



Calcium levels in finishing cattle rations
by Randall Keith Dew

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE
in Animal Science

Montana State University

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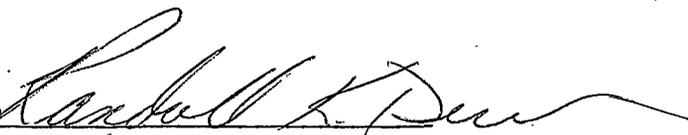
Abstract:

Four feeding trials were conducted with finishing steers to evaluate the effect of ration calcium level on feedlot performance, free-choice, high-calcium mineral consumption, fecal alkalinity, fecal pH, fecal starch content, and carcass merit. In trial I, 64 head of 324 kg. Simmental cross-bred steers were fed a 92% ground barley-8% roughage finishing ration ad libitum for 119 days. The steers were allotted to four treatments which consisted of the following: 1) .3% calcium in the ration, 2) .3% calcium in the ration + free-choice mineral, 3) .6% calcium in the ration, and 4) .6% calcium in the ration + free-choice mineral. Daily gain, feed per gain, daily ration intake, free-choice mineral consumption, fecal pH, fecal alkalinity, fecal starch content, and carcass merit were not found to be significantly different ($P > .05$) among treatments. Fecal starch was found not to be correlated ($P > .05$) with fecal pH. In trial II, 48 head of 275 kg. cross-bred steers were fed an 85% ground barley and wheat, 15% roughage finishing ration for 192 days. The steers were allotted to four treatments which consisted of the following: 1) .15% calcium, 2) .3% calcium, 3) .6% calcium, 4) .9% calcium in the ration dry matter. Among the four treatments there was no significant ($P > .05$) difference found in daily gain, feed per gain, daily feed intake, or fecal starch content. Fecal pH for steers fed treatment 4 (6.7) was greater ($P < .01$) than for cattle fed treatments 1 (6.1) and 2 (6.2). Fecal starch was found to be negatively correlated ($r = -.38$; $P < .01$) with fecal pH. Regression analysis indicated that 38% of the variation of fecal pH was due to a treatment effect. Quality grade for cattle fed treatment 4 was lower (11.5 vs. 12.5 and 12.4) than for cattle fed treatments 1 ($P < .01$) and 3 ($P < .05$). Also cattle fed treatment 4 had a lower marbling score ($P < .01$) than did cattle fed treatment 3. In trial III, 40 head of 235 kg. cross-bred steers were fed a high-roughage, low-grain growing ration for 56 days. The roughage was fed ad libitum and the grain mix intake limited to 1.0% of the steers' body weight per day. The steers were allotted to one of four treatments which consisted of the following: 1) .24% calcium, 2) .6% calcium, 3) 1.0% calcium, and 4) 1.9% calcium in the ration dry matter. Average daily gain, feed per gain, and daily ration intake were not found to be significantly affected ($P > .05$) by the four treatments. In trial IV, the steers used in trial III were fed an 85% ground barley and wheat, 15% roughage finishing ration for 178 days. The same ration calcium level treatments fed in trial II were used in trial IV. Neither of the four treatments were found to significantly ($P > .05$) improve daily gain, feed per gain, daily ration intake and carcass merit, or reduce fecal starch content. Steers fed treatment 4 did have a higher ($P < .05$) fecal pH (6.6 vs. 6.2) than did steers fed treatment 1. Regression analysis indicated that 24% of the variation in fecal pH ($P < .01$) was due to a treatment effect.

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CALCIUM LEVELS IN FINISHING CATTLE RATIONS

by

RANDALL KEITH DEW

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

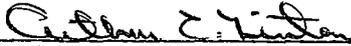
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ABSTRACT

Four feeding trials were conducted with finishing steers to evaluate the effect of ration calcium level on feedlot performance, free-choice, high-calcium mineral consumption, fecal alkalinity, fecal pH, fecal starch content, and carcass merit. In trial I, 64 head of 324 kg. Simmental cross-bred steers were fed a 92% ground barley-8% roughage finishing ration ad libitum for 119 days. The steers were allotted to four treatments which consisted of the following: 1) .3% calcium in the ration, 2) .3% calcium in the ration + free-choice mineral, 3) .6% calcium in the ration, and 4) .6% calcium in the ration + free-choice mineral. Daily gain, feed per gain, daily ration intake, free-choice mineral consumption, fecal pH, fecal alkalinity, fecal starch content, and carcass merit were not found to be significantly different ($P > .05$) among treatments. Fecal starch was found not to be correlated ($P > .05$) with fecal pH. In trial II, 48 head of 275 kg. cross-bred steers were fed an 85% ground barley and wheat, 15% roughage finishing ration for 192 days. The steers were allotted to four treatments which consisted of the following: 1) .15% calcium, 2) .3% calcium, 3) .6% calcium, 4) .9% calcium in the ration dry matter. Among the four treatments there was no significant ($P > .05$) difference found in daily gain, feed per gain, daily feed intake, or fecal starch content. Fecal pH for steers fed treatment 4 (6.7) was greater ($P < .01$) than for cattle fed treatments 1 (6.1) and 2 (6.2). Fecal starch was found to be negatively correlated ($r = -.38$; $P < .01$) with fecal pH. Regression analysis indicated that 38% of the variation of fecal pH was due to a treatment effect. Quality grade for cattle fed treatment 4 was lower (11.5 vs. 12.5 and 12.4) than for cattle fed treatments 1 ($P < .01$) and 3 ($P < .05$). Also cattle fed treatment 4 had a lower marbling score ($P < .01$) than did cattle fed treatment 3. In trial III, 40 head of 235 kg. cross-bred steers were fed a high-roughage, low-grain growing ration for 56 days. The roughage was fed ad libitum and the grain mix intake limited to 1.0% of the steers' body weight per day. The steers were allotted to one of four treatments which consisted of the following: 1) .24% calcium, 2) .6% calcium, 3) 1.0% calcium, and 4) 1.9% calcium in the ration dry matter. Average daily gain, feed per gain, and daily ration intake were not found to be significantly affected ($P > .05$) by the four treatments. In trial IV, the steers used in trial III were fed an 85% ground barley and wheat, 15% roughage finishing ration for 178 days. The same ration calcium level treatments fed in trial II were used in trial IV. Neither of the four treatments were found to significantly ($P > .05$) improve daily gain, feed per gain, daily ration intake and carcass merit, or reduce fecal starch content. Steers fed treatment 4 did have a higher ($P < .05$) fecal pH (6.6 vs. 6.2) than did steers fed treatment 1. Regression analysis indicated that 24% of the variation in fecal pH ($P < .01$) was due to a treatment effect.

Chapter 1

INTRODUCTION

The existence of the beef industry as it is known today is threatened by such factors as rising feed costs, interest rates, labor costs and reduced consumer demand with increased competition of meat from other species. The challenge facing the beef industry was expressed by Dr. W. T. Berry, Jr., executive vice president of the National Cattlemen's Association, who said in 1981, "Beef producers have lost their market to the tune of 20 percent since 1974, beef consumption in this country has dropped from 96 lb. per person to 78 lb. of beef at the retail level. We are in a protein battle and are being out produced, out processed and out merchandised by protein products with a lower price." The search for ways to increase economy and efficiency in all phases of beef production must be intensified in response to the various economic pressures being placed on the industry.

The cattle feeder, in particular, is one component of the beef industry whose livelihood is threatened by these economic pressures. Many advancements have been made over the years in maximizing production and improving the efficiency of feeding cattle for slaughter. The most obvious improvement has been a shift from high-roughage, low energy diets to more energy-dense rations consisting primarily of cereal grains and a limited amount of roughage. The more energy-dense

cereal-grain based diets (comprised of at least 80 percent cereal grain) would allow a faster and more economical gain versus grass or high roughage fattened cattle. As recently as 30 to 35 years ago, a typical cattle finishing ration would have consisted of only 40 to 50 percent grain and 50 to 60 percent roughage.

As the feeding of high grain diets became a more common practice, researchers noted that expected rates and efficiencies of production were not always realized (Noller, 1978). In fact, ration digestibility was found to decrease 10 percent or more when high-grain, low-roughage diets have been fed ad libitum to ruminants (Wheeler et al., 1975).

Several digestive disorders inherent with the feeding of high-grain diets are thought to be the major cause of reduced ration digestibility and animal performance. The primary physiological anomaly associated with high-grain diets is the prevalence of acidic conditions throughout the digestive tract of ruminants consuming diets high in readily soluble carbohydrates such as starch. Exogenous buffers have long been used in ruminant nutrition in an effort to combat this acidity and return the pH of the digestive tract to a level conducive for optimum nutrient utilization (Wheeler, 1980a).

Until recently, the focus of attention in the use of buffers has been in the control of pH in the reticulorumen with little concern for the pH environment of the small intestine. However,

recent research has provided evidence that elevating levels of calcium in ruminant rations using limestone (calcium carbonate) results in a higher pH in the small intestine, and improved performance and ration digestibility (Wheeler and Noller, 1977). This increase in small intestinal pH was accompanied by a reduction in the amount of starch appearing in the feces. In addition, the pH of the small intestine was found to be reflected in the pH of the feces.

Researchers have theorized that acidic conditions prevalent in the small intestine hamper the action of the enzyme alpha amylase on rumen-bypassed starch. Therefore, theoretically, ration digestibility and animal performance should be improved by the use of an exogenous buffer such as limestone which is known to be an effective small intestinal buffer.

In an effort to further define the effects of increased calcium levels in finishing cattle rations, four feeding trials were conducted with the following objectives under consideration:

1. Determine whether or not finishing cattle would exhibit improved performance and carcass merit if fed a level of calcium above that recommended by the National Research Council.
2. Determine whether or not ration calcium levels and calcium to phosphorus ratios less than those recommended by the National Research Council affect feedlot performance.
3. Determine whether or not increased calcium intake would affect fecal pH, fecal alkalinity, and the amount of starch in the fecal dry matter, and whether or not these

variables were related to feedlot performance or each other.

4. Determine whether or not ration calcium level would influence the daily intake of a free-choice, high-calcium (21 percent calcium and 7 percent phosphorus) mineral mix.

The subject of this thesis encompasses the results of those four feeding trials in light of the preceding objectives.

The review of literature will deal with the characteristics of high-grain, low-roughage diets fed to ruminants and the various digestive disorders associated with their consumption. The primary disorder to be considered is the reduction of pH throughout the entire ruminant digestive tract and the effect on ration starch digestion. The sites of starch digestion in the ruminant digestive tract will also be discussed. The review will conclude with various citations of the use of limestone as a lower tract buffer and calcium levels in ruminant rations.

Chapter 2

REVIEW OF LITERATURE

Degradation of Starch in the Digestive Tract

Ingested starch is catabolized primarily in the rumen utilizing hydrolytic enzymes produced by micro-organisms, or will be degraded in the small intestine via enzymes secreted in pancreatic fluid in the small intestine, Keller, et al. (1958).

Ruminal Degradation of Starch

In the rumen, starch is considered to be rapidly digested (Hungate, 1966). Rumen micro-organisms produce alpha amylase, an enzyme that will attack the interior of starch molecules. The end result will be the production of maltose, dextrans, and oligosaccharides (French, 1973). Since glucose is not formed directly from the action of this alpha amylase, micro-organisms must also produce maltase and dextrinase enzymes to yield glucose.

Bacteria will provide the principal means whereby starch is degraded to glucose, and glucose in turn fermented to steam-volatile organic acids and lactic acid. The bacteria species of Streptococcus bovis, Bacteroides amylophilus, Bacteroides ruminicola, Succinimonas amylolytica and Selenomonas ruminantium are known to include many starch digesting strains (Hungate, 1966). The Streptococcus bovis strain has been identified as producing an alpha amylase as well as

sucrose phosphorylase, isomaltase, and lactic dehydrogenase. The Bacteroides amylophilus strain is capable only of attacking starch and not glucose. The Succinimonas amylolytica strain, like the Bacteroides amylophilus strain, is unable to ferment glucose, but can act on hydrolysis products of starch (Hungate, 1966).

A large portion of the glucose formed in the rumen is fermented via the Embden - Meyerhof glycolytic pathway to steam volatile organic acids, primarily acetic, propionic, and butyric (Baldwin, 1965). Acids produced in smaller quantities include formic, isobutyric, 2-methylbutyric, valeric and isovaleric (Church, 1969). These acids are then absorbed through the rumen wall into the portal blood and utilized as an energy or glucose source by the ruminant (Blaxter, 1962). Vetter and Stifel (1971) found significant levels of fructose-1-phosphate, fructose-1,6-diphosphate aldolases, hexokinase, glucokinase, fructose-1,6-diphosphatase, pyruvate kinase and glucose-6-phosphate dehydrogenase in the rumen of corn fed steers.

Protozoa to a lesser extent will digest ration starch. The Entodinium species has been found to be the predominant protozoa in grain fed ruminants (Hungate, 1966). Mould and Thomas (1958) found that protozoa will synthesize starch in the form of amylopectin. The workers also determined the presence of alpha amylase, maltase, and amylo-1,6-glucosidase in protazoa cell extracts taken from sheep. Heald (1951), in studies with sheep, determined an

insignificant amount (5 to 6 g//24 hr.) of glucose was presented to the small intestine from protozoa. However, it should be noted the sheep in this trial were on all chopped hay diets with no grain. Weller and Gray (1954) also concluded that protozoa make insignificant contributions of glucose to the small intestine. Hungate (1966) stated that the protozoa will meet about one percent of the daily carbohydrate requirements of the host.

Small Intestinal Digestion of Starch

The means by which starch is degraded in the small intestine to glucose appears to be quite similar between the ruminant and monogastric animals. In both species the pancreas will secrete an aqueous and an organic phase of fluid into the duodenum by the common bile duct (Hill, 1970). However, it appears that in addition to the common bile duct, ruminants also possess a major duct from the pancreas to the duodenum, thereby providing two routes for pancreatic secretions to the small intestine (Wass, 1965).

The aqueous phase is high in sodium bicarbonate and will provide the major means of buffering the small intestine from acids produced in the rumen and the abomasum. The organic phase will contain the enzymes and zymogens responsible for digestion such as: trypsinogen, chymotrypsinogen, procarboxypeptidase A and B, and carboxypeptidase B; nucleolytic enzymes such as ribonuclease and deoxyribonuclease;

lipolytic and amylolytic enzymes. The amylolytic enzymes such as alpha amylase will comprise less than two percent of the enzymes present in the pancreatic secretions. This is considered extremely low compared to the concentration of amylolytic enzymes present in the pancreatic fluid of man (Keller et al., 1958).

Pancreatic alpha amylase catalyzes the hydrolysis of the alpha 1-4 linkages in the interior of the starch polymers presented to the small intestine. The products of this hydrolysis will be maltose, maltotriose and alpha limit dextrans (since most of the ingested starch is amylopectin). The majority of amylase activity takes place in the intestinal lumen (Gray, 1970). Dextrinase and maltase enzymes will then catalyze the hydrolysis of the maltose, maltotriose and alpha limit dextrans to glucose (Siddons, 1968). Most likely this hydrolysis takes place within the intestinal columnar cells (Gray, 1970). In the presence of adenosine triphosphate (A.T.P.) and hexokinase, glucose is phosphorylated and actively transported across the cell membrane (Hele, 1950; Gray, 1970).

In the monogastric animal the absorption of glucose begins in the duodenum and is completed in the proximal 100 cm. of the jejunum (Borgstrom et al., 1957). Hembry et al. (1967) in studies with mature sheep found that the greatest amount of glucose uptake occurred in the jejunum. These workers also noted that amylase was the second most abundant carbohydrase enzyme in the small intestine next to maltase;

and concluded that since maltase was plentiful, complete hydrolysis of starch is more dependent on amylase acidity. Absorption of glucose from the colon was found to be extremely low.

Borgstrom et al. (1957), in intestinal intubation studies with humans, found a wide variation in the concentration of enzymes over the length of the intestine. Hembry et al. (1967), in studies with sheep, found the mucosa of the jejunum contained the greatest amount of all enzymes with the duodenum containing the least.

Large Intestinal Digestion of Starch

Significant amounts of starch escape rumen fermentation and are digested in the large intestine. However, Waldo (1973) indicated that the capacity of the large intestine to digest starch is not well defined.

Karr et al. (1966) suggested that on high concentrate diets more starch may reach the small intestine of cattle than is able to be utilized. In their study, total tract digestion of starch ranged from 97.7 to 98.8 percent, indicating the carbohydrates passing the small intestine undigested were digested quite well in the large intestine. It was also noted 4.3 g/kg b.w. ^{3/4} of starch was presented in the large intestine, 83 percent of which was digested in this region of the gut. With increasing levels of starch in the ration, post-ruminal digestion of starch remained high, but increasing

amounts were digested in the large intestine. McNeill et al. (1971), in trials with various forms of sorghum grain, found an average of 6.5 g/kg. b.w.^{3/4} of starch was presented to the large intestine of 370 kg. Angus steers, of which 88 percent was digested.

The mode of starch digestion in the large intestine is primarily that of fermentation by anaerobic micro-organisms, with the subsequent production of steam volatile organic acids such as acetic, propionic, and butyric. These acids are absorbed across the large intestinal wall in the same manner as those produced in the rumen and utilized as an energy source by the ruminant (Orskov et al., 1970).

In considering the economy of post-ruminal starch digestion, starch degraded via enzyme catalysis in the small intestine with the subsequent uptake of glucose will be more efficient than the fermentation of starch in the large intestine. Armstrong et al. (1960) infused glucose into either the rumen or abomasum of sheep fed a basal ration of dried grass. Rumen infused glucose was utilized with 54.5 percent efficiency, with 42.3 kilocalories fat stored per 100 kilocalories of glucose administered. The abomasal infused glucose that bypassed rumen fermentation was utilized with 71.5 percent efficiency with 61.6 kilocalories of fat stored on the animal per 100 kilocalories of glucose administered.

In addition to energy losses from heat, and gasses produced from fermentation, microbial nitrogen synthesized would also be lost as no

digestion of microbes would take place beyond the large intestine. In studies with sheep, Orskov et al. (1970) determined that 1.6 g. of nitrogen was excreted in the feces for every 100 g. of carbohydrate fermented in the large intestine.

Carbohydrase Activity and Development in the Young Ruminant

The young ruminant apparently has limited abilities to degrade starch in the small intestine due to limited amounts of amylase and maltase being produced. Dollar and Porter (1957) gave oral solutions of glucose, lactose, sucrose, maltose, dextrans, and soluble starch to young dairy calves. The workers found that during the first four weeks of life the calves utilized only glucose and lactose. At nine weeks of age the calves were able to utilize maltose. The results of this study indicate, that in the young calf, amylase and maltase activity is very low, and lactase activity very high. Huber et al. (1961), using calves 22 to 600 days old, introduced slurries of glucose, lactose, maltose, sucrose, amylose, amylopectin, flojel (acid treated starch), and tapioca starch orally. Starch, maltose, and sucrose were poorly utilized in contrast to glucose and lactose that were well utilized in the small intestine. Lactose utilization decreased markedly with age. Maltase levels increased up to 6 to 8 weeks of age. Blood sugar responses to treatment were twice as great at 6 to 8 weeks of age than at 2 to 4 weeks of age. Walker (1959) found little amylase activity and no sucrose activity in

young lambs. However, amylase activity was found to increase with age.

Henschel et al. (1963) gave 10 g. each of several carbohydrate treatments to 4 to 6 month old calves. The carbohydrates administered were: raw wheat starch, maltose, lactose, sucrose and glucose. Only two percent and 14 percent of the glucose and lactose respectively were recovered at the proximal end of re-entrant intestinal cannulas. As much as 60 percent of the raw wheat starch and 62 percent of the sucrose were recovered. With the addition of amyloglucosidase to the starch treatments, only seven percent of the raw wheat starch was recovered. Larsen et al. (1956) also found a limited ability of calves to utilize corn starch post-ruminally and noted very limited amylase activity in this area. Siddons (1968) noted that in young calves amylase activity increased with age and reached a maximum at 101 days of age. Maltase activity was found to be independent of age and quite similar between the adult and calf.

Cereal Grain Starch in Ruminant Rations

The primary cereal grains fed to ruminants in the United States are: corn, barley, sorghum, wheat, and oats. Starch present in each cereal grain expressed as a percentage of dry matter is as follows: corn, dent, yellow, all analysis, 71.3 percent; barley, all analysis, 63 percent; sorghum, all analysis, 70 percent; wheat, all analysis, 63 percent; oats, all analysis, 50 percent. Corn and

sorghum account for about 80 percent of the starch from concentrates fed to ruminants with slightly more than 35 million metric tons of starch consumed by domestic animals in the United States in 1970 (Waldo, 1973). Eighty-three percent of this starch was consumed by cattle on feed (54 percent) and milk cows (29 percent).

In plants, starch exists as granules in cells known as plastids (Banks and Greenwood, 1975). French (1973) described these discrete water insoluble starch particles or granules as being from 1 μm to well over 100 μm in diameter. Gray (1970) indicated that starch existed in these granules in two molecular forms, that of amylose and amylopectin. Approximately 20 percent of cereal grain starch is amylose and 80 percent amylopectin. Amylose is a homogenous, polymerized molecule consisting of D-glucose units linked via alpha 1-4 glycosidic bonds (French, 1973). Each molecule will be comprised of approximately 1000 D-glucose residues and prefers a coiled helix confirmation with 6 glucose residues per turn (Everett and Foster, 1959; Metzler, 1972). Amylopectin is a highly branched molecule consisting of 1000 to 500,000 D-glucose residues. Amylopectin is similar to amylose in that the vast majority of the glucose residues are linked to each other via alpha 1-4 bonds. However, in amylopectin branch points or chains will occur linked by alpha 1-6 glycosidic bonds. These chains will occur every 25 to 30 glucose units, and consist of 20 to 25 glucose molecules. The alpha 1-6 linkages will

comprise up to 4 to 5 percent of the total linkages present in amylopectin (Oser, 1965).

The majority of ingested starch is fermented in the rumen by anaerobic micro-organisms to steam volatile fatty acids. Microbial fermentation can also take place in the ceacum and colon of the lower gut. In either case, these acids are absorbed through the gut wall into the portal blood stream and utilized in the liver as an energy or carbon source (Baldwin, 1965). Propionic acid serves as the principal source of glucose for the ruminant but acetic and butyric are considered ketogenic (Topps et al., 1968).

The means by which ration starch is utilized as an energy source depends on where digestion takes place. Significant amounts of starch will also undergo enzymatic degradation to glucose in the small intestine in a manner similar to that of the monogastric animal. The end result is the uptake of glucose in the small intestine (McDonald, 1969). In this digestion, the inefficiencies of fermentation resulting from heat, carbon dioxide and methane production are not present (Armstrong et al., 1960).

Site and Extent of Starch Digestion in the Ruminant Digestive Tract

It has become increasingly apparent that the lower gut (small intestine, ceacum and colon) makes a significant contribution to the

nutritional well being of the ruminant (Noller, 1978). Henschel et al. (1963) concluded through studies with young steers there was extensive carbohydrate digestion occurring post-ruminally due to digestive enzyme action and bacterial fermentation. McCullough (1973) speculated that the gain and feed efficiency advantage of whole corn versus flaked corn diets was due to an increased rumen by-pass of whole corn to the small intestines. McCullough's speculation was based upon his review of several experiment station research trials. Poutiainen et al. (1971) when feeding young steers a mixed diet of barley and grass hay versus grass hay only, thought it interesting that 14 percent more of the mixed diet was digested in the ceacum, and resulted in a 12 percent greater carcass weight gain.

The site of starch degradation in the gastro-intestinal tract appears to be influenced by four factors. These factors are as follows: 1) the level or proportion of grain to roughage in the ration, 2) the level of intake, 3) the type of grain processing and 4) the type of cereal grain fed.

The Influence of the Grain to Roughage Ratio

In general, as the proportion of grain to roughage in a ration increases greater quantities of starch escape rumen fermentation. Zinn and Owens (1980a) fed a 40 percent hay, 60 percent rolled corn

diet to steers fitted with dual re-entrant cannulas in the small intestine. The workers found 443 g. of starch escaping rumen fermentation from this diet. When the hay was reduced to 20 percent of the ration, and the corn increased to 80 percent, undigested starch leaving the abomasum more than doubled to 956 grams. Poutianen et al. (1971) found similar results with young calves. In this study the amount of dry matter escaping rumen fermentation increased 14 percent when 50 percent barley was included in a previously all dried hay diet. Macrae and Armstrong (1969) found that an increase of rolled barley from 33 to 66 percent in rations fed sheep increased the starch escaping to the proximal duodenum from 17.5 to 26.5 grams per 24 hours. Topps et al. (1968) fed either all hay or hay plus 298 g. of starch to sheep in order to evaluate the influence of the presence of concentrate on digestible energy disappearance in the gastro-intestinal tract. There was nine percent less digestible energy disappearing in the reticulo-rumen, omasum, and abomasum, and 16 percent more digestible energy disappearing in the small intestine in the hay plus starch diet than the all hay diet. Tucker et al. (1968) found as much as 35 percent of dietary starch escaped rumen fermentation in four wethers fed diets ranging from 20 to 80 percent corn. These workers noted that post-ruminal digestion of starch was very efficient with only 20 to 26 g. of starch appearing in the feces regardless of the level of corn in

the diet. Karr et al. (1966) fed yearling Angus steers rations consisting of 19 to 35 percent starch, and found that 16 to 38 percent of the starch escaped rumen fermentation. It was noted in this study that as starch intake increased digestibility decreased in the small intestine, and increased in the large intestine. Teeter et al. (1980) found that with 554 kg. Angus steers fed whole corn no roughage diets significant amounts of starch escaped rumen, and post-ruminal digestion, and appeared in the feces. The amount of undigested starch present in the feces was reduced 85 percent when 40 percent roughage was added to the ration in the form of cottonseed hulls or alfalfa hay.

In contrast, other workers have shown forage level in the ration to have little effect on the extent of ruminal bypass of starch. Topps et al. (1969) fed diets of increasing starch content to steers and found the amount of starch reaching the abomasum undigested varied little among diets. It should be noted that ration intake was restricted in this study which has been shown to limit the bypass of starch from the rumen (Wheeler et al. 1975). Nicholson and Sutton (1969) fed diets with either 80:20 or 25:75 ratios of concentrate to roughage to sheep. The diets with the highest proportion of concentrate showed only a slight increase in the amount of undigested starch reaching the duodenum. All but 5 to 11 percent of the starch was fermented in the rumen. However, there is evidence rumen

fermentation in sheep is more extensive than cattle (Armstrong and Beever, 1969).

The Influence of the Level of Ration Intake

Although with high grain rations, substantial amounts of ration starch escape rumen degradation, most of the work cited in the preceding section indicate total tract starch digestion is complete and efficient. Most of the previously cited studies report total tract digestibilities of starch at 90 to 100 percent, with little or no loss of starch in the feces (Waldo, 1973). However, Wheeler (1980a) indicated that the majority of these trials were done with animals fed at or near maintenance levels of ration intake. Therefore, in many trials, stresses are not placed on the ruminant similar to those found when full feeding high concentrate rations.

Karr et al. (1966) noted that total tract digestion of ration starch was from 97 to 99 percent regardless of the level of starch in the ration. In these trials, only 12 to 62 g. of starch appeared in the feces. Tucker et al. (1968) noted total tract digestibility of starch was from 94.5 to 98.4 percent. Orskov et al. (1969), in trials conducted using different forms of corn or barley fed to sheep, noted a mean of only one percent of ration starch appearing in the feces, and total tract digestion of starch from 99.2 to 99.3 percent. It should be noted that in one lamb, 25 percent of the

dietary starch escaped rumen fermentation in this study.

Wheeler et al. (1975) fed rations of forage-concentrate ratios of 75:25, 60:40, 45:55, and 30:70 to Holstein cows. When these rations were fed at maintenance levels of intake, starch digestibility averaged 96.2 to 96.8 percent. Starch appearing in the feces at this level of intake was only 5 percent of the fecal dry matter. When the rations were fed at 2.3 to 3.2 times maintenance level of intake, starch digestibility decreased and ranged from 84.7 to 88.1 percent. The percentage of starch appearing in the feces increased to 13.4 percent of the fecal dry matter. Wheeler et al. (1976) again fed high concentrate diets ad libitum to lactating dairy cows and noted that the percent of fecal starch ranged from 19.0 percent for barley rations up to 40.0 percent for corn based diets. In another study with crossbred steers fed ad libitum a high moisture corn and silage ration, Wheeler and Noller (1976b) found the percent of starch in the fecal dry matter as high as 32.4 percent.

Zinn and Owens (1980a) fed a 20 percent roughage, 80 percent rolled corn diet to Angus steers at two levels of intake. At an intake of 1.5 percent of body weight/day, 338 g. of ration starch was presented to the small intestine. Increasing the intake to 2.0 percent of the steers bodyweight/day increased the amount of starch presented to the small intestine to 956 g./day. Watson et al. (1972b) fed what were considered a low level (5.08 kg. dry matter/24 hr.) and

a high level (8.6 kg. dry matter/24 hr.) of rolled barley rations to mature cows. In the low level diet, 91.4 percent of the ration starch was digested before the duodenum, and 9.0 percent in the small intestine. The workers indicated an appreciable amount of dietary starch escaped rumen fermentation with the high level of intake, 75.8 percent of which was digested in the small intestine, 22.5 percent fermented in the ceacum, and only 1.7 percent appeared in the feces.

Orskov et al. (1969) found that when intake of rolled barley or rolled barley plus grass hay diets was decreased from ad libitum to 70 percent of ad libitum intake, the amount of starch escaping the rumen undigested decreased an average of 38 percent. Little et al. (1968) infused 200, 400, and 600 g. of starch into the abomasum of steers twice daily in order to estimate the digestion of starch in high concentrate rations. The workers found that as the level of ration starch increased the digestibility of starch in the small intestine decreased, with greater quantities being recovered in the posterior ileum and the feces.

Nicholson and Sutton (1969) fed .9, 1.7 and 2.3 multiples of maintenance intake of high grain rations to sheep. In this study, all but 5 to 11 percent of the ration starch was fermented in the rumen regardless of the level of intake. As mentioned earlier, this may be due to the species used since rumen digestion in sheep is

apparently more extensive than in cattle (Armstrong and Beever, 1969).

The Influence of Grain Processing

Various methods of processing cereal grains for livestock has continued to improve the palatability or the utilization of grains. There are at least eighteen different means of processing grain, including grinding, steam rolling, pelleting, flaking or dry rolling (Hale, 1973).

Grains that have undergone extensive processing will be digested more thoroughly in the rumen (McCullough, 1973). McNeill et al. (1971) evaluated the digestibility of sorghum grain processed by four different methods. The sorghum grain was either dry ground, steam flaked, reconstituted whole kernel and ground prior to feeding or micronized. Ruminal starch digestion was greatest for steam-flaked sorghum and least for the dry ground form.

Galyean et al. (1976) compared the digestibilities of four processed forms of corn. Evaluated were dry rolled, steam flaked, ground ensiled high moisture corn, and acid-treated high moisture whole corn. The workers found that the ground high moisture, and steam flaked corn had greater total tract digestibility reflecting greater degradation in the rumen. There was no difference in the digestibility of starch in the small intestine among any of the different methods of processing.

Beever et al. (1970) fed diets of four parts corn and one part dried grass to sheep. The corn was either ground or steam flaked. Starch digestion in the rumen was 95.6 percent for the steam-flaked corn and only 77.7 percent for the ground corn. When the steam flaked form was fed, only .8 g./24 hr. of starch appeared in the feces. Total tract digestibility of starch was still 99.6 and 99.9 percent for the ground and steam flaked forms respectively, despite 22 percent of the starch passing the rumen undigested from the ground corn diet. McCullough (1973) fed either flaked corn or whole corn to yearling steers and found rumen, small intestine, ceacum and colon and total tract starch digestibility of 91.1 percent, 7.9 percent, 0.9 percent, and 97.6 percent for the flaked corn diet and 61.1 percent, 34.0 percent, 2.5 percent and 99.8 percent for the whole corn ration.

Macrae and Armstrong (1969) found that, in trials with sheep, more undigested whole barley versus rolled barley appeared in the feces. Orskov and Fraser (1972) noted that rumen breakdown of pelleted barley was greater than whole barley in sheep feeding trials. MacLeod et al. (1972), in studies with growing steers, found that when whole barley diets were fed, there was a 10 percent reduction in dry matter and nitrogen digestibility when compared to the digestibility of rolled barley. Orskov et al. (1969) fed either flaked corn, ground corn, or cracked corn to sheep and found that undigested starch reaching the abomasum was twice as great for the

lambs fed ground or cracked corn as for those fed the flaked-corn diets.

The Influence of the Type of Cereal Grain Fed

Waldo (1973) indicated corn, sorghum, wheat, oats, and barley as the most commonly used cereal grains. The location and extent of starch digestion will also depend in part on the type of grain used in the ration.

Kay et al. (1972) fed pelleted diets of either whole wheat, whole corn, whole barley or whole oats to 100 to 400 kg. Holstein steers. The amount (g./day and percent of intake) of undigested starch passing the abomasum was: 395 g. (17 percent), 1008 g. (40 percent), 398 g. (19 percent) and 417 g. (27 percent) for the wheat, corn, barley and oats diets respectively.

Barley is more extensively degraded in the rumen than is corn. Watson et al. (1972a) fed rolled barley or ground and pelleted corn to mature cows. The barley and corn rations contained an average of 73.0 percent and 74.8 percent apparent digestible energy. The percentage of apparent digestible energy disappearing before the duodenum, in the small intestine and the ceacum and colon was 65.0 percent, 23.0 percent and 13.6 percent, respectively for the barley ration. Corresponding values for the corn diets were 54.4 percent, 34.7 percent and 12.0 percent. Orskov et al. (1971a) fed diets

consisting of rolled barley and various protein levels to sheep fitted with abomasal and ileal cannulas. The workers noted that even when fed at near ad libitum intake, 93 percent of the barley starch was digested in the rumen. Orskov et al. (1971b) studied various rumen characteristics associated with barley or corn diets fed to sheep. The rumen fermentation values for the barley and corn were 91.0 percent and 78.0 percent, respectively. The amount of corn digested in the small intestine varied from 2 to 37 percent of the ration intake. When large quantities of starch escaped rumen fermentation, an average of 6 percent of ingested starch was fermented in the large intestine, and up to 2.0 percent appeared in the feces. These fermentation values are in close agreement with Waldo (1973), who indicated barley, flaked corn, steam flaked sorghum, wheat and oat starches were about 94 percent fermented in the rumen. Ground corn starch was said to be about 74 percent fermented in the rumen.

Tyrrell et al. (1972) compared barley and corn for efficiency of fattening 416 kg. yearling heifers. The workers found little difference in energy utilization between barley and corn. Metabolizable energy for corn was used with 53.2 percent efficiency and for barley 47.5 percent efficiency. It was noted that as intake increased for both barley and corn, available metabolizable energy decreased.

Sorghum starch is said to be the cereal grain starch most resistant to rumen digestion. The extent of rumen degradation will

be influenced by endosperm types of sorghum. This factor is exemplified by the following endosperm types for sorghum and their associated rumen fermentation values: corneous, 48 percent; normal, 18 percent; waxy, 75 percent; and floury, 80 percent (Waldo, 1973). McGinty and Riggs (1968) studied the digestion co-efficients of eight different varieties of sorghum grain when fed to steers. The co-efficients of digestion ranged from 50.0 percent to 71.58 percent. McNeill et al. (1971) fed dry-ground, steam-flaked, reconstituted or micronized forms of sorghum grain as four treatments to Angus steers. They found rumen fermentation values varied greatly according to type of processing. These values were 42.25 percent, 66.28 percent, 82.23 percent, and 43.38 percent for the dry ground, steam flaked, reconstituted and micronized forms, respectively. There was no difference noted in total tract digestibility of starch. Holmes et al. (1970) fed steamed or pressure steamed sorghum grain to sheep and cattle. Both the steamed and pressure steamed forms of the sorghum had rumen fermentation values of 90 and 95 percent respectively and total tract digestibility of 97 percent.

The extent of ruminal starch digestion for wheat starch is thought to be similar for barley. Oat starch is also thought to be readily attacked in the rumen (Waldo, 1973).

Digestive Irregularities and High Grain Diets

Digestive irregularities are often associated with high intakes of high-grain, low-roughage rations. These digestive anomalies include: 1) the development of acidic conditions in the reticulorumen small and large intestine, 2) a marked reduction in the production of alkaline, buffering saliva, 3) an accelerated rate of passage through the digestive tract at high intakes, and 4) a possible decrease in the activity of pancreatic alpha amylase resulting in poor hydrolysis of undigested starch presented to the small intestine (Noller, 1978). Wheeler (1980a) indicated the major digestive anomaly is the development of acidic conditions in the digestive tract. The acidic condition in combination with the other digestive disorders cause an unfavorable environment to exist in the gastrointestinal tract for the optimum utilization of nutrients.

Reticulorumen pH

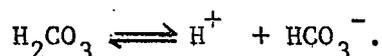
The pH of the reticulorumen area is the result of volatile fatty acid (VFA) production and absorption, level of feed intake, and saliva production (Wheeler, 1980a). Reticulorumen pH is maintained within the pH 5.5 to 7.3 range. Values associated with the lower end of this range (pH 6.0 and below) often accompany reduced feed intake, reduced reticulorumen motility, and impaired fermentative capabilities for the rumen micro-organisms (Trenkle, 1979). Protozoal populations are lost or greatly diminished as pH

drops. Hungate (1966) found protozoa were unable to survive at pH 5.5. Reduced pH conditions in the reticulorumen often precede the the production of lactic acid (pKa 3.8) from increased numbers of Streptococcus and Lactobacillus organisms. The production of large amounts of lactic acid often results in sudden death syndrome or lactic acidosis in feedlot cattle (Uhart and Carroll, 1967).

Reticulorumen Buffer Systems

The ruminant must possess a means of maintaining a pH environment conducive to microbial growth because large amounts of volatile fatty acids are produced which are found to yield pH values of 2.78 to 3.03. Three major systems the ruminant utilizes to buffer this acidity include the following: 1) the exchange of bicarbonate across the rumen wall, 2) the blood buffer system, and 3) the salivary buffer system (Bartley, 1975).

Kay and Hobson (1963) described the initial step of the bicarbonate exchange system in the reticulorumen as the diffusion of carbon dioxide (CO₂) across the rumen wall. Carbonic anhydrase, an enzyme abundant in animal tissue, would catalyze the hydration of CO₂ to carbonic acid (H₂CO₃) (Metzler, 1977). Carbonic acid is a weak acid and would dissociate into the bicarbonate (HCO₃⁻) and hydrogen ion (H⁺) in the following manner:



The result of the dissociation of carbonic acid is the establishment

of a conjugate acid-base system between carbonic acid and the bicarbonate ion (Trenkle, 1979).

The blood buffering system is present in the plasma and erythrocytes, and maintains blood pH at pH 7.4 despite the absorption of substantial amounts of volatile fatty acids from the reticulorumen. Erythrocytes such as hemoglobin make use of the bicarbonate buffer system, and the imidazolium group of the amino acid histidine as proton acceptors. Blood plasma will make use of the phosphate buffer system ($\text{H}_2\text{PO}_4^- / \text{HPO}_4 = \text{pKa } 7.2$) but obtains 75 percent of its buffering capabilities from the bicarbonate system (Trenkle, 1979).

Kay and Hobson (1963) described the role of the salivary buffer system as being a first-line defense against acidity in the reticulorumen from the production of organic acids. McManus (1959) diverted saliva from the reticulorumen of sheep and noted VFA levels rose from 60 to 115 molar equivalents / liter of rumen fluid. The pH of the reticulorumen environment decreased from 6.7 to 6.2 after the saliva was diverted. When saliva was not diverted, VFA levels decreased approximately 30 molar equivalents and the pH increased slightly. Similar effects were shown in later work by McManus (1962) when saliva was prevented from entering the reticulorumen of sheep that were fitted with esophageal cannulas.

Saliva is a mixture of secretions originating from the parotid, submaxillary, buccal, inferior molar, sublingual and labial glands

(Trenkle, 1979). Saliva is strongly alkaline with a pH of 8.1 because the secretions of the parotid inferior molar, and buccal glands are strongly buffered with bicarbonate and phosphate (Bartley, 1975). The bicarbonate buffer system is the primary means used in saliva to buffer reticulorumen acidity. Saliva is most effective as a buffer in the pH range of pH 6 to 7 (Trenkle, 1975).

Reticulorumen Acidity and Volatile Fatty Acid Production

The volatile fatty acids are produced in the reticulorumen in sufficient quantities to provide 60 to 80 percent of the metabolizable energy required by the ruminant (Thorlacius and Lodge, 1973). Organic acids produced in such quantities would have a marked effect on reticulorumen acidity unless they are sufficiently absorbed or neutralized (Trenkle, 1979). Briggs et al. (1957), in studies with rumen fistulated sheep, found an inverse relationship existed between volatile fatty acid levels and reticulorumen pH. Balch and Rowland (1957) also found an inverse relationship existed between volatile fatty acid levels and reticulorumen pH in their studies with Shorthorn cows.

The reticulorumen concentration of volatile fatty acids is in the range of 60 to 120 millimoles / liter of rumen fluid. The concentration of volatile fatty acids in the reticulorumen can reach a maximum of 200 millimoles / liter of rumen fluid, especially

when high concentrate finishing rations are fed. Passive uptake of volatile fatty acids occurs across the squamous, stratified, reticulorumen epithelium. The diffusion of volatile fatty acids across the reticulorumen wall is dependent on their concentration in the blood (Trenkle, 1979). The reticulorumen epithelium is more permeable to the unionized than the ionized form of the volatile fatty acids. The pKa of the VFA is low (2.7 to 3.03); therefore, absorption will tend to increase as reticulorumen pH decreases (Thorlacius and Lodge, 1973). Sutton et al. (1963) using rumen fistulated calves, 16 to 21 weeks of age, studied the absorption of VFA across the reticulorumen wall at different pH levels. Phosphoric acid or sodium hydroxide was used to adjust the reticulorumen pH environment. Absorption at pH 5.0 was more than double the rate of absorption at pH 6.6 and four times the rate of absorption at pH 8.0. These findings suggest that as pH in the reticulorumen decreases, blood VFA levels could increase to a point where absorption would be hindered because of rapidly increasing concentrations in the blood.

High-grain diets are readily fermented in the reticulorumen, resulting in the rapid production of volatile fatty acids. The relationship between ration characteristics and reticulorumen VFA levels is aptly described in the following quote by Church (1969), "However, it is probably safe to conclude that the ingestion of

immature grass, increasing amounts of carbonaceous or protein supplements, increasing levels of feed intake, and pelleted roughages tend to result in higher VFA levels." Phillipson and McAnally (1942) demonstrated the differences in the effect of roughage versus concentrate on reticulorumen pH and VFA levels when 100 g. of starch or cellulose were infused into the reticulorumen of sheep. The infused corn starch caused a prolonged decrease in reticulorumen pH and a steady sustained rise in the VFA levels. The cellulose infusion caused no such effect on pH or VFA levels. Kern et al. (1974) demonstrated that near neutral conditions (pH 6.9) existed in the reticulorumen of steers fed an all roughage diet consisting of timothy hay. Luther and Trenkle (1967) fed all-roughage rations to lambs and noted a pH of 6.5 in the reticulorumen. These workers added 40 percent concentrate to the diet and noted that pH levels in the reticulorumen decreased to pH 6.2.

Diets consisting of part grain or all grain will usually result in increased VFA levels and decreased pH in the reticulorumen. Briggs et al. (1957) used rumen fistulated sheep to demonstrate the effect of including grain in a ration on reticulorumen pH and VFA levels. The sheep first received an all roughage ration which caused reticulorumen VFA levels to increase to a maximum of 104 millimoles / liter of rumen fluid and pH level to decrease to 5.85. The sheep were then adapted to a high grain diet

(70 percent wheat grain, 30 percent roughage, and 85 g. of starch) which caused reticulorumen VFA levels to rise to a maximum of 153 millimoles / liter of rumen fluid and pH to drop as low as 4.5. Phillipson (1942) found results similar to Briggs' results after feeding four types of rations to rumen fistulated sheep. The diets were composed of the following: oats and bran; pasture grass; grass hay; or mangold and cabbage. The mangold and cabbage diet was considered a high-concentrate diet high in reticulorumen soluble carbohydrates such as starch. The mangold and cabbage diet caused a rapid fall in reticulorumen pH accompanied by increased VFA levels.

Work by Thompson et al. (1967) suggests ration particle size will influence reticulorumen pH and VFA levels. The workers fed Angus steers ground or flaked corn with no hay, or with 1.8 kg/day of either chopped or long hay. Steers fed corn and long hay had significantly higher rumen pH values (pH 6.3) and lower VFA levels (126.5 millimoles / liter of rumen fluid) than steers fed the corn plus ground hay diet (pH 5.9 and VFA level of 155.7 millimoles / liter of rumen fluid). Shaw et al. (1960) fed two groups of eight Holstein steers ground corn with coarsely chopped alfalfa hay (diet 1) or flaked corn fed with finely ground alfalfa hay (diet 2). Diet 2 caused a twofold increase in reticulorumen VFA levels (1357.4 mg./100 ml. rumen fluid) over diet 1 (580.4 mg./100 ml. rumen fluid). Reticulorumen pH was not measured in this study. Rhodes and Woods

(1962) fed long stem alfalfa hay to sheep and noted a reticulorumen pH level of 6.1. The same type hay was subsequently finely ground and pelleted, with ground corn added to the diet. The pelleted hay and corn diet caused rumen pH to decrease to 5.8. There was little difference in total VFA levels between the hay and pelleted hay and corn diet, but the molar percent propionic acid did increase when the hay and corn ration was fed. Noller (1980) would interpret the difference in reticulorumen pH between the diets to the greater production of propionic acid which is often associated with reduced pH in the reticulorumen. Esdale and Satter (1972) decreased the reticulorumen pH of Holstein cows from 6.2 to 5.6 and found the molar percentage of propionic acid to increase from 19.8 to 37.2 percent. The molar percent of acetic acid decreased from 68.5 to 43.0 percent. Bailey (1961) would indicate the effect of ration particle size on reticulorumen pH and VFA production to be due to a decrease in saliva production and reduced buffering characteristics in the reticulorumen.

The level of ration intake also influences reticulorumen pH and VFA production. Rumsey et al. (1970) fed steers all concentrate diets consisting of cracked corn. The levels of ration intake were at .5, 1.0, 1.5, and 2.0 percent of steer bodyweight per day. Reticulorumen pH and VFA levels (millimoles / liter of rumen fluid) for each increasing level of intake were as follows: 6.2, 115.9;

6.2, 136.6; 5.9, 163.2; and 5.7, 183.9. Bath and Rook (1963) increased the intake of all roughage rations fed to cows from 4.5 to 9.1 kg./hd./day. The higher level of intake caused reticulorumen VFA levels to increase from 7.4 to 10.5 molar equivalents / 100 ml. or rumen fluid. Reticulorumen pH decreased from 6.65 to 6.3 as intake increased to 2.0 percent of bodyweight.

Acidity in the Lower Gastro-intestinal Tract

The pH environment of the lower gastro-intestinal tract of the ruminant was thought to be of little consequence to its nutritional well being (Noller, 1978). However, Harrison and Hill (1962) noted in their studies with sheep that the duodenum is a highly acidic environment which is poorly buffered by pyloric, duodenal, and pancreatic secretions. The workers concluded that enzyme activity in the small intestine would be limited due to the acidic conditions. Wheeler and Noller (1977) indicated the desirable pH of the small intestine to be from pH 6.5 to 7.0. This pH range theoretically would allow for the optimum activity of pancreatic alpha amylase and the efficient degradation of starch bypassing the reticulorumen undigested. These workers demonstrated in slaughter studies with cattle and sheep that acidic conditions prevail not only in the reticulorumen but also in the small and large intestine in ruminants fed high grain rations, and that little change in pH occurs through

the lower tract to the feces. In one trial, Holstein steers were fed all-concentrate diets, ad libitum, consisting of either rolled barley, whole kernal corn, or cracked corn. The pH of the reticulorumen (RR), small intestine (SI), colon (C), and feces (F) for each of the three respective diets were as follows: RR: 5.84, 5.64, 5.38; SI: 6.18, 5.75, 5.75; C 6.17, 5.93, 5.82; F: 6.11, 5.93, 6.00. Wheeler et al (1976) fed eight crossbred ram lambs a pelleted, 80 percent corn grain diet for 84 days. The lambs were evenly divided into two groups with one group fed ad libitum, and the second group fed at maintenance intake of digestible energy. The pH levels of the small intestine for both the ad libitum and maintenance intake groups were 6.16 and 6.25. Wheeler and Noller (1977) found there was no significant difference ($P > .10$) between the pH of the small intestine and the feces in their studies. They concluded that the pH of a fecal grab sample was an excellent indicator of pH in the small intestine. Ferreira et al. (1980) also found no significant difference between fecal pH and small intestinal pH in their studies with Holstein heifers and calves.

Kern et al. (1974) demonstrated that near neutral conditions not only prevail in the reticulorumen, but also in the small and large intestine of steers fed all timothy hay diets at two percent of bodyweight per day for 30 days. The pH of the reticulorumen (RR), small intestine (SI), Cecum (CE), and terminal colon (TC) were the

following : RR: 6.0; SI: 7.3; CE: 7.0; TC: 7.2. Armstrong and Beever (1969) noted that the pH in the jejunum of sheep fed grass hay cubes ranged from pH 7.2 to 7.9. Ben Ghedalia et al. (1974) added 600 g. of concentrate to a vetch hay diet fed to sheep and noted the pH did not increase to 7.7 until the terminal ileum.

Digestion in nonruminants such as humans takes place primarily by enzyme catalysis in the small intestine. The acidity arising from the acid secretions of the stomach is effectively buffered by pancreatic and intestinal secretions. Borgstrom et al. (1957) noted with humans that the pH of the stomach ranged from 2.5 to 3.0, but increased immediately in the duodenum to 6.0. Kay (1969) demonstrated the ruminant does not have the same buffering capabilities in the small intestine as the nonruminant. In his studies with sheep, Kay noted the secretions from the duodenum and jejunum were weakly alkaline and contained very little bicarbonate. The pH in the intestine of these sheep was found to increase gradually from 2.4, .05 meter from the pylorus to 5.2, 2 meter beyond the pylorus to 7.8, .3 meter before the caecum.

Copious and continuous influxes of acid chyme from the reticulorumen and abomasum combined with the weakly alkaline nature of the secretions entering the small intestine produce the lower pH often existing in the small intestine (Noller, 1978). The abomasum is comparable to the simple stomach in nonruminants, with the pH

remaining close to 3 (Phillipson, 1977). The acid chyme leaving the abomasum is a continuous process and is only partially neutralized in the small intestine (Harrison and Hill, 1962). The secretion of hydrochloric acid from the abomasum was found to increase as intake increased in studies with sheep by Ash (1961). Using an innervated fundic pouch of the abomasum, the workers measured the secretion of hydrochloric acid. Increasing the intake of a dried grass hay diet from 700 g. to 1100 g. per day increased the secretion of hydrochloric acid from 15 to 45 molar equivalents per 24 hours. The increased ration intake also increased the rate of passage of acid chyme from the abomasum from 130 to 250 milliliters / 30 minutes, with a maximum outflow of 934 milliliters / hour. Harrison and Hill (1962) noted the rate of passage of material through the duodenum of sheep increased from 13.3 to 26.0 milliliters per hour when feeding was increased from once per day to three times per day. The workers did not state whether or not the amount of ration was also increased. The preceding work suggests the common practice of full feeding rations to ruminants would increase the rate of digesta passage and the secretion of hydrochloric acid from the abomasum to the small intestine.

Impaired Saliva Production

Normally, large quantities of saliva are produced by ruminants

daily. Putnam et al. (1966a) found the production of saliva in 350 kg. beef steers varied from 33.5 to 54.1 liters per day. Bailey (1961) collected and dried boluses from the reticulorumen and estimated the daily saliva output of a mature cow to range from 98 to 190 liters per day. Kay (1959) estimated sheep will secrete from 6 to 16 liters of mixed saliva per day.

The accepted practice of feeding processed high-energy, low-fiber rations to ruminants often results in a marked reduction in salivary secretion and reticulorumen pH (Emmanuel, 1968). This reduction in saliva production is due primarily to decreased time spent chewing or ruminating (Bartley, 1975). Putnam et al. (1966b) fed four steers (average weight 400 kg.) a ration consisting of 89 percent hay at 1.5 percent of bodyweight daily intake. The hay was coarsely ground, or finely ground (10 millimeter screen) and pelleted. Saliva secretion decreased from 2.0 to 1.4 liters / hr., and reticulorumen pH decreased significantly ($P < .10$) when the steers were fed the pelleted hay. The workers also demonstrated the effect of roughage level on saliva production and reticulorumen pH. The hay was reduced to 25.0 percent of the ration with 63.0 percent cracked corn added to the diet. Saliva secretion decreased from 2.0 liters / day for the all roughage ground hay diet to 1.5 liters / day for hay diet which included grain. The pH of the reticulorumen also decreased from pH 6.7 to 6.3. Baily (1961) also found that

