nitrogen	60.4	70.0	51.6	57.1	5.1	65.2[h]	54.3[g]	56.0	63.5	3.6
ADF	34.6	43.5	25.0	40.4	2.9	39.1[h]	32.7[g]	29.8[c]	42.0[d]	2.
NDF	39.9	47.5	19.4	41.1	4.1	32.2[e]	48.8[f]	28.2[e]	44.3[f]	2.
Hemicellulose	49.3	55.2	19.4	42.5	7.9	52.6[h]	30.9[g]	32.2[g]	48.8[h]	5.6

[a] MM = multiple of maintenance.

[b] Standard error of the mean.

[cd] Means within heading with different superscripts differ statistically ($P < .01$).

[ef] Means within a heading with different superscripts differ statistically ($P < .05$).

[gh] Means within a heading with different superscripts differ statistically ($P < .10$).

TABLE 3. EFFECTS OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH PRAIRIE HAY

	Intake-roughage level interaction					Intake[a]		Roughage level (%)		
Intake level[a]	1.1MM	1.1MM	1.85MM	1.85MM		1.1	1.85	10	50	SEM[b]
Roughage level	10%	50%	10%	50%	SEM[b]					
Digestibility: Organic Matter	82.2	72.6	77.1	65.9	2.0	77.4[f]	71.5[e]	79.7[d]	69.2[c]	1.4
Starch	93.7	93.9	89.2	78.7	3.9	93.8[f]	84.0[e]	91.5	86.3	2.8
Nitrogen	68.5	64.2	66.1	57.0	3.2	65.3	61.5	67.3[h]	60.5[g]	2.2
AFD	44.2	37.2	54.3	56.3	3.4	44.2	46.7	40.7[c]	55.3[d]	2.4
NDF	54.3	65.0	58.2	53.2	6.4	59.6	55.7	56.3	59.1	4.5
Hemicellulose	62.5	82.9	75.4	48.2	13.4	72.7	61.8	69.0	65.5	9.5

[a] MM = multiple of maintenance.

[b] Standard error of the mean.

[cd] Means within a heading with different superscripts differ statistically ($P < .01$).

[ef] Means within a heading with different superscripts differ statistically ($P < .05$).

[gh] Means within a heading with different superscripts differ statistically ($P < .10$).

TABLE 4. EFFECTS OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH COTTONSEED HULLS

	Intake-roughage level interaction					Intake[a]		Roughage level (%)		
Intake level[a]	1.1MM	1.1MM	1.9MM	1.9MM		1.1	1.9	10	50	SEM[b]
Roughage level	10%	50%	10%	50%	SEM[b]					
Digestibility:										
Organic Matter	82.8[h]	68.3[g]	73.8[gh]	68.0[g]	2.1	75.5[i]	70.9[h]	78.2[d]	68.2[c]	1.5
Starch	97.7[e]	97.7[e]	90.8[f]	96.3[e]	1.1	97.7[e]	93.6[d]	94.2[e]	97.0[f]	0.8
Nitrogen	67.6	55.0	62.6	54.4	2.5	61.3	58.5	65.1[d]	54.7[c]	1.7
ADF	24.0	42.2	27.1	43.6	8.5	33.1	35.3	25.6[g]	42.9[h]	6.0
NDF	36.2	48.0	45.9	44.6	6.7	41.0	45.8	40.2	45.2	4.7
Hemicellulose	55.2	61.3	56.0	49.0	5.6	58.2	51.3	55.4	55.1	4.0

[a] MM = multiple of maintenance.

[b] Standard error of the mean.

[cd] Means within a heading with different superscripts differ statistically ($P < .01$).

[ef] Means within a heading with different superscripts differ statistically ($P < .05$).

[gh] Means within a heading with different superscripts differ statistically ($P < .10$).

TABLE 5. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH SORGHUM SILAGE

	Intake-roughage level interaction					Intake[a]		Roughage level (%)		
Intake level[a]	1.2MM	1.2MM	2.0MM	2.0MM		1.2	2.0	10	50	SE
Roughage level	10%	50%	10%	50%	SEM[b]					
Digestibility:										
Organic Matter	73.3	76.0	69.6	65.2	5.0	74.6	67.4	71.4	70.6	3.0
Starch	83.9	90.2	79.7	76.7	5.4	87.1	78.2	81.8	83.4	3.8
Nitrogen	67.5	66.2	63.8	60.4	3.9	66.8	62.1	65.7	63.3	2.8
ADF	26.2	34.2	49.0	46.5	7.5	37.6	40.4	30.2[c]	47.7[d]	5.5
NDF	33.3	42.7	52.4	43.5	8.3	42.9	43.1	37.3	48.6	5.9
Hemicellulose	40.2	59.8	41.0	33.6	9.4	50.0	37.3	40.5	48.6	6.6

[a]MM = multiple of maintenance.

[b]Standard error of the mean.

[cd]Means within a heading with different superscripts differ statistically ($P < .01$).

TABLE 6. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH CORN SILAGE (GRAIN VARIETY)

	Intake-roughage level interaction					Intake[a]		Roughage level (%)		
Intake level[a]	1.28MM	1.28MM	2.15MM	2.15MM		1.38	2.15	10	50	SE
Roughage level	10%	50%	10%	50%	SEM[b]					
Digestibility:										
Organic Matter	79.4	80.2	67.8	76.6	2.6	79.8[f]	72.2[e]	73.6	78.4	1.8
Starch	89.2	92.1	77.4	90.4	3.0	90.7[h]	83.9[g]	83.3[e]	91.3[f]	2.1
Nitrogen	72.8[h]	79.6[h]	55.5[g]	69.7[h]	4.2	71.6[h]	62.6[g]	64.1	70.2	2.9
ADF	46.2	56.2	44.8	56.0	3.3	51.2	50.4	45.5[e]	56.1[f]	2.
NDF	54.8[f]	55.5[f]	40.6[e]	52.0[f]	1.9	55.1[d]	47.1[c]	48.7[e]	53.7[f]	1.
Hemicellulose	61.3	54.0	40.0	43.5	3.5	57.7[f]	42.0[e]	52.2	48.7	2.

[a]MM = multiple of maintenance.

[b]Standard error of the mean.

[cd]Means within a heading with different superscripts differ statistically ($P < .01$).

[ef]Means within a heading with different superscripts differ statistically ($P < .05$).

[gh]Means within a heading with different superscripts differ statistically ($P < .10$).

TABLE 7. EFFECT OF INTAKE AND ROUGHAGE LEVEL ON DIGESTIBILITY WITH CORN SILAGE (FORAGE VARIETY)

	Intake-roughage level interaction					Intake[a]		Roughage level (%)		
Intake level[a]	1.3MM	1.3MM	2.0MM	2.0MM	SEM[b]	1.3	2.0	10	50	SE
Roughage level	10%	50%	10%	50%						
Digestibility:										
Organic Matter	82.6	74.1	74.1	71.6	2.9	78.4	72.9	78.4	72.9	2.
Starch	92.9[d]	84.8[c]	86.6[cd]	88.5[cd]	2.5	89.7	86.6	88.8	87.6	1.8
Nitrogen	74.6	68.3	69.9	64.4	3.6	72.2	66.3	71.4	67.2	2.6
ADF	48.2	53.6	47.0	47.5	5.0	50.9	46.7	47.6	50.1	3.5
NDF	50.0[cd]	54.0[d]	54.8[d]	43.8[c]	3.6	52.0	48.5	52.1	48.9	2.5
Hemicellulose	51.3	54.6	56.2	39.0	5.6	53.0	46.4	53.4	46.8	4.0

[a]Multiple of maintenance.

[b]Standard error of the mean.

[cd]Means within a heading with different superscripts differ statistically ($P < .01$).

TABLE 8. PARTIAL CORRELATION COEFFICIENTS FOR THE PROTEIN LEVEL AND PROTEIN SOURCE STUDY--CHAPTER IV

	DMD	STADIG	NDIG	ADFDIG	NDFDIG	NEMDIG
DMD	--	.32	.51[x]	.57[x]	.71[x]	.35[z]
STADIG		--	.26	-.16[y]	-.08[x]	.03
NDIG			--	.42[y]	.54[x]	.07
ADFDIG				--	.59[x]	-.15[x]
NDFDIG					--	.60[x]
HEMDIG						--
BLOOD GLUCOSE	.39[z]	.01	.35[z]	.27	.08	.06
BUN	.24	.03	.35[z]	.05	.06[z]	.03
Rumen NH	.36	.06	.06	.02	.37[z]	.12
Rumen pH	.01[z]	-.08	.12	.01	.12	.19
Acetate	.37[z]	.30	.16[z]	-.19[x]	-.28[z]	.02
Propionate	.47[y]	.01	.36[z]	.63[x]	.37[z]	-.16
Butyrate	.03	.26	.08	-.22	.04	.10
Isobutyrate	.12	.13	.04	-.06	-.07	-.01
Valerate	.04	.25	-.11	-.15	.24[y]	.17
Isovalerate	.29	.01	-.32	-.57	-.49[y]	.03[z]
Caproate	.10	.05	-.11	-.05	.43[y]	.39[z]

	Acetate	Propionate	Butyrate	Isobuyrate	C_5	IC_5	C_6
Acetate	--						
Propionate	-.46[y]	--					
Butyrate	-.63[x]	-.31	--				
Isobutyrate	.05	-.17	-.14	--			
Valerate	-.52[x]	-.11	.67[x]	-.17	--		
Isovalerate	.12	-.64	.21	.06	-.11	--	

[x]Statistically significant ($P < .01$).

[y]Statistically significant ($P < .05$).

[z]Statistically significant ($P < .10$).

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