THE NET ABSORPTION AND SECRETION OF DRY MATTER, WATER SODIUM, POTASSIUM, CALCIUM, MAGNESIUM, AND ZINC THROUGHOUT THE GASTROINTESTINAL TRACT OF SHEEP

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ABSTRACT

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By

Dale Elton Bauman

The sites within the gastrointestinal tract where absorption and secretion occur are not well known, especially in the mature ruminant. In the present study, a nonabsorbable marker technique (Cr_2O_3) was used to determine the site and extent of net absorption and secretion of certain dietary nutrients as digesta passed through the gastrointestinal tract. One prerequisite for this technique is that the indicator move through the tract with the nutrient under study. Therefore, nutrient flux patterns were studied at two different time periods (postprandial) to establish if the flux patterns were the same.

Sixteen individually penned sheep were fed one of four different hay diets. The roughage diets were siberian reed grass, reed canary grass, alfalfa early cut (cut 6/25/65), and alfalfa late cut (cut 7/16/65). All sheep were fed constant amounts of their respective diet at 12 hour intervals. Sheep were trained so that the amount offered was consumed in a one-hour period.

At the end of the one-hour feeding period, a gelatin capsule containing 1.0 gram Cr_2O_3 was given, and this time was considered to be zero time. After 10 days of Cr_2O_3 dosing, one-half of the sheep were sacrificed at 6 hours postprandial and the remainder at 12 hours. The gastrointestinal tracts were removed and divided into nine segments

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by ligation, and contents of the sections weighed and sampled.

Daily dry matter consumption averaged 16.3, 22.5, 28.5, and 21.7 g/kg body weight for sheep fed the siberian reed, reed canary, alfalfa early cut, and alfalfa late cut respectively. No differences were apparent in the pH values of digesta from those sheep sacrificed at 6 hours or 12 hours postprandial. The gastrointestinal digesta accounted for 18.7% and 17.4% respectively of the body weight for sheep sacrificed at 6 hours and 12 hours postprandial.

Rate of passage for the different diets as determined by amount of Cr_2O_3 in the tract, indicated the grass diets averaged 1.11 days while the corresponding value for the alfalfa diets was 0.89 days.

Dry matter and Cr_2O_3 distribution data coupled with the flux pattern of dry matter, indicated the method of giving Cr_2O_3 in a gelatin capsule did not give adequate mixing with the diet in the rumen. Therefore nutrient flux patterns found in the rumen were of limited value. However, mixing appeared to be complete by the time digesta had passed to the abomasum.

The overall flux patterns between the sheep sacrificed at 6 hours and 12 hours postprandial were in very good agreement for every nutrient studied, thereby suggesting that the Cr_2O_3 was moving through the digestive tract at the same rate as the nutrients studied. Since chromium oxide is water insoluble, it seems likely that from the abomasum on through the hind gut, the digesta must be moving as a water-digesta-slurry complex.

Fifty percent of dry matter was absorbed as digesta passed through the stomach (rumen, reticulium, omasum, and abomasum). Dry matter was secreted into the proximal portion of the small intestine and reabsorbed as

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as digesta passed through the remainder of the small intestine so that digestibility of the roughage diets averaged 50%.

A net absorption of H_2O, Na, K, Zn, Ca, and Mg occurred in the stomach. A large net secretion of H_2O, Na, K, and Zn occurred in the proximal small intestine with minimum estimates of daily secretion being 12.0 liters, 26.5 g, 27 g, and 107 mg respectively. Calcium and magnesium were also secreted into the proximal small intestine, but were of less relative magnitude than the other nutrients mentioned. A net absorption of water, Na, K, and Zn occurred in the remainder of the small intestine with H_2O, Na, and lesser amounts of K being absorbed in the large intestine. There was no net absorption of Ca or Mg from the small intestine or large intestine.

It appears that the major portion of the dietary mineral was absorbed in the stomach for every mineral studied. The small intestine absorbed the greatest quantity of H_2O, Na, K, and Zn, but was merely reabsorbing the large secretions which occurred in the proximal portion of the small intestine.

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INTRODUCTION

Mineral constituents in the ruminant amount to 4-6% of its body weight with the proportions of the different minerals in the adult animal being very similar for all species. The role of such minerals in the body is very diverse and yet very important. Minerals are found as an essential part of the body's structure; they are involved in body regulatory functions such as pH and osmotic balance with this function being very important in the rumen of ruminants; minerals are constituents of some enzymes and activators of other enzyme systems. In fact, the specific roles and the extent of these roles for the different minerals in the body is just beginning to be understood.

Five main factors influencing the amount of nutrient that an animal obtains from a ration are the concentration of the nutrient in the ration, the amount of the ration consumed, the extent of digestion, the rate of passage, and the rate of absorption. Although these factors are all interrelated, the process of absorption forms the basis of this thesis.

Absorption of a compound may be defined as removal or an efflux of that compound from the gut either by diffusion or by active transport, while secretion may be defined as emitting into the gastro-intestinal tract or influx of a constituent into the medium or lumen. For example, the absorption of calcium from the small intestine would be an efflux of calcium from the gut lumen while secretion of calcium i

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into the gut lumen would be an influx of calcium. However, this is complicated by the fact that both absorption and secretion may be, and probably are occurring simultaneously and with most techniques one can measure only net absorption or net secretion. When results show that a net absorption of calcium has occurred in the small intestine this means that an actual absorption of calcium has occurred but simultaneously no secretion has occurred or that a secretion less than absorption has occurred. In most textbooks and in this thesis the term absorption should be taken to mean net absorption while secretion should be interpreted to mean net secretion or accumulation of nutrient within the organ specified.

The process of absorption of minerals from the gastrointestinal tract requires that the mineral in the ingesta be available in a chemical and physical form for absorption and also that the gastrointestinal tissue has the ability to act as an absorbing surface. These two requirements do not seem to be complicated, in fact Ingelfinger (87) has calculated that the human small intestine has a potential absorbing surface area larger than half a basketball court. If an animal can absorb a molecule the size of an amino acid or a fat micelle then surely a small mineral ion should be absorbed.

Mineral absorption however, is not as simple as would seem at first glance. One is amazed to find that a ruminant can suffer from milk fever or a calcium deficiency and still be absorbing only 20-40% of the dietary calcium. The same situation is found in a magnesium deficiency where magnesium tetany results while the animal is absorbing only 10-30% of the dietary magnesium passing through the tract.

Most physiology and nutrition textbooks state that the absorption

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of minerals occurs in the small intestine (64, 129, 167). An exception to this is Hungate (81), who states that absorption of polyvalent mineral ions occurs mainly in the abomasum. An examination of the research on mineral absorption in ruminants indicates a severe lack of information on comparative absorption processes and the extent of absorption along the entire tract. No definite answer is available on the specific site of mineral absorption and the comparative importance of the various gastrointestinal tract sections nor on possible aids to increase absorption in certain sections of the gastrointestinal tract.

The author's hope is that this thesis might provide some insight into the overall process of mineral absorption in the ruminant animal.

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REVIEW OF LITERATURE

Absorption and Secretion Study Techniques

The history of the development of techniques for the study of absorption and digestion is both fascinating and stimulating. In 1864 Thiry, as quoted by Wilson (167), created a new era in research by surgically preparing an intestinal fistula which permitted absorption experiments in an unanesthetized animal. Ten years later a German investigator, Eugene Wildt, as quoted by Hyden (84), studied absorption and secretion of several of the ash constituents (Na, K, Ca, Mg, Fe, P, S and Cl) by using the silica in the diet as a reference material.

Over the years research techniques for studying absorption have been improved and modified. These techniques fit into the following general categories:

1) Perfusion of isolated organs.
2) Everted sac technique.
3) Tissue slices or strips.
4) Arterio-venous difference.
5) Permanent fistulas in the gastrointestinal tract combined with the use of a reference material.
6) Non sacrifice of the animal combined with the use of a reference material.

7) Sacrifice of the animal combined with the use of a reference material.

Perfusion studies of isolated organs are done by isolating the organ and perfusing a known solution through the organ and measuring changes in nutrient concentration. This technique allows the researcher to control the flow rate of a known perfusate. However, maintenance of normal physiological situations is difficult to achieve with this technique.

Everted sac techniques and tissue slice methods are similar to the perfusion of an isolated organ, in that changes in concentration of a known solution are measured to determine absorption. Also an even greater problem exists in extrapolating the experimental results to physiological conditions. Because of their simplicity the everted sac and the tissue slice techniques have been used extensively for the study of absorption of sugars and amino acids. Wilson (167) and Crane (39) have reviewed the use of these techniques.

The A-V(arterio-venous) differences are obtained by sampling the blood supply flowing into an organ or area and sampling the blood returning from that organ or area. Then by determining the concentration change and multiplying this by the blood flow rate one obtains the amount of a compound absorbed per unit time. This method is used by relatively few investigators due to surgical difficulties and problems in measuring blood flow rate. Several organs have more than one supply and return of blood making it difficult to quantitate entire blood exchange when more than one vein and artery are involved. The A-V difference method lends itself to repeated sampling but it is very difficult to maintain physiological conditions.

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Permanent fistulas at various points along the gastrointestinal tract yields knowledge of absorption processes without sacrificing the animal. However, it is difficult to pinpoint the exact site of absorption and secretion, i.e., an ileum cannula provides information on net flux processes which occurred to that point but yields no information on which of the areas of the alimentary tract preceding the ileum are involved in giving the resulting net flux.

By feeding a reference material mixed in the diet and collecting fecal samples for analysis, one can calculate apparent absorption but this gives no data as to influx and/or efflux of the nutrient at different sites along the gastrointestinal tract.

The final technique listed is sacrifice of the animal combined with use of a reference material. In this method the digestive tract may be subdivided into sections and by comparison of the compound and reference material concentrations, results can be obtained as to net absorption or net secretion. Thus the net influx and net efflux may be followed by comparing progressive sections of the gastrointestinal tract. This method has the disadvantage that the animal has to be sacrificed.

In order to obtain information as to the exact sites of net absorption and secretion of organic and inorganic ions and the importance of these sites in relation to the rest of the gastrointestinal tract, one must use a series of permanent fistulas or the animal sacrifice technique.

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Reference Materials Used in Absorption and Secretion Studies

Reference substances differ widely from one another and may or may not be water soluble. They may be constituents of the normal diet or may be added to the ration. There are however, certain characteristics which all reference materials should possess. These desired characteristics are:

1) Indicator should exhibit no influence on the normal digestive processes of the animal or exhibit any unpalatable properties.
2) Indicator analysis should be relatively simple giving good duplication.
3) Indicator should be nonabsorbed from the alimentary tract to any significant extent with 100% of the dose fed recovered in the feces.
4) Indicator should move through the digestive tract at the same rate of passage as the nutrient under investigation.

The importance of a reference material possessing these four characteristics cannot be overstressed. A classic illustration of a reference material not meeting the desired characteristics is $BaSO_4$. Barium Sulfate was used in early studies on absorption processes but was found to exhibit laxative characteristics which greatly changed the rate of passage (101).

The first man to use an indicator or reference material to study absorption in the gastrointestinal tract apparently was Eugene Wildt in 1874 (84). Working with sheep, Wildt used the silica in the ration as a reference material. A few of the various reference materials that have been used in absorption studies are iron oxide, silica, chromium oxide,

dyes, barium sulfate, insoluble ash, glass beads, lignin, cerium-144, and polyethylene glycol. Summaries of reference substances used and examples of their use in absorption studies have been written (28, 37, 89).

Chromium oxide (Cr_2O_3) is one of the most widely used reference materials (4, 37, 46, 54, 122, 171). Analysis is relatively simple with several methods being available (18, 93, 164). Fecal recoveries of Cr_2O_3 generally range from 95-100% of the dose given. A review of several studies on chromium absorption is found in Nutrition Reviews (146). The results showed that trivalent Cr was 99.6% recovered in the feces whereas divalent Cr was slightly absorbed. Chromium Oxide can be mixed in the diet as a powder, in pellet form or impregnated on paper strips and has been reported to travel with the dry matter in the digestive tract (34, 83). The fact that Cr_2O_3 does travel with the dry matter of the digesta should be considered when it is to be used as a reference material for water soluble constituents.

Lignin has been used in absorption studies by a number of workers (46, 66, 171) with recoveries being 90-100%. Lignin is difficult to define with different methods of lignin analysis giving different results. Yang and Thomas (171) using the VanSoest method for lignin analysis found that Cr_2O_3 and lignin gave similar results in absorption studies except for the rumen wherein all ratio values were reduced when Cr_2O_3 was used as the marker.

Polyethylene glycol (PEG) is another indicator that has often been used and has been generally considered to travel with the liquid fraction of the digesta. PEG is a highly polymerized long-chain compound with a w

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molecular weight of about 4000 and a general formula $CH_2OH-(CH_2-O-CH_2)_n-CH_2OH$ (84). PEG recoveries vary with many investigators reporting almost 100% recovery of consumed marker in feces (28, 84),with other investigators reporting recoveries of 85-92% (33, 139). Corbett *et al*. (34) reported difficulty in analysis for PEG. Smith (139) worked with calves having a fistula at the distal end of the small intestine and found a 100% recovery of the PEG dose at this point but only a 90% recovery in the feces, suggesting a 10% destruction in the large intestine. When a wide range of concentrations of polyethylene glycol were fed, Smith (141) found no significant effect on animal digestion or on transit time of the digesta. The idea that PEG is water soluble and moves with the liquid fraction of the digesta is generally accepted but no published data showing the percent of PEG associated with the ultrafiltrable portion of the digesta in any gut section could be found. This idea is questioned by the work of Coombe and Kay (31) which indicated that PEG was retained slightly though significantly longer than stained straw in the small intestine.

Stained feeds (31, 48, 141) and pectin (62) have also been used as reference materials in absorption studies but generally recoveries have been low thus making their use of limited value.

Several radioisotopes have been used as references in studying absorption. Radioactive indicator use creates a problem in disposal of excreta and disposal of the animal since under present Food and Drug Administration regulations these animals cannot be returned to a normal life with the herd or sold on the open market.

Cerium-144 recoveries ranged from 93 to 119% (27, 58, 83). Research indicated that the cerium-144 was absorbed on and bound to

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the dry matter (58, 83) although Cragle and colleagues (37) indicated it was water soluble. Cragle and co-workers further found that Cr_2O_3 and Ce-144 gave similar results in young and old animals when used as reference materials.

Yttrium-91 has been used in rats and chickens to study digestion and absorption with fecal recoveries of 96-101% (82, 101). Yttrium-91 has not been used for ruminant studies.

Downes and McDonald (43) used a Chromium-51 complex of ethylene-diamine tetraacetic acid as a soluble rumen marker and found 85-91% recovery in feces with an additional 5% being lost in the urine.

The reference materials commonly used in absorption studies generally fit the first three characteristics necessary for a reference material. That is, they have no effect on the normal digestive processes at the concentration used, they give repeatable results in their determinations, and they are relatively nonabsorbed. However a problem arises in deciding whether the reference substances and the nutrient under study travel along the gastrointestinal tract at the same rate. One method of determining if the nutrient and the reference material are traveling at the same rate is to look at the fecal concentrations of both at different times after feeding. If the nutrient and reference substance travel at the same rate then the ratio of one concentration to another should remain constant. Rate of passage, involving mineral studies is further complicated by the fact that the fraction of digesta with which the mineral travels is unknown. Thus in mineral studies one assumes that the mineral and marker travel together or that they are in constant equilibrium. Movement as a water-digesta-slurry complex might also be possible. Horvath (80) in a paper given at a recent symposium, discussed this problem. He stated that "it is likely that at least two indicators are required; one for the fluid phase and one for the solid phase of the ingesta and that the proportion of the nutrient in each phase would also need to be determined". In order to compare different indicators and their rate of passage Horvath (80) simultaneously fed Cr_2O_3, Cr-51-EDTA and PEG to sheep for eight days prior to sacrifice. The alimentary tract was divided into 9 segments and Mg-28 absorption calculated. The three indicators did not give the same results. Huston and Ellis (83) on the other hand found that Ce-144, Cr_2O_3, and polyethylene glycol did not differ significantly as reference materials in rate of passage studies.

There is a possibility that the mucosa epithelium of the digestive tract may be shed in sacrificed animals depending on the sacrifice technique. Badary _et al_. (7) reported there was a marked shedding of the duodenal epithelium in animals that were shot and bled but that very little shedding of epithelium occurred in the abomasum or the remainder of the small intestine. Thus if the indicator was bound to the epithelium mucosa it would be released into the lumen, resulting in an error in net efflux and influx calculations. This problem has been investigated only in the case of Ce-144, by Miller _et al_. (109). They found 92% of the total alimentary tract Ce-144 was bound to the ingesta while 0.5, 0.3 and 0.05 percent of the daily dose of Ce-144 was bound to the rumen, omasum, and abomasum tissue respectively. This work was done with calves fed a hay and concentrate diet.

Definitive research comparing the rate of passage of indicators (soluble and water insoluble), nutrients, and digesta (liquid, solid r

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and slurry) is needed.

Absorption and Secretion in the Gastrointestinal Tract of Ruminants

Dry Matter

The dry matter eaten by a ruminant may be considered to traverse the digestive tract in three stages (60). First, the food mixes with saliva and is swallowed in the rumen where it is fermented by microorganisms and a large portion of the organic matter is degrated and absorbed. Therefore in the rumen one finds intake, passage, nutrient absorption, fermentation, secretion, and synthesis going on simultaneously. Second, the food residues, saliva, and microorganisms themselves pass on to the abomasum and small intestine where they are exposed to acid and enzyme secretions of the animal. Finally, what remains flows into the large intestine where it is subjected to microbial attack a second time following which the undigested residues are excreted.

The dry matter of a diet is usually considered to be everything except the water. This makes it difficult to compare different rations in dry matter flux along the digestive tract because the constituents comprising dry matter and the percent of these constituents in different diets may vary widely. The net flux of dry matter or other nutrients in a diet has been shown to be further complicated by the fact that many physical parameters affect ruminant digestion. For example Meyer (106) concluded that the physical form of the ration influenced total digestibility by its effect on food intake, rate of passage, rate of digestibility, as well as the effect of physical form of the ration on the end products of digestion.

Results with different diets indicated that from 23 to 70% of the dry matter fed disappeared in the stomach (12, 79, 105, 133) and 12 to 34% in the hind gut (12, 133). One can calculate from Yang and Thomas' data (171) that an average of 71% of the dietary dry matter disappeared in the stomachs of calves. They also reported an average secretion of dry matter into the upper small intestine of 658% of abomasal dry matter levels with a gradual absorption of dry matter occurring in passage through the remainder of the digestive tract.

Results have indicated that as intake increased the percent of dry matter digested in the stomach decreased (65) and also that the percent of dry matter digested by the stomach increased as succulent feed replaced roughages (133). Sineshchekov (133) reported for every kilogram of dry matter consumed there were 10 to 15 liters of chyme entering the intestine in all farm animals. The chyme was 25% dry matter and the daily volume of chyme entering the intestines was about one-half the weight of the animal itself.

Research on organic matter digestion indicated that 63 to 69% of the total digested organic matter disappeared in the stomachs of cows and sheep fed hay or high starch diets while the same value decreased to 43 to 46% for ruminants fed high straw diets (22, 120). Bruce and colleagues (21) found similar results with re-entrant cannulae indicating that 68% of the digested organic matter disappeared in the stomach. These same researchers also determined that 20% of the digested organic matter disappeared in the small intestine and 12% in the large intestine. Yang and Thomas (171) studied net flux of organic matter along the entire alimentary tract of calves. They reported a 78% net absorption of organic matter in the rumen, and a large net secretion of organic matter into the upper small intestine. They further reported that a gradual absorption of organic matter occurred primarily in the remainder of the small intestine but also in the large intestine.

Hale et al. (67) determined that about 43% of the dietary cellulose was digested in the stomach of ruminants. Other research indicated that 70 to 90 percent of the total cellulose digested was digested in the stomach of ruminants with the remainder being digested in the cecum and large intestine (21, 60, 61, 67). Hale and co-workers (67) reported the soluble portions of the diet were rapidly digested during the first 6 hours after feeding while the greatest proportion of digestion of cellulose took place during the 6 to 12 hours post feeding period in experiments with cows fed a beet pulp and alfalfa hay diet.

Campling and co-workers (22) concluded that 59 to 65% of the total digestible crude fiber of hay and straw diets was digested in the reticulo-rumen while Ridges and Singleton (123) reported the crude fiber disappearance in the stomach of ruminants amounted to 85 to 100% of the total crude fiber digested. Yang and Thomas (171) studied crude fiber flux along the entire alimentary tract in calves, using Cr_2O_3 and lignin as the reference materials. They reported a net absorption of crude fiber from the reticulo-rumen of 40% of the total fiber in the ration with the percent digested being significantly greater for high fiber diets as compared to low fiber diets.

Water

Water is necessary for all animal life with most tissues containing 70 to 90% water (103). The rumen itself may hold 10-25% of total body water of the ruminant and can act as a water store in times of H_2O deprivation (72). The water requirement of animals can be met from three sources; (1) water contained in the food, (2) water consumed as drinking water, and (3) the metabolic water formed in the body as a result of oxidation in the tissues. The body must receive sufficient water to balance its losses in addition to the amount required for formation of new tissues or products. It is evident that factors such as temperature, urine volume, and many others influence the water loss causing a wide variation in requirement. The factors affecting water losses are summarized in articles by Leitch and Thomson (96) and by Cuthbertson (40).

Saliva is the source of a large portion of ruminal water. Estimates indicated that the total salivary secretions of sheep and cattle were 10 and 150 liters per day respectively (10, 90). Wilson (166) estimated the volume of saliva entering the rumen each day represented more than twice the volume of fluid usually present in the rumen at any one time.

Water balance into and from the rumen has not been studied, possibly due to the problem of determining water intake and the fact that water is so readily available. In the omasum, 31 to 80% of the water in rumen digesta was absorbed with the average value being about 60%, indicating the importance of the omasum in water absorption (9, 63, 171).

The design of the omasum is such that it would seem possible for some of the material passing from the reticulum to reach the abomasum via the omasal groove, without entering between the leaves of the omasum. Gary and colleagues (63) observed the starch: lignin ratio in the rumen, omasum and abomasum contents and concluded that only very small amounts of reticular contents pass directly to the abomasum. Gray et al. also determined by nitrogen: lignin ratios of successive organs, that the mechanical process of squeezing liquid from the ingesta in the omasum contributed very little to the increase in concentration of the residual plant solids in the omasum. This indicated the decrease in water in the omasum was due to a real absorption of water.

Secretion of water can occur in the abomasum (9, 84, 171). Badawy and co-workers (9) reported that the increase in water content in the abomasum was 123-197% over that found in the omasum. Masson et al. (102) calculated that five liters of abomasal juice were secreted into the abomasum of the sheep each day. Ridges et al. (123) using a cannula two inches below the pylorus in goats, reported that 12-15 liters of fluid were added per day to the stomach. Hogan and Phillipson (79) estimated the water secretion into the stomach of sheep was six liters per day.

Net absorption of water has been shown to occur along the remainder of the gastrointestinal tract in many species with the large intestine playing a primary role (20, 79, 84, 139, 171). Bruce et al. (21) used cannulae with chromium sesquioxide as the reference material and concluded that the small intestine absorbed most of the water, phosphorus, potassium, and chloride present in the duodenal digesta while the large intestine absorbed most of the remaining water and chlorine. Bruce *et al*. pointed out that in the small intestine, water was secreted in bile, pancreas secretions and other intestinal secretions. Goodall and Kay (60) found that 88% of the water entering the large intestine of sheep was absorbed.

Water has been generally considered to be passively absorbed along the entire gastrointestinal tract being drawn from the lumen as an osmotic consequence of potassium and sodium flux into the body. Recently, water was shown to be actively absorbed in the small intestine of dogs (161) but whether this is true in the ruminant and the relative importance of this process to net water absorption of the animal is not known.

Water *per se* may influence absorption and secretion of various minerals. Although this has not been widely studied, especially in the case of ruminants, Suttle and Field (153) reported that in sheep intra-ruminal additions of water decreased fecal magnesium and increased urinary magnesium excretion.

Sodium

The distribution of Na in the tissues is markedly different from that of potassium. First, the sodium ion can enter the mineral lattice of the bone and is found there in concentrations of 4 grams Na per kg of bone (40). Secondly, sodium is mainly found in the extracellular fluids and is the predominant basic element concerned in neutrality regulation. Sodium salts circulate through the body with Na making up 93% of the basic ions of the blood serum (103).

Normal ruminant rations are low in sodium and must be supplemented to supply sufficient Na to meet requirements. Even with unsupplemented rations the main source of ruminal sodium was not the diet but salivary secretions (11, 118, 144). Ruminant animals have a marked ability to conserve sodium ions. When fed diets deficient in sodium ruminants decreased the Na losses via the feces to almost zero and also reduced Na and Cl urinary losses (20, 160).

Van Weerden (160) found that the contents of the abomasum were slightly hypotonic with respect to blood. At the beginning of the small intestine there was a sharp increase until marked hypertonicity was attained, which gradually declined with distal movement of digesta until the contents approached isotonicity in the rectum. Under several different feeding regimes, Smith (142) found that digesta from calves and cows approached an isotonic state with regard to the blood by the end of the small intestine. Changes in sodium and chlorine concentrations of the digesta were found to be the main factors in the tonicity change.

Perry and co-workers (119) examined the flux of sodium along the entire gastrointestinal tract of calves fed concentrate or concentrate plus hay rations. They reported a three fold net secretion of Na in the rumen and a large net absorption of Na in the omasum (calculated to be 76% average net absorption of Na as compared to the diet). They further found a slight secretion of Na in the abomasum but a 3-4 fold net secretion over rumen levels in the first section of the small intestine. This large secretion of sodium was reabsorbed throughout the remainder of the small intestine with a further net absorption occurring in the large intestine. This resulted in a 78-80% net absorption of Na for the diet.

Yang and Thomas (171), working with calves and using lignin as an indicator, found that sodium was absorbed in the rumen, lower small intestine, and rectum, whereas a sodium secretion occurred in the abomasum and upper small intestine. However, they also found a net secretion of Na in the cecum and first section of the small intestine.

Research involving young calves with re-entrant fistulas at various positions in the small intestine indicated that a considerable net amount of endogenous sodium was added to the digesta, partly before the small intestine was reached, but mainly in the upper one-half of the small intestine (111). The net absorption of sodium was 53% by the time digesta reached the end of the small intestine in calves fed milk diets.

Smith (139) also used cannulae and reported that 40% of the Na was absorbed by the time the digesta reached the end of the small intestine and almost 100% was absorbed by the end of the large intestine. Goodall and Kay (60) indicated that 96% of the sodium entering the large intestine of sheep was absorbed while Hyden (84) determined that secretion of Na occurred in the duodenum and absorption occurred mainly in the cecum and large intestine when PEG was used as the reference material. Hyden (84) also indicated that the sites of absorption for H_2O, Na and Cl were similar. Bruce et al. (21) however, found that the small intestine absorbed most of the H_2O, Cl, P and K while the large intestine absorbed most of the Na and continued the absorption of H_2O and Cl.

Perfusion studies using isolated rumens have indicated that active transport of sodium occurred in the rumen epithelium in the direction of lumen to blood (41, 147). The active transport was against an electrochemical and concentration gradient but there was disagreement on the specific mechanism involved. Stevens (147) determined that a calculation of partial sodium conductances indicated that part of the Na was transported by "cation exchange diffusion" with the partner ion being chlorine. Dobson (41) disagreed with this as he could find no suitable partner ion. Other investigators reported that hypertonic conditions, as found after feeding or solute loading, stimulate the absorption of sodium from the rumen (145). Active absorption of sodium has also been demonstrated in the small intestine of rats (29, 30) and sheep (20).

The complexities involved in the sodium transport system are just beginning to become evident and understood. Skou (134) has done a large amount of research on sodium transport and his results indicate that potassium was involved in the sodium absorption mechanism. He further isolated an enzyme responsible for part of the steps in the absorption system. Still other workers have shown that calcium transport depends on sodium transport with the phosphoproteins being indicated as the sodium carriers (88). Future research should indicate whether the same mechanism accounts for Na absorption along the entire gastrointestinal tract or whether the several different mechanisms postulated by various research groups might be operative in different tissue sites.

Potassium

Except for purified or other diets high in starch, the possibility of a dietary deficiency of potassium in ruminants is remote since naturally used ingredients have a K (potassium) level well in excess of the body needs. The main source of potassium in the rumen is from the diet and not due to potassium in salivary secretions (11). The opposite is true for sodium indicating that the saliva is the main source of Na in the rumen. Potassium is found in the body mainly as a cellular constituent and differs from most elements since the amount of K in the bones is negligible (40).

Van Weerden (160) found that the concentration of potassium was greater in the gastrointestinal tract than in the blood and concluded that passive diffusion of potassium could occur along the entire tract.

Sperber and Hyden (144) reported that the potassium concentration in the rumen was five times that in plasma, suggesting that this element passively diffuses across the rumen epithelium. However Perry et al. (119) found calves fed concentrate or concentrate plus hay diets showed no net absorption or secretion of potassium from the rumen when Cr_2O_3 or Ce-144 was used as the reference material. One can calculate from the data of Perry and colleagues (119) that the calves fed these diets had an average net absorption of 43% of the dietary K by the time the digesta had passed through the abomasum. Perry and co-workers further found a large net secretion of potassium in the proximal small intestine which resulted in the K level in this region being 280% of the dietary potassium level. The potassium was gradually absorbed as the digesta passed along the remainder of the small intestine and through the large intestine so that the net absorption of the dietary potassium for the entire digestive tract was 75-80%.

Smith (139) found similar results when PEG was used as the reference material. His results indicated potassium along with water and chlorine was absorbed prior to a cannula at the distal end of the small intestine so that net absorption of K was 80-95% of the intake. Further potassium absorption occurred in the large intestine so that a total apparent absorption for the diet was approximately 100%.

Care and Van't Klooster (25) also found that absorption of potassium occurred in the small intestine by use of intestinal loops. Other research has shown that the small intestine absorbed potassium more extensively than it did sodium while the large intestine absorbed sodium much more completely than potassium during passage through the digestive tract (21, 60, 111).

Urine was found to be the major pathway of potassium excretion accounting for approximately 90% of total potassium excretion in ruminants (103). Telle and colleagues (155) working with sheep, found the skin was also an important excretion site with potassium excretion via the skin being independent of intake.

Recent research has indicated that potassium may be involved in "grass tetany" of adult ruminants. Hypomagnesaemia often resulted when the ration was changed suddenly from hay to spring grass. Results indicated the higher the potassium levels in the grass, the lower the plasma magnesium and the greater the incidence of grass tetany (20, 55, 154). Other workers have found no connection between potassium level of the grass and hypomagnesaemia (73, 126).

Calcium

The mineral of greatest amount in the body is calcium with 99% of the body Ca contained in bone (36). This compares to 80% of the body phosphorus and 60-70% of body magnesium contained in the bone.

Apparent absorption of calcium from the diet varies with age of the ruminant. Very young ruminants have an apparent absorption of 90-99% (44, 68, 97), while older animals have an apparent absorption of 8-50% (44, 68, 69, 97).

The rumen was shown to be relatively impermeable to Ca. Dobson (41, 42) indicated that the electrical potential difference between the rumen contents and plasma prevented any passive diffusion of Ca from the rumen to the plasma. Storry (151) and Phillipson (121) could not demonstrate a net loss of Ca or Mg ions from the rumen even with solutions that were sufficient to overcome the electrical potential and concentration gradients. However, Yang and Thomas (171) reported the rumen absorbed 75% of the dietary Ca in calves fed low and high fiber diets.

Cragle and Chandler (27, 37) reported that calcium was absorbed (66% of the dietary Ca absorbed) from the abomasum of young calves as determined by the use of Ce-144 as the reference material. Other work using similar techniques, indicated that net secretion of Ca in some calves and a net absorption of Ca in other calves occurred in the abomasum (119, 171). Yang and Thomas (171) found the abomasum absorbed 44% of the Ca entering this organ in one experiment while a second experiment indicated a 73% secretion of Ca in the abomasum.

These same authors also found a large net influx of Ca in the upper small intestine and a gradual net absorption occurring along the remainder of the small intestine. This same large net secretion of calcium in the proximal small intestine and gradual calcium absorption from the remainder of the small intestine was indicated by other workers with ruminants (27, 37, 119, 121) and monogastrics (3,110).

Smith (139) determined in young calves, that 86% of the calcium in the diet was absorbed by the time the digesta reached the end of the small intestine with this value decreasing as the animal increased in age.

In most research the large intestine of ruminants had no net absorption of calcium (27, 36, 37, 119, 139). However, Yang and Thomas (171) reported a 25% net absorption of the Ca entering the large intestine in one trial and a 49% net secretion of Ca in another trial.

Metabolic fecal calcium loss in ruminants did not vary with current calcium intake and thereby suggested that secretion of calcium into the gastrointestinal tract was constant over varying calcium intakes (99, 172). In contrast, the intestinal secretion of phosphorus did vary with level of P intake thus secretion of phosphorus appears to play a major role in maintenance of phosphorus homeostasis (99, 172).

Many factors have been shown to influence Ca availability, absorption, and retention. Good reviews of the factors affecting availability and absorption of calcium and calcium interactions with other minerals have been written (70, 78, 80, 157). Hoekstra (78) concluded that if another element, hormone, vitamin, or any material was to have an interaction with Ca or any other ion then it must interact in the diet, at the site of absorption, at the site of excretion, or at the tissue level.

Although the interactions of Ca with other minerals and substances are many, only a few of the more important and well established interactions will be reviewed.

Vitamin D was determined to aid calcium absorption at the site of absorption in monogastrics (92, 130, 169) and in ruminants (139).

Magnesium (1, 26, 70, 130) and zinc (35, 56, 74, 128, 158) were both shown to interfere with Ca at the site of absorption and perhaps also at the cellular level.

Calcium and phosphorus have long been known to interact with each other in the diet and this phenomenon has been reviewed by several authors (75, 163). Ruminants can tolerate wider combinations and total amounts of dietary calcium and phosphorus than non-ruminant species (99, 168, 173). Young and co-workers (173) reported that a wide dietary Ca: P ratio had no apparent effect on phosphorus absorption when P was adequate, but when P was low in the diet both calcium and phosphorus absorption were decreased.

Insolubility of calcium-phosphorus salts in the small intestine has for years been used to explain the mechanism of mutual antagonism of dietary Ca and P upon the absorption of one another. However, Hoekstra (78) points out in a review that the problem appears to be much more complicated than this.

To be absorbed, calcium in the diet must be separated from the complexes in which it occurs in the diet and rendered soluble and ionizable (95). The pH of the digesta was found to affect the proportion of Ca which was ultrafiltrable (59, 151, 152). Oberleas and co-workers (112) found no Ca: phytate complexes when the pH was below 3.7. Storry (151, 152) determined that practically all of the Ca in the abomasal contents of sheep was ultrafiltrable because of the high H^+ ion concentration. He further found as the pH increased there was less Ca and Mg available (152). Storry proposed that the binding was due to a surface adsorption phenomena and that an increased pH resulted in dissociation of active groups which resulted in a greater net negative charge upon the digesta and therefore the binding of calcium and magnesium ions by electrostatic attraction. Other results with calves, pigs, and rats indicated that the greatest absorption of calcium occurred in the small intestine and abomasum where the percent ultrafiltrable calcium was the highest and the pH was the lowest (3, 37, 110). Smith (143) reported the contents from ileal cannulae in calves contained 63-93% of the calcium as non-ultrafiltrable calcium.

The need for the availability of dietary calcium to exist in a form in which it can be absorbed was evidenced further by research with calves, where the apparent absorption of calcium was 90%, 37.5%, and 92% when switched from milk, hay plus grain, and milk diets respectively (97). The results of this same research indicated the Ca retention of an older cow was increased from 8% up to 23% by the addition of dried skim milk to the ration.

In monogastrics, calcium was absorbed by active transport from the small intestine lumen with the transport system being specific for calcium or magnesium (129). Although not studied as thoroughly in ruminants, results indicated that no more than a fraction of the calcium and magnesium absorbed by the small intestine could be absorbed by simple diffusion of the free ion (131). Other research indicated Ca and Mg interfere with the absorption of one another in the mid-ileum region of sheep and these authors suggested magnesium may be absorbed from much of the ileum of sheep by a process of facilitated diffusion involving a limited carrier system which was common to calcium (26).

Magnesium

Magnesium is of particular importance in ruminant nutrition where, except in very young animals, this element is poorly absorbed by ruminants and clinical deficiency symptoms sometimes occur under normal management conditions. The animal's body contains about 0.05 percent magnesium with this being distributed 60% in the skelton, 40% in the soft tissues, and about 1% in the extracellular fluids (127). A review on the magnesium role in biological systems has been written by Aikawa (2) and others. Since magnesium is primarily an intracellular ion and is an important cofactor in the activity of many enzyme systems especially phosphorylating systems, one finds abnormalities of intermediary energy transfer when animals are deprived of dietary magnesium (16, 165).

The extent of dietary magnesium absorption in ruminants has been found to be low even when the animal was deficient in magnesium. Smith (135, 137) reported the magnesium absorption in magnesium deficient calves was less than 50%. The normal absorption of Mg from the diet has been reported to be about 25-40% in young calves (139) and lambs (50, 104) with this decreasing to 5-25% in older animals (24, 52, 54, 100). Smith (138, 139) used animals which had been cannulated at the distal end of the small intestine, to study the difference in magnesium absorption in young and old animals. He found that both young and old animals absorbed the same percent of magnesium from the area preceding the cannula but older animals absorbed no magnesium from the large intestine while the young animals (2 to 5 weeks old) absorbed 40-70% of the magnesium which escaped absorption in the small intestine. These findings were confirmed by Cragle and colleagues (38) using the sacrifice technique combined with Cr_2O_3 or Ce-144 as the reference material. Recent research has indicated that the lack of absorption by the large intestine in older animals may be due to changing from liquid diets to hay plus concentrate diets as the animal matures. In animals fed hay and grain diets, the magnesium reaching the large intestine was largely bound (143).

Secretion of magnesium in the ruminant gastrointestinal tract was shown to occur in saliva, gastric secretions, and pancreatic secretions (150) with estimates of Mg secretion into the digestive tract ranging from 100 to 250 mg per sheep per day (50, 54, 100). Phillipson and Storry (121) had also reported Mg secretion into the jejunum and ileum using tracer techniques. Using Ce-144 as the reference material for calves, Cragle and co-workers (36, 119) indicated the net secretion of magnesium into the proximal small intestine was 1.5 times the Mg found in the diet. The quantity of Mg and Ca secreted into the proximal small intestine was such that a net absorption of these elements could not be detected in passage through the upper small intestine.

The reticulo-rumen of sheep has been found to be permeable to radioactive magnesium (23) but there appears to be no significant net uptake of magnesium by this organ in the sheep (23, 121) or the calf (119, 136) on normal diets. However, Care and Van't Klooster (26) found the rumen may play an important role in net magnesium absorption of a diet supplemented with magnesium.

Cragle and Perry (36, 119) reported absorption of dietary magnesium to be 38% by the time ingesta reached the omasum of calves fed either a concentrate or a hay plus concentrate diet. Care and Van't Klooster (26) found no net absorption of magnesium from the abomasum using an abomasal pouch perfused with an artificial abomasal solution.

The small intestine has been reported to absorb magnesium, but research using techniques to find the specific area of the small intestine involved has indicated different results. Field (51) concluded the middle one-third of the small intestine was the most important in sheep. Perry and co-workers (119) found the net secretion of Mg in the proximal small intestine of 150% of the diet was gradually absorbed in passage through the remainder of the small intestine with little or no net absorption of magnesium occurring in the large intestine. The overall apparent absorption of magnesium was 35%.

Phillipson and Storry (121) also reported a gradual absorption of magnesium throughout the small intestine in sheep. Care (26) used PEG as the reference material combined with re-entrant intestinal loops in sheep and determined the ileum was the major site of net magnesium absorption under normal dietary conditions. He also concluded that Ca and Mg interfere with the absorption of one another in the mid-ileum region inferring that in this region these elements may have a common absorption mechanism.

Stewart and Moodie (148) calculated absorption of magnesium using the A-V difference method by isolating the organs and the blood supply to these organs. They concluded that although magnesium was absorbed mainly from the duodenum and ileum, absorption could occur from any part of the gastrointestinal tract. Their technique however, was open to the criticism that osmotic forces arising from the introduction of large quantities of magnesium salts (112 grams) into the isolated gut sections could have contributed to the observed A-V difference.

Much of the research in magnesium efflux and influx has been done with radioactive Mg. Research reported by Field (51) has cast some doubt on several of the assumptions used in estimating endogenous magnesium and magnesium flux by the use of Mg-28. He found Mg-28 and dietary Mg were not evenly distributed and their ratio was not uniform throughout the tract. Since dietary magnesium would not be all ionic, the values reported for absorption from Mg-28 studies would represent the absorption of ionic radioactive magnesium only. This was further complicated by the fact that there was an exchange of Mg-28 with the magnesium in the gut mucosa thus causing a decreased specific activity of lumen Mg both by decreasing the numerator and increasing the denominator in the specific activity calculation. Therefore calculated apparent absorption may be neither absorption or secretion but merely a result of the exchange reaction. If these phenomenons are confirmed then many ideas developed from earlier investigations using Mg-28 will need re-evaluation.

The physical form of the diet affects the amount of magnesium absorbed. Smith (140, 141) determined that the greater the transit time of the diet the greater the percent of magnesium absorbed. He was working with calves and noted a large animal variation but observed that individual calves were very repeatable.

It has been generally accepted that in order to be absorbed magnesium needs to be in the ionic form. An important condition which governed the release of dietary magnesium into a soluble or ultrafiltrable form was the low pH in the abomasum (57, 59, 151, 152). Analysis of abomasal contents revealed that almost all the Mg was present in an ultrafiltrable form, whether sheep were fed hay or spring grass (152). Smith (143) also found that 100% of the magnesium was ultrafiltrable at pH of 2 to 3 and that the percentage of ionic magnesium decreased progressively to about 75% at pH 6.0. This lead him to conclude that in the small intestine the concentration of ionic magnesium in the digesta at the absorption site was the main factor controlling the amount absorbed at any given time.

A fall in the concentration of ultrafiltrable Mg unrelated to a pH change in the digesta of the duodenum and ileum has been reported. Smith (143) determined the magnesium in ileal contents was 34-74% non-ultrafiltrable. The extent of the magnesium bound was dependent on two processes, one dependent upon phosphate and the other not.

Nitrogen has been reported to play a role in Mg absorption of sheep as Stillings _et al_. (149) found absorption of magnesium was 18-24% for sheep fed low nitrogen forages (2.35% nitrogen) while apparent absorption of Mg was 11-16% for sheep fed high nitrogen forages (4.06% nitrogen). Head and Rook (71) found a relationship between high rumen ammonia and low magnesium availability but the mechanism for this effect remains unknown.

A deficiency of magnesium can occur in ruminants resulting in hypomagnesaemia. Summaries of the deficiency symptoms have been written by Wilson (165) and Rook (127).

Zinc

Zinc was first shown to be a component of carbonic anhydrase in 1939 (91). Since this time zinc has been found to be an integral part of other enzymes and functions in a wide range of cellular enzymes. The enzymes involved were reviewed by Underwood (159).

Zinc absorption studies indicated that a very low level of this element was absorbed. Feaster et al. (49) found only 3-10% of the dietary radiozinc was absorbed by steers fed either low or high zinc diets while research by Cragle and Miller (37, 107) indicated apparent absorption for radiozinc of 12% in cows, 20% in growing calves, and 55% in one week old calves.

The only research on the sites of zinc efflux and influx in passage along the gastrointestinal tract was done by Cragle and coworkers (37, 107) using both Cr_2O_3 and Ce-144 as reference materials. They found approximately 35% of the daily administered zinc-65 was absorbed from the abomasum, whereas there was a net secretion of radiozinc into the first segment of the small intestine which raised the zinc level to 280% of the dietary level. Net zinc absorption occurred throughout the remainder of the small intestine, with no absorption or excretion occurring below the cecum.

The range in apparent absorption of 12 to 55% for various age groups was further investigated by Cragle and colleagues (37, 107). They reported no significant differences between age groups in absorption from the upper small intestine but found that the differences in apparent absorption were due to differences in the extent of efflux in the lower small intestine. All animals had a net absorption of Zn in the lower small intestine, but the older the animal, the less extensive was this absorption. These same investigators also reported a positive correlation between dry matter digestibility and zinc absorption which suggested a relationship between zinc and the undigested residues in the digestive tract.

A zinc deficiency in ruminants can occur. Zinc deficiency was characterized in lambs by Ott et al. (117) while Miller and co-workers (108) characterized the deficiency in calves. Normally a zinc deficiency has not been reported to occur even in animals pastured on zinc deficient soils although Legg (94) observed typical manifestations of zinc deficiency in calves, yearlings, and adult cows pastured under certain range conditions in British Guiana. A diet containing 20 ppm of zinc was adequate in preventing deficiency symptoms in calves and cows (94, 108).

Zinc toxicity was also characterized in ruminants in a series of four papers by Ott et al. (113, 114, 115, 116). In sheep, heifers, and steers the toxic level was about 1000 ppm in the diet.

Interrelationships of zinc with other minerals have been shown to be numerous and not well understood. A high calcium diet was found to decrease zinc absorption and zinc turnover in rats, mice, and dogs (35, 56, 74, 98, 128). Forbes (56) indicated that this interference occurred in the lumen at the site of absorption. Becker and Hoekstra (15) found an increased zinc absorption when Vitamin D was given to rats. They concluded from absorption, distribution, and turnover data that this probably resulted, not from a direct effect of the vitamin, but from a homeostatic response to an increased need for zinc which accompanied enhanced skeletal growth and calcification.

Hoekstra (78) summarized many of the mineral interrelationships and emphasized the fact that there was a great deal of conflicting data in this area. He pointed out that various investigators had reported that zinc interfered with copper absorption, copper interfered with zinc absorption, zinc interfered with calcium absorption and calcium interfered with zinc absorption. The interference picture was further complicated by the fact that other research indicated that copper (125-200 ppm) in the diet will alleviate zinc deficiency symptoms in swine (77, 124). Very little research on mineral interrelationships with zinc has been done in ruminants.

Zinc was excreted in most species in the feces regardless of whether it was ingested or injected (49, 132).

EXPERIMENTAL PROCEDURE

General Design

Sixteen sheep were randomly assigned and fed one of four different chopped hay rations. The rations were siberian reed grass, reed canary grass, alfalfa cut June 25, 1965 (alfalfa early cut) and alfalfa cut July 16, 1965 (alfalfa late cut). The hay rations were fed to individually penned sheep for a period of 20 days and feedings took place twice a day at equal 12 hour intervals. For the last eight days the intake was adjusted to a constant amount so there would be no feed refusal or weigh-back after one hour. Therefore, the sheep were trained so that an exact amount fed was eaten entirely within a one hour period. This was done to obtain a constant intake and to reach an equilibrium of food passage within the animal.

Immediately following the one hour feeding period, a gelatin capsule was given using a balling gun. This time was considered as zero hours after feeding. The gelatin capsule contained 1.0 g of chromium oxide and 0.5 g of cerous sulfate. The practice of giving the capsule twice daily at zero hours after feeding was initiated ten days before sacrificing the animals.

Eight of the sixteen sheep were sacrificed at 6 hours and the remainder at 12 hours postprandial, with two sheep on each ration being sacrificed at each interval as shown in Table 1. The sheep were killed by stunning with electrical current and bled immediately by severing the jugular vein. The digestive tract was removed and ligatures placed between the different segments and at short intervals of the small intestine in order to prevent movement of the digesta. The gastrointestinal tract was then divided into nine sections as follows:

(1) Rumen - including the the reticulum

(2) Omasum

(3) Abomasum

(4) Small Intestine 1 [The small intestine was divided into

(5) Small Intestine 2 thirds on the basis of length]

(6) Small Intestine 3

(7) Cecum

(8) Large Intestine 1 [The large intestine was divided into

(9) Large Intestine 2 two sections at the point where fecal pellets were formed]

The digesta in each section was quantitatively removed, weighed, mixed, and sampled. Determinations of pH were made immediately by the use of a Beckman Model G pH meter with a glass electrode assembly. The entire contents of each section (except for the rumen, where an aliquoit was taken) were then frozen immediately and stored until freeze dried.

The digesta samples were dried using a Virtis (tray type) freeze drier with a 60^{o} F temperature being maintained on the plates. Following this the gastrointestinal tract samples were ground to a fine powder using a Wiley Mill with a 40 mesh screen and stored at room temperature until samples were ashed and analyzed.

Table 1. Rations fed and time of sacrifice.

Ration	Sheep Number	Time of Sacrifice (Hours Postprandial)
Reed Canary Grass	2	6
	4	6
	9	12
	14	12
Siberian Reed Canary Grass	1	6
	3	6
	7	12
	13	12
Alfalfa Late (cut 7/16/65)	5	6
	8	6
	11	12
	16	12
Alfalfa Early (cut 6/25/65)	6	6
	10	6
	12	12
	15	12

Elements were solubilized using a wet ashing procedure. One gram aliquots of dry matter were weighed in duplicate and ashed. Dry matter was determined by oven drying the freeze-dried samples for 48 hours at 55° F. Twenty-five ml of nitric acid were added to the one gram samples and the mixture boiled for two hours to remove the readily oxidizable material. This was followed by the addition of six ml of perchloric acid and continued heating and boiling for another four hours. Great care was taken to oxidize first with nitric acid and then perchloric acid in order to avoid an explosion. Following the ashing with nitric and perchloric acid the mixture was diluted to 100 ml using deionized distilled water. The diluted liquid samples were stored in plastic four ounce bottles and subsamples taken for the various mineral determinations as needed.

Mineral contamination was minimized by rinsing all glassware three times with a 20% HCl-deionized water solution, followed by three rinses with deionized distilled water.

Mineral Analyses

Mineral determinations were done by atomic absorption or by flame emission using a Jarrel Ash, series 83-360 atomic absorption/flame spectrometer. A hydrogen-air flame was used. Data in Table 2 indicates the wavelengths employed for each element and other analytical information.

Calcium and magnesium concentrations of the ashed digesta samples were determined by atomic absorption at 4227 Å and 2852 Å respectively. Strontium chloride was added to the aliquoits used for Ca and Mg analysis in order to eliminate interferences which resulted primarily from phosphorus. The calcium standard was made by disolving $CaCO_3$ in deionized water while the magnesium standard was made by dissolving pure Mg shavings in a small amount of HCL and then diluting to a desired volume with deionized water.

Chromium analysis was by far the most difficult because experimental evidence obtained during this study showed that substances normally contained in the diet interfere in chromium emission. The method of adding 500 ppm of Ca to minimize interferences (164) resulted in a 90% recovery of added standard solutions. Therefore, a combination of 500 ppm of Ca and internal Cr standards was used. This resulted in approximately 100% recoveries as shown by data in Table 3. This meant that the samples from each sheep were analyzed and compared to the internal chromium standard made using the hay diet that each particular sheep was fed. Cr_2O_3 was used to make the chromium standard although several sources of Cr were tested and all gave standards that were comparable.

Table 2. Method of mineral analysis, wavelength, concentration range, and elements added to minimize interferences.

Element	Method Of Analysis	Wavelength (Angstroms)	Analysis* Concentration	Elimination of** Interferences
Ca	Absorption	4227	5 to 20 ppm	10,000 ppm Sr
Cr	Emission	4254	2.5 to 10 ppm	500 ppm Ca
K	Emission	7665	1.5 to 5 ppm	-------------
Mg	Absorption	2852	0.5 to 2.5 ppm	10,000 ppm Sr
Na	Emission	5890	1 to 15 ppm	-------------
Zn	Absorption	2138	0.2 to 1.5 ppm	-------------

*Concentration range in which response was approximately linear
**Final concentration in sample needed to minimize interferences

Sodium and potassium concentrations were determined by flame emission at 5890 Å and 7665 Å respectively, with no interferences being encountered. The sodium and potassium standards were made by using the respective chloride salts.

The zinc standard was made by dissolving pure zinc ribbon in a small volume of HCl and then diluting to the desired concentration. Zinc analysis was determined by atomic absorption at 2138 Å, with no interferences being encountered. Special attention was given in zinc analysis in order to avoid contamination from glassware and other materials used.

Recoveries of standard additions were determined and the data are shown in Table 3. This was done by randomly selecting four or five different gastrointestinal tract samples and adding a known concentration of standard to each selected sample. Samples were then analyzed and the percent recoveries of the added standards were calculated.

Table 3. Recoveries of standard additions of each element to selected gastrointestinal digesta samples.

Tract Segment	Element and Percent Recovery					
	Ca	Cr	K	Mg	Na	Zn
Rumen	------	100.0%	102.5%	------	103.0%	94.0%
Omasum	106.0%	------	------	104.8%	100.0%	------
Abomasum	104.0%	98.5%	104.2%	------	------	96.0%
SI-1	94.0%	------	------	102.4%	------	94.0%
SI-2	------	103.0%	------	------	------	100.0%
SI-3	------	------	100.0%	96.7%	97.6%	104.0%
Cecum	104.0%	------	102.0%	104.0%	------	------
LI-1	100.0%	------	------	------	104.0%	------
LI-2	------	101.5%	100.0%	98.9%	104.0%	108.0%

All gastrointestinal segment samples were divided into two separate samples and these duplicated samples were carried through separate weighing, wet ashing, dilution, and analysis procedures. The agreement between analysis was very reasonable for the duplicate gastrointestinal samples.

Calculation of Absorption and Secretion

Absorption and secretion as pointed out previously, are difficult terms to define and as interpreted in this study might best be termed net absorption and net secretion. Chromium oxide was used as the reference material since it has been found to be relatively nonabsorbed and fits most of the qualifications described for a reference material in the Review of Literature.

To calculate net absorption and/or net secretion, Equation 1 was used. By definition, the diet would have a ratio value of 1.0. A ratio value greater than 1.0 in any segment of the digestive tract would indicate a net secretion of a particular nutrient into the gastrointestinal tract up to that segment while a value less than 1.0 would indicate that a net absorption of the nutrient had occurred up to that section. The efflux and influx of the particular nutrient in successive segments of the gastrointestinal tract would be indicated by a decrease or an increase respectively, in the ratio values between two successive segments.

(Equation 1)

$$\text{Ratio Value} = \frac{\left[\dfrac{\text{nutrient concentration in segment}}{\text{reference concentration in segment}}\right]}{\left[\dfrac{\text{nutrient concentration in diet}}{\text{reference concentration in diet}}\right]}$$

Since the hay fed was the major source of dry matter, potassium, and magnesium, Equation 1 was used as stated to calculate the net flux of these nutrients along the digestive tract. However, in the calculation of the net flux patterns of water, sodium, zinc, and calcium, Equation 1 was modified so that the rumen ratio value equaled 1.0. The reason for this change was that in addition to the amount of the above nutrients in the hay ration, an unmeasured amount of each nutrient was supplied the sheep either ad libitum (water) or as a supplement (trace mineralized salt and dicalcium phosphate). This modification of Equation 1 to set the rumen ratio value to equal 1.0 did not change the flux pattern, but rather it merely adjusted the magnitude of the ratio value by a better estimate of the actual amount of water, sodium, zinc, and calcium consumed by the sheep.

The overall digestibility or the apparent absorption of a dietary nutrient in its passage through the entire alimentary tract would therefore be 1.0 minus the fecal ratio value, with this multiplied by 100 to change the value to a percentage basis.

The net amount of nutrient secreted or absorbed as digesta passes through successive segments of the digestive tract can also be calculated as was done by Perry _et al_. (119). This calculation was used to estimate the amount secreted into the proximal small intestine. A net ratio value was first determined as shown by the formula of Equation 2.

(Equation 2) $$\text{Net Ratio Value} = \begin{bmatrix}\text{SI-1} \\ \text{Ratio value}\end{bmatrix} - \begin{bmatrix}\text{Abomasum} \\ \text{Ratio Value}\end{bmatrix}$$

Since the ratio value of the diet would be 1.0 and the net ratio value would be relative to the dietary concentration of nutrient, then Equation 3 can be used to calculate secretion of the particular nutrient per day.

(Equation 3)

$$\begin{bmatrix}\text{Net Secretion}\\ \text{mg/day}\end{bmatrix} = \begin{bmatrix}\text{Net Ratio}\\ \text{Value}\end{bmatrix}\begin{bmatrix}\text{Dry Matter}\\ \text{Intake g/day}\end{bmatrix}\begin{bmatrix}\text{Diet Concentration}\\ \text{mg/g D.M.}\end{bmatrix}$$

For example, one can calculate the net secretion of potassium into the proximal small intestine for sheep fed reed canary grass. The net ratio value would be 0.85 (1.15 minus 0.30) using data from Table 13. The average intake for sheep fed reed canary grass was 1052 grams dry matter per day (Table 4) and the concentration of potassium in the diet was 30.6 mg per gram dry matter (Appendix Table 17). Using Equation 3, the net secretion of potassium in the proximal small intestine would equal 27.4 grams per day.

RESULTS AND DISCUSSION

Feed Consumption

Dry matter consumption data for each of the 16 sheep fed the four hay diets is indicated in Table 4. Intake was constant for 10 days before sacrifice in an attempt to reach an equilibrium in rate of passage. Results shown in Table 4 indicate that the daily intake varied from 14.6 to 32.5 grams of dry matter per kilogram body weight except for sheep #8 whose daily intake was 190.5 grams of dry matter per day (4.4 grams dry matter per kilogram body weight). Prior to the 10 day period of constant intake, sheep #8 was eating amounts similar to the other sheep. However after the beginning of the dose with the Cr_2O_3 capsule, the sheep's intake decreased and blood was found on the balling gun after the dosing. When slaughtered, sheep #8 had necrotic tissue around the throat area. Due to the decreased intake as a result of the necrotic condition, the values for sheep #8 were discarded in computations of dry matter in the digestive tract as a percent of daily intake and in chromium distribution in the digestive tract as a percent of daily intake. All other calculations and data include all 16 sheep.

Intake of sheep fed siberian reed grass averaged the least (16.3 grams dry matter per kg body weight) and sheep fed early cut alfalfa had the greatest intake (28.5 grams dry matter per kg body weight), while those fed canary grass and late cut alfalfa averaged about the same intake (22.5 and 21.7 grams dry matter per kg body weight respectively - Table 4). This was similar to the pattern found by Ingalls (85), where consumption of sheep fed a legume diet was significantly greater than those fed all grass roughage diets. In the present trial the sheep fed legume hay diets averaged 25.5 grams daily dry matter intake per kilogram body weight while the sheep fed grass roughage diets averaged 19.1 grams daily dry matter intake per kg body weight.

Table 4. Dry matter consumption of four hay diets.

Diet	Sheep Number	Body Weight (kg)	Dry Matter Intake	
			g/day	g/day/kg B.W.
Reed Canary Grass	2	44.0	993.4	22.6
	4	47.4	984.3	20.8
	9	49.8	1137.0	22.8
	14	46.0	1093.2	23.8
Siberian Reed Canary Grass	1	39.9	580.6	14.6
	3	49.6	1014.5	20.5
	7	42.0	639.6	15.2
	13	35.9	541.3	15.1
Alfalfa (late cut)	5	52.8	1250.4	23.7
	8	42.9	190.5	4.4
	11	42.2	710.6	16.8
	16	35.7	880.0	24.6
Alfalfa (early cut)	6	44.0	1338.1	30.4
	10	50.0	1623.9	32.5
	12	39.6	911.7	23.0
	15	46.5	1301.8	28.0

pH of Gastrointestinal Digesta

No differences were apparent in the pH values for the same alimentary tract segment between the sheep sacrificed at 6 hours after feeding and those sacrificed at 12 hours postprandial (Table 5). Average pH of the rumen (6.45) and the omasum (6.46) was the same for all sheep. Progressing along the digestive tract the pH was lower in the abomasum averaging 4.19 and then increased to an average of 6.36, 7.14, and 7.53 in successive small intestine segments. The pH averaged about neutral in the lower gut being 7.09 in the cecum and 7.23 in the large intestine.

Table 5. pH of gastrointestinal digesta.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	12 hours
Rumen	6.38	6.31	6.49	6.59	6.44	6.45
Omasum	6.26	6.20	6.83	6.55	6.43	6.49
Abomasum	4.00	3.76	4.23	4.74	4.15	4.22
SI-1	6.20	6.38	6.61	6.23	6.43	6.28
SI-2	7.25	7.24	7.08	6.99	7.23	7.05
SI-3	7.62	7.50	7.22	7.57	7.35	7.60
Cecum	7.00	7.30	7.09	6.93	7.10	7.08
LI-1	7.27	7.39	7.22	7.02	7.20	7.25

The rumen, omasum, and abomasum segments of the digestive tract were found to have a slightly lower pH for the grass diets as compared to the same respective segments of sheep fed the alfalfa diets.

The significance of pH in mineral absorption is discussed more thoroughly in the section entitled Integrated Results and Discussion.

Wet Digesta Distribution in Gastrointestinal Tract

Wet digesta in the rumen of the sheep fed the four forage diets accounted for 66.2 to 73.8% of the total wet digesta in the alimentary tract (Table 6). Sheep sacrificed at 6 hours after feeding had 74.1% of the alimentary tract wet digesta in the rumen while the corresponding value was 69.1% for sheep sacrificed 12 hours postprandial. Ingalls et al. (86) found a similar decrease of 5% in wet rumen digesta with 76% being in the rumen at 6 hours and 71% at 12 hours after feeding in sheep fed similar roughage diets. Boyne et al. (19) reported that in sheep fed a mixed concentrate and hay diet, the total weight of wet rumen digesta decreased only slightly from 0 to 6 hours postprandial but decreased about 40% from 6 to 12 hours after feeding. Level of intake has been shown to affect rumen contents by changing rate of passage. Blaxter (17) reported that the physical form of the diet changed the rate of passage and also that an increased intake of a given diet caused a faster rate of passage. In the present experiment all gastrointestinal sections beyond the rumen contained comparatively more wet digesta at 12 hours than at 6 hours after feeding (Table 6). An average of the wet digesta distribution in the digestive tract of all sheep was 71.6% in the rumen, 1.9% in the omasum, 4.4% in the abomasum, 9.3% in the small intestine, 5.0% in the cecum, and 8.0% in the large intestine. One can calculate from Boyne and co-workers data (19), distribution values of 70.0, 1.5, 8.2, 8.4, 8.2, and 3.7 percent for the same respective digestive tract sections of sheep fed a mixed concentrate and forage ration.

The amount of wet digesta in the alimentary tract expressed as a percent of body weight (Table 7) indicated that even with animals fed

Table 6. Distribution of wet digesta in gastrointestinal tract expressed as a percent of total wet digesta in entire tract.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	12 hours
Rumen	73.8	72.6	73.8	66.2	74.1	69.1
Omasum	1.6	1.8	2.2	1.9	1.5	2.2
Abomasum	5.0	4.8	2.7	5.0	4.2	4.6
SI-1	1.7	1.5	2.2	2.7	1.7	2.3
SI-2	2.6	3.3	2.2	3.7	2.5	3.4
SI-3	4.4	3.5	4.4	4.9	3.9	4.7
Cecum	4.6	5.4	4.7	5.2	4.6	5.4
LI-1	5.7	5.5	6.9	8.7	6.6	6.9
LI-2	0.6	1.5	1.0	1.7	0.9	1.5

Table 7. Distribution of gastrointestinal wet digesta as a percent of body weight and dry matter as a percent of daily intake.

Tract Segment	Wet Digesta as Percent of Body Weight		Dry Matter as Percent of Daily Intake	
	6 hours	12 hours	6 hours*	12 hours
Rumen	13.8	12.0	84.5	74.5
Omasum	0.3	0.4	2.5	3.4
Abomasum	0.8	0.8	3.7	4.0
SI-1	0.3	0.4	1.6	1.8
SI-2	0.5	0.6	2.5	3.2
SI-3	0.7	0.8	3.3	3.5
Cecum	0.9	0.9	4.7	5.4
LI-1	1.2	1.2	7.3	7.8
LI-2	0.2	0.3	1.9	3.5
TOTAL	18.7	17.4	112.0	107.1

*Average of seven sheep as sheep #8 values were discarded a limited amount of food (restricted to the exact amount completely consumed in a one hour period), the wet digesta in the entire tract still represented an average of 18.1% of the total live weight. Other workers (46, 86, 162) have reported that wet digesta of the alimentary tract constituted from 12-25% of the live weight in cattle and sheep. The sheep in the present trial had 12.0-13.8% of body weight as wet digesta in the rumen (Table 7), which corresponds to the 11-18% reported by previous investigations from this institution (86, 156).

Dry Matter Distribution in Gastrointestinal Tract

The rumen contained most of the dry matter in the gastrointestinal tract (Table 8) averaging 72.3% for all sheep. Yang (170) reported that 53-72% of total alimentary tract dry matter was in the rumen of calves, while other investigators (8, 19, 125) found similar values of 52-75% in the rumen of sheep. The percent of the total gastrointestinal tract dry matter found in the rumen has been shown to be affected by both the diet (17) and time after feeding (19, 47). Results shown in Table 8 indicate the decrease in the rumen dry matter as a percent of the total digestive tract dry matter was from 75.0% at 6 hours postprandial to 69.5% at 12 hours. Boyne *et al*. (19) reported the rumen dry matter decreased from 75% at 6 hours after feeding to 60% at 12 hours postprandial for sheep fed a concentrate and hay ration. As with the wet digesta distribution, the rumen dry matter expressed as a percent of total digestive tract dry matter was less in the sheep sacrificed 12 hours postprandial than in sheep sacrificed at 6 hours, but these corresponding values were greater in all other gastrointestinal segments.

The total dry matter in each segment when expressed as a percent of daily dry matter intake is also shown in Table 7. The total dry matter in the tract represented 112.0% of daily intake at 6 hours postprandial and decreased to 107.1% at 12 hours. One would expect a decrease from 6 to 12 hours because of absorption (digestion) of dry matter and excretion of undigested dry matter residues. However estimation of the decrease is difficult because of dry matter secreted into the digestive tract and differential rates of passage through the digestive tract.

Table 8. Distribution of dry digesta in gastrointestinal tract expressed as a percent of total dry matter in entire tract.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	74.6	72.7	74.3	67.5	75.0	69.5
Omasum	2.3	2.6	3.0	2.7	2.1	3.2
Abomasum	3.8	4.1	2.1	3.4	3.0	3.7
SI-1	1.5	1.3	1.4	2.1	1.5	1.7
SI-2	2.4	2.8	1.7	3.1	2.0	3.0
SI-3	3.1	2.4	3.3	3.6	2.9	3.3
Cecum	4.5	4.9	4.5	5.1	4.5	5.1
LI-1	6.6	5.8	7.5	9.1	7.1	7.3
LI-2	1.4	3.4	2.0	3.5	1.9	3.2

Chromium Oxide Distribution in Gastrointestinal Tract

The chromium oxide distribution in the digestive tract is shown in Table 9 where the distribution is expressed as a percent of the daily chromium oxide intake. Since the sheep were fed twice daily at 12 hour intervals and were fed the same amount at each feeding, and since Cr_2O_3 had been fed at each meal for ten days before sacrifice, an equilibrium should have been established in which the quantity of inert chromium oxide indicator fed each day was the same as the quantity of inert chromium oxide excreted each day. In fact, from the period of 0-12 hours after eating one would expect to find 50% of the daily chromium oxide intake excreted with the other 50% being excreted in the period from 12-24 postprandial, assuming that a daily equilbrium in rate of passage had been attained. One would also expect the sheep sacrificed at 6 hours postprandial to have a greater total of Cr_2O_3 in their digestive tract than those sacrificed at 12 hours after feeding. However, results indicated that 98.1% of the daily intake was found in the digestive tract of those sheep sacrificed at 6 hours postprandial compared to 102.2% of the daily intake of Cr_2O_3 in those sheep sacrificed at 12 hours (Table 9). Since the 6 hour and 12 hour values are similar, the major portion of chromium oxide and digesta excreted by the sheep between meals must have been excreted from 0-6 hours after eating.

Miller _et al_. (109) found that 99% of the daily Cr_2O_3 dose was recovered in fecal excretions after the fifth day when calves were dosed twice per day while the corresponding value for Ce-144 was 97%. More important, they reported no hourly variations as to fecal excretion of either Cr_2O_3 or Ce-144, with an average of 8.5% of the

Table 9. Relative distribution of chromium oxide in the gastrointestinal tract of sheep expressed as percent of daily Cr_2O_3 intake.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	48.6	66.2	39.7	37.6	54.4	42.5
Omasum	2.3	4.0	4.3	2.6	3.0	3.4
Abomasum	8.6	9.9	3.8	9.8	7.3	9.2
SI-1	0.8	0.7	1.2	1.4	1.0	1.1
SI-2	2.0	2.9	1.9	2.3	2.0	2.6
SI-3	4.3	3.5	5.4	4.6	4.2	4.6
Cecum	10.6	13.5	8.9	9.7	8.8	12.6
LI-1	15.5	15.4	16.6	16.8	13.6	18.2
LI-2	3.9	9.3	4.1	6.2	3.8	8.0
TOTAL	96.6	125.4	85.9	91.0	98.1	102.2
Passage Rate (Days)	1.11		0.89		1.00	

daily dose of reference substance being excreted each two hour period throughout the day. Blaxter (17) however, reported that with ruminants given their rations in two equal meals at exactly 12 hour intervals the rate of feces production was not constant over a 24 hour period. He concluded that the magnitude of the diurnal variation in fecal excretion depended upon level of intake and physical form of the diet. In Blaxter's experiments sheep fed a diet similar to the one used in the present experiment had more fecal excretion from 0-6 hours after feeding than from 6-12 hours postprandial. Evidently feeding schedule must be considered as a factor influencing diurnial fecal excretion in addition to level of intake and form of diet.

Since Cr_2O_3 is not absorbed to any significant extent then excretion must equal consumption. Furthermore since chromium oxide administration was done every 12 hours with a constant amount at each time, then the amount excreted in 12 hours must be the same as the amount given in the dose every 12 hours. However different diets have different rates of passage, so if the reference material moved with the diet then the total amount of Cr_2O_3 present in the digestive tract at a time just prior to the next feeding would be directly related to the rate of passage. If 200% of the daily intake of Cr_2O_3 is found in the alimentary tract immediately prior to feeding than the diet could be considered to pass through the gastro-intestinal tract in 2 days. In the present experiments the sheep sacrificed at 12 hours postprandial represent the situation at the beginning of the next feeding. However, since the 6 hour and 12 hour postprandial values for the "percent of daily Cr_2O_3 intake in the digestive tract" were similar (Table 9), all sheep were used in estimation of the diet rate of passage. The average percent of the daily intake of Cr_2O_3 found in the alimentary tract for all sheep (6 hour and 12 hour) was 100.2%, therefore the sheep averaged 1.00 days for a given meal to pass through the digestive tract (Table 9).

The rate of passage for the different roughage diets as shown in Table 9 indicated that the alfalfa rations averaged 0.89 days in passing through the digestive tract while the corresponding value for the grass diets was 1.11 days. The faster rate of passage found for the alfalfa diets can partly be explained by intake. The average intake (Table 4) of sheep fed the grass diets was 873 grams per day as compared to 1145 grams for the sheep fed the alfalfa diets. It has been established that as the intake of a particular diet increased, the retention time of feed residues in the gastrointestinal tract decreased (17, 31, 32). Balch and Campling (13) have summarized much of the research in this area and concluded that while the factors involved in determining rate of passage were many and complex, an increased intake resulted in a decreased retention time primarily as a result of an increased flow of digesta from the reticulo-rumen. Examination of the chromium oxide distribution in the alimentary tract (Table 9) indicated the major difference in the chromium oxide distribution occurred in the reticulo-rumen section. Sheep fed reed canary grass and siberian reed grass averaged 48.6% and 66.2% of the daily Cr_2O_3 intake in this section while the corresponding values were 39.7% and 37.6% for sheep fed late and early cut alfalfa diets respectively.

As pointed out previously the chromium oxide passage through the digestive tract would be directly related to the rate of passage of digesta. Assuming Cr_2O_3 moves with the digesta and is neither absorbed nor secreted from the rumen then disappearance of Cr_2O_3 from the rumen would be the same as digesta passage from the rumen. The sheep consumed 50% of their daily chromium oxide every 12 hours at meal time. Sheep sacrificed 12 hours postprandial were being sacrificed just prior to feeding. Therefore the amount of chromium oxide in the rumen of sheep at zero hours would be the 12 hour value (42.9% from Table 9) plus 50% (percent daily Cr_2O_3 intake at a feeding) or a total of 92.5%. The disappearance from the rumen from

0-6 hours after feeding would therefore be 92.5% minus the rumen 6 hour value (54.4% in Table 9) or 38.1%. In the period from 6-12 hours postprandial 11.9% of the daily chromium oxide intake passed from the rumen (54.4 minus 42.5%). Therefore three times as much digesta passed from the rumen in the period 0-6 hours after feeding as in the period 6-12 hours postprandial.

The total Cr_2O_3 in the alimentary tract expressed as a percent of daily intake averaged 100.2% for all sheep (Table 9) while the total dry matter averaged 109.6% (Table 7). If chromium oxide was inert and dry matter was digested (i.e. absorbed), one would expect a smaller percent for dry matter in the digestive tract. However this reasoning overlooks the fact that dry matter is being secreted into the gastrointestinal tract as digestive secretions and cell desquamation. These percentages point out that the dry matter flux into the alimentary may be sizeable. The flux of dry matter is discussed more thoroughly in the section on Dry Matter Flux under Results and Discussion.

The distribution of chromium oxide within the sections of the digestive tract when expressed as a percent of the total gastrointestinal Cr_2O_3 is shown in Table 10. The sheep sacrificed 6 hours postprandial had 53.5% of the digestive tract chromium oxide in the rumen with this value decreasing to 41.9% for sheep sacrificed at 12 hours postprandial. As expected the gastrointestinal segments beyond the rumen had a greater percent of the total Cr_2O_3 in the digestive tract at 12 hours postprandial than at 6 hours, indicating passage of digesta along the alimentary tract with time.

The amount of chromium oxide in the rumen represented a greater proportion of the total Cr_2O_3 in the digestive tract for sheep fed the grass diets, averaging 51.1% of the total Cr_2O_3 in the digestive tract, than the corresponding value of 44.3% for sheep fed the alfalfa diets. This again reinforces the fact that the rate of passage from the rumen was greater for the alfalfa diets as compared to the grass rations.

The average distribution of chromium oxide for all 16 sheep (Table 10) indicated that 47.7% of the total Cr_2O_3 in the digestive tract was in the rumen. The same values for the other digestive tract segments were 3.4% in the omasum, 8.1% in abomasum, 7.8% in small intestine, 10.9% in the cecum, and 22.4% in the large intestine. Miller and Cragle (107) working with calves fed hay and concentrate diets, reported a much greater percent of the total digestive tract Cr_2O_3 and Ce-144 in the omasum and less in the abomasum. They found that the distribution for Cr_2O_3 and Ce-144 were similar. One can calculate from their data that the distribution of total digestive tract Cr_2O_3 was 45.1%, 31.3%, 1.7%, 5.0%, 5.2%, and 11.6% in the rumen, omasum, abomasum, small intestine, cecum, and large intestine respectively. Other research by investigators from the same station reported the total digestive tract Ce-144 distribution was 52-55% in the rumen, 17-20% in the omasum, and 2-4% in the abomasum for calves and cows fed hay and concentrate rations (14, 37, 107, 109). Reasons why the omasum contained 10 times the inert reference material in those studies than the present study and reasons why the abomasum contained three times less are difficult to explain. A slower rate of passage was indicated for the Miller and Cragle study (107) by the fact that total Cr_2O_3 in the tract was 156.7% of the daily chromium

Table 10. Chromium oxide distribution in the gastrointestinal tract of sheep expressed as percent of total Cr_2O_3 in the tract.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	50.6	51.6	47.3	41.3	53.5	41.9
Omasum	2.4	3.3	4.9	2.8	3.2	3.5
Abomasum	8.7	8.1	5.1	10.2	7.5	8.6
SI-1	0.9	0.6	1.3	1.5	1.1	1.2
SI-2	2.1	2.3	1.6	2.5	1.8	2.5
SI-3	4.5	2.8	5.4	5.3	4.4	4.6
Cecum	10.8	11.1	10.8	10.6	9.6	12.2
LI-1	16.1	12.6	18.6	18.8	14.9	18.1
LI-2	3.8	7.7	5.1	6.9	4.1	7.7

oxide intake. Miller and Cragle were studying radiozinc flux and although the Cr_2O_3 distribution in the omasum and abomasum were very different from the present study, they obtained a similar zinc flux pattern as indicated in the section entitled Zinc Flux under Results and Discussion.

Additionally the distribution of Cr_2O_3 might provide an indication of its value as a reference material for absorption/secretion studies. As with any inert indicator, there are serious difficulties in ascertaining an indicator's value. A possibility always exists that the chromium oxide could accumulate in a particular segment of the digestive tract, perhaps by adhering to the tissue or by binding preferentially to some digestive secretion or fraction of the dry matter in that section. The result that 8.1% of the Cr_2O_3 was found in the abomasum (Table 10) may indicate that an accumulation of reference material occurred. However, since the percent of total digestive tract dry matter in the abomasum is 3.4% (Table 8) and one would expect from 40-60% dry matter disappearance from the ruminant stomach (rumen, reticulium, omasum, and abomasum), the Cr_2O_3 amount in the abomasum does not seem unreasonable.

Miller et al. (107) investigated the problem of reference substance accumulation to digestive tract tissue with Ce-144. They found the 0.5%, 0.3%, and 0.05% of the daily dose of radiocerium were bound to the tissue of the rumen, omasum, and abomasum respectively, for calves fed hay plus concentrate diets. Chromium oxide binding to the tissue was not investigated in this study, but this same research and other research reported from the same research station has indicated that Cr_2O_3 and Ce-144 have a similar distribution in, and rate of passage through the digestive tract (37, 107, 109).

Dry Matter Flux

Patterns of flux for dry matter in sheep fed the four roughage diets were similar (Table 11). The data on dry matter flux for the sheep sacrificed at 6 hours postprandial and those sacrificed at 12 hours indicated very similar net flux patterns. These data are represented graphically in Figure 1. A large net secretion of dry matter which averaged 176% of that contained in the diet occurred in the rumen by the ratio value calculations. This is unlikely since established data has indicated that 23 to 70% of the dry matter disappears in the stomach of the ruminant with the major portion of this disappearance occurring in the reticulo-rumen (12, 79, 105, 171). One possible explanation for the large ratio value of the rumen would be that the Cr_2O_3 given in the gelatin capsule was settling to the bottom of the rumen resulting in a higher percentage of the Cr_2O_3 binding to the finer particles of the rumen dry matter and therefore passing from the rumen quicker than the average for the entire dry matter. This would result in the ratio value calculation for the rumen being larger than expected since the chromium oxide would be leaving the rumen more rapidly than the dry matter. However, if this occurred the process must be fairly constant in order to explain almost identical net flux patterns observed with sheep sacrificed at 6 hours or 12 hours postprandial. Results seem to

Table 11. Dry matter ratio values in the gastrointestinal tract sections of sheep fed all forage diets.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	1.66	1.54	2.29	1.56	1.68	1.84
Omasum	1.05	0.80	0.90	0.94	0.81	1.03
Abomasum	0.46	0.58	0.57	0.41	0.45	0.56
SI-1	1.99	2.51	1.62	1.69	2.03	1.80
SI-2	1.24	1.32	1.43	1.19	1.31	1.27
SI-3	0.78	0.95	0.84	0.67	0.85	0.77
Cecum	0.46	0.48	0.60	0.46	0.55	0.45
LI-1	0.46	0.50	0.60	0.46	0.57	0.45
LI-2	0.45	0.47	0.59	0.49	0.55	0.45

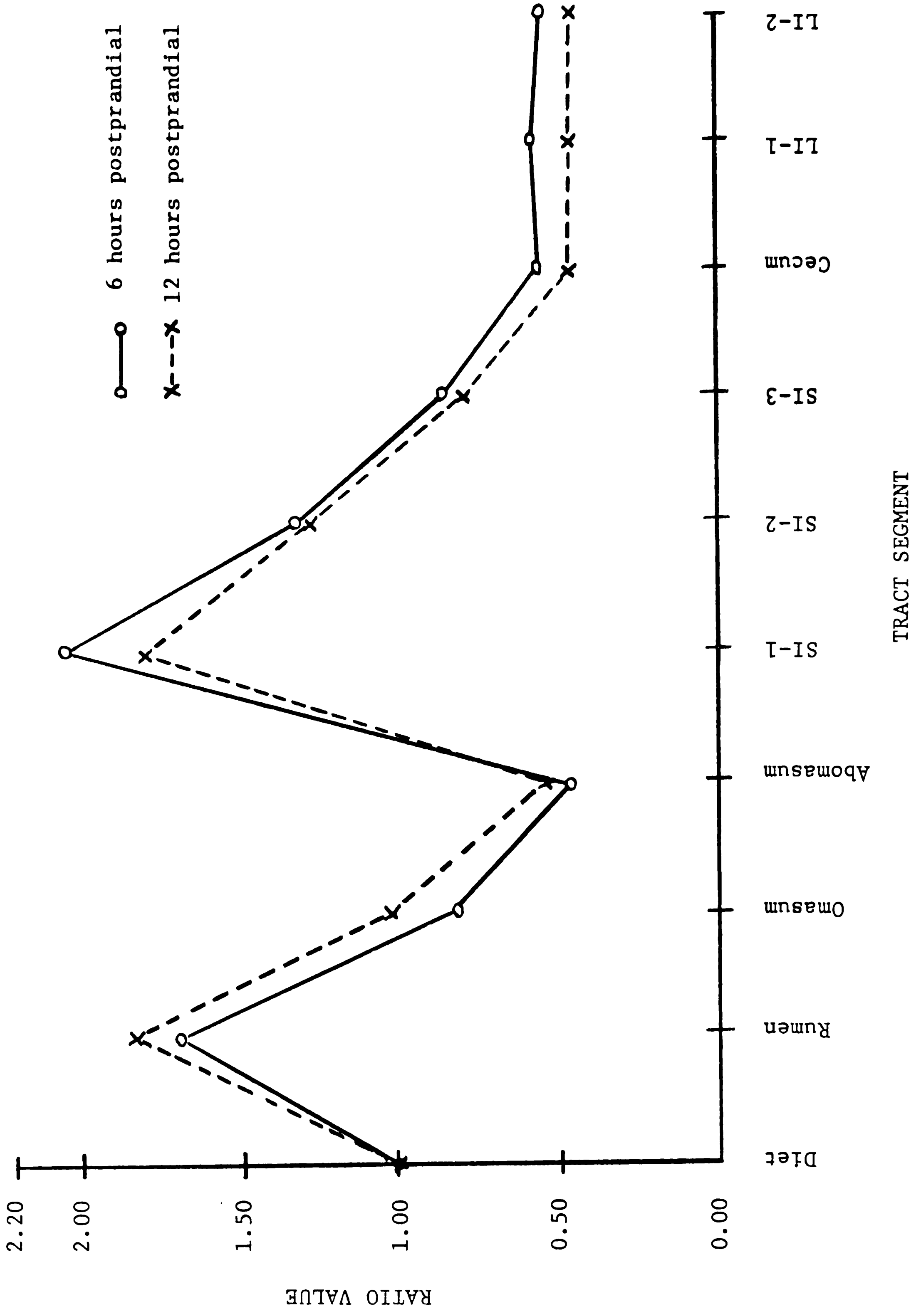
indicate that there was inadequate mixing of Cr_2O_3 with the dry matter in the rumen so that the true net flux of dry matter in the rumen was not determined. The method of dosing with Cr_2O_3 in a gelatin capsule was probably the cause of this inadequate mixing.

The dry matter disappearance of digesta passed through the stomach averaged 50% (Figure 1). Other investigators have indicated the dry matter disappearance in the stomach of ruminants ranged from 23-70% depending upon the particular diet, with an approximate average of 50-60% for roughage diets (12, 79, 105, 171). Since the abomasal ratio values in the present trial gave an average dry matter digestion value of 50% to this point (Table 11) which is similar to other research, it seems logical to conclude that the flux pattern of dry matter was probably representative of total dry matter from the abomasum through the remainder of the digestive tract.

Values shown in Table 11 indicate that a large net dry matter secretion occurred in the proximal small intestine of the sheep while a gradual net absorption of dry matter occurred as digesta passed through the remainder of the small intestine and the first segment of the large intestine. Similar results in the proximal small intestine of calves were reported by Yang and Thomas (171). Their results indicated a net secretion of dry matter in the proximal small intestine which amounted to 685% of the dry matter levels in the abomasum.

The approximate digestibilities of the forage diets can be calculated by designating the pellets of "LI-2" section of the digestive tract as feces. The digestibility of the roughage averaged 50% by this method of calculation, however the sample was small since "LI-2" digesta amounted to 1.9% of the daily intake in the 6 hour

Figure 1. Dry matter flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.


6 hours postprandial
12 hours postprandial
RATIO VALUE
0.00
0.50
1.00
1.50
2.00
2.20
TRACT SEGMENT
Diet
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2

sheep and 3.5% of the daily intake in the 12 hour sheep (Table 7). These same hay rations averaged 62% digestibility for different sheep in a digestion trial experiment.

Water Flux

Since H_2O intake by the sheep was not measured the ratio values were adjusted so that the rumen ratio value equaled 1.0 (Table 12). A large net absorption of water occurred in the omasum averaging 64% of the water found in ruminal digesta (range of 57-73% for the different roughage diets). Other research indicated the omasum absorbed from 31 to 80% of the water in the rumen digesta with an average of approximately 60% (9, 63, 171).

Only a small net secretion of water occurred in the abomasum (5% over water in omasal digesta). This was in contrast to the findings of Badawy and co-workers (9), who reported that the water content in the abomasum amounted to 197% of the levels in the rumen. Masson et al. (102) and Hill (144) calculated that 5 liters of abomasal juice were secreted into this organ each day in sheep while other research reported 6 and 12-15 liters of fluid were added each day to the stomach of sheep (79) and goats (123), respectively.

Omasal digesta had a dry matter content of 18.6% while that in the abomasal digesta averaged 10.3% dry matter in the present trial. This would seem to indicate that water was being secreted by the abomasum and that the results concerning water flux as calculated by the use of Cr_2O_3 as the reference material were in error. However this can be explained by the research of Ash (5, 6), where he determined there was a differential flow of fluid and solid material from the

Table 12. Water ratio values in the gastrointestinal tract sections of sheep fed all forage diets.

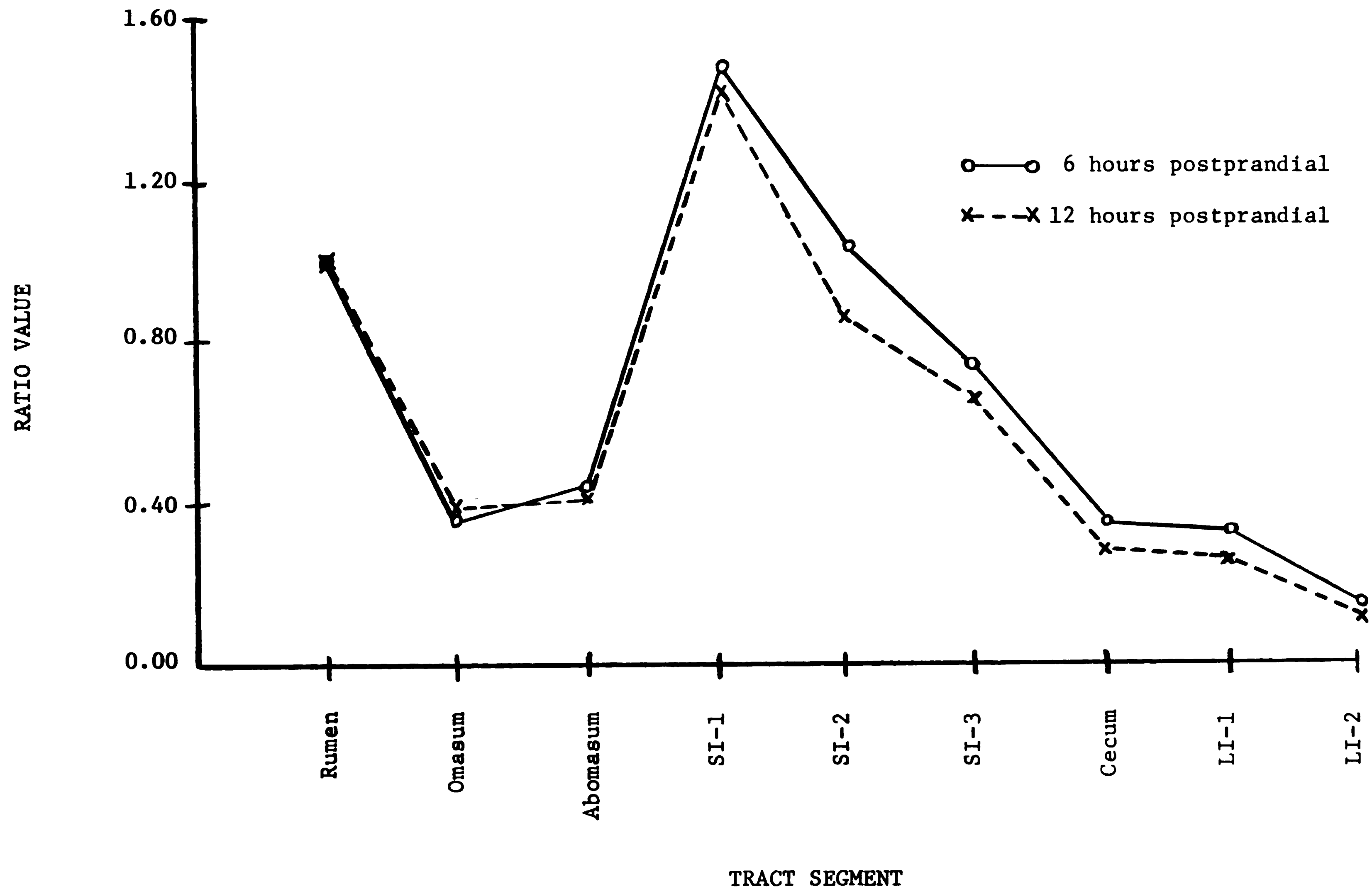
Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.43	0.34	0.27	0.41	0.34	0.38
Abomasum	0.43	0.47	0.34	0.40	0.42	0.40
SI-1	1.40	1.85	1.18	1.32	1.47	1.40
SI-2	0.85	1.09	0.86	0.96	1.03	0.85
SI-3	0.71	0.93	0.51	0.62	0.74	0.65
Cecum	0.31	0.36	0.29	0.31	0.35	0.28
LI-1	0.25	0.31	0.23	0.30	0.32	0.24
LI-2	0.11	0.12	0.12	0.14	0.14	0.11

omasum. His results dramatically illustrated this when under certain conditions gushes of cool fluid flowed from the omasum during or immediately after drinking. Also any net dry matter absorption greater than water absorption would result in a lowered percent of dry matter in the digesta of the abomasum. Results shown in Table 12 do not mean that no "secretion" occurred into the abomasum but rather that no "net secretion" occurred.

Practically the same net flux pattern was found at 6 hour and 12 hour postprandial (Figure 2) indicating the reference substance provided a very good representation of water flux into and from the digestive tract.

A large net secretion of water occurred in the proximal small

Figure 2. Water flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.


1.60
1.20
0.80
0.40
0.00
RATIO VALUE
6 hours postprandial
12 hours postprandial
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2
TRACT SEGMENT

intestine so that the ratio value in digesta from this segment averaged 144% of the value for water in the rumen. This water was gradually absorbed as digesta passed through the hind gut, with a rapid absorption from the small intestine and a continued absorption from the large intestine (Figure 2). Estimation of the net secretion of water in the first section of the small intestine over water levels in abomasum following the method of Perry et al. (119), indicated an average of 12.0 liters of water per day was secreted in this region. This estimate of secretion would be a minimal estimate because of possible reabsorption in this segment of the small intestine, since this section of the small intestine amounted to one-third the length of the entire small intestine.

The apparent absorption of water by the entire alimentary tract averaged 87.5% of the ruminal water (Figure 2).

Sodium Flux

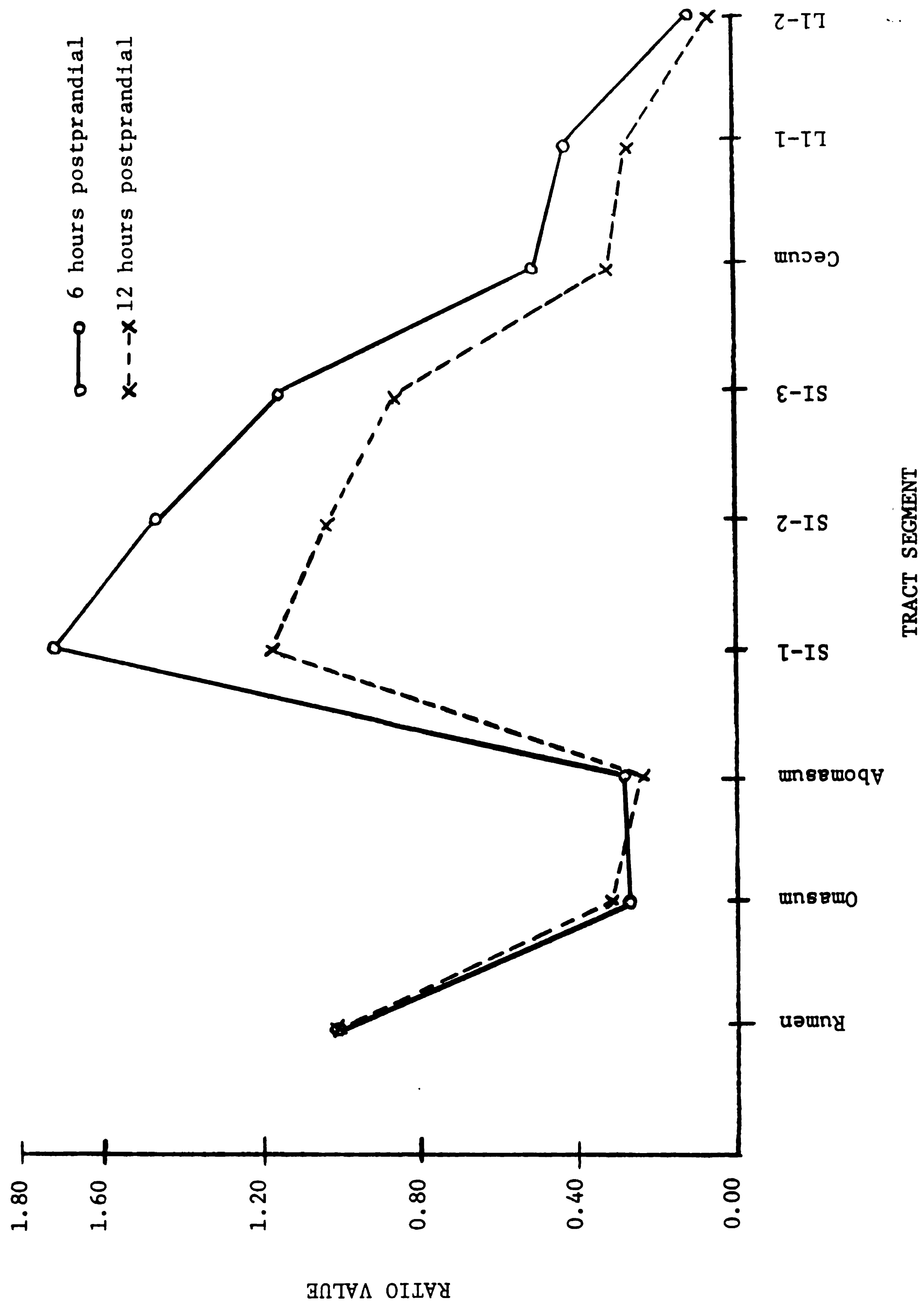
Secretion or absorption of sodium into the rumen was not determined in this study since the rumen ratio values were adjusted to equal 1.0 because the total sodium intake was not known. A large absorption of Na occurred in the omasum (averaging 70% of rumen ratio values) while no net change in the flux of sodium occurred in the abomasum (Table 13). This agrees with the findings of Perry et al. (119), who reported a 76% average absorption of dietary Na in the omasum of calves fed concentrate or hay plus concentrate diets.

Sodium has been reported to be secreted in large amounts in the upper small intestine with gradual reabsorption of Na occurring as digesta passed through the remainder of the small intestine (111, 119, 171). Results reported in Table 13 indicate that a large amount of sodium was secreted into the proximal portion of the lumen of the small intestine resulting in Na ratio values of 145% of the ratio values of the rumen. An estimation of the net secretion in this segment of the gastrointestinal tract revealed that a minimum of 26.5 grams of sodium per day was secreted (estimates for the four roughage diets ranged from 22.6 to 30.2 grams Na per day). A similar estimate for calves by Perry et al. (119), was 133 grams of sodium per day. Absorption of ruminal sodium amounted to 68% by the end of the small intestine (Table 13). Research involving calves with re-entrant cannulae at the distal end of the small intestine, indicated that 40-53% of dietary sodium was absorbed up to this point (111, 139).

Table 13. Sodium ratio values in the gastrointestinal tract sections of sheep fed all forage diets.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	12 hours
Rumen	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.35	0.31	0.21	0.30	0.28	0.31
Abomasum	0.27	0.29	0.23	0.24	0.28	0.23
SI-1	1.53	1.96	1.02	1.29	1.73	1.17
SI-2	1.40	1.61	0.97	1.03	1.47	1.03
SI-3	1.21	1.37	0.74	0.73	1.16	0.87
Cecum	0.47	0.52	0.37	0.33	0.51	0.33
LI-1	0.38	0.45	0.32	0.30	0.45	0.28
LI-2	0.11	0.10	0.12	0.07	0.13	0.07

Figure 3. Sodium flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.



6 hours postprandial
12 hours postprandial
RATIO VALUE
1.80
1.60
1.20
0.80
0.40
0.00
TRACT SEGMENT
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2

Absorption of sodium continued in the cecum and large intestine with an average of 90% of the ruminal sodium level being absorbed in the entire digestive tract. This is comparable with other results of 72-100% absorption of dietary sodium in ruminants (119, 139, 171).

A graphic illustration of the 6 hour and 12 hour postprandial data for the net flux of sodium is shown in Figure 3. Large differences in Na flux in the upper two-thirds of the small intestine were found between those sheep sacrificed at 6 hours and 12 hours postprandial. This may indicate some differences in rate of passage between sodium and chromium oxide in this area of the alimentary tract. This phenomena may also be caused by relatively more secretion of Na into the small intestine at 6 hours than at 12 hours. However the overall trends for sheep sacrificed at 6 hours and 12 hours remain the same.

Potassium Flux

The net flux of potassium is shown in Table 14. A small net secretion of potassium(16%)occurred in the rumen. This compares favorably with results of Baily (11), which indicated that potassium entered the rumen in salivary secretions, but that the main source of rumen potassium was the diet. Perry _et al_. (119) reported no appreciable changes in ruminal potassium flux as compared to the diet in calves fed concentrate or concentrate plus hay diets. However, calves which received a semipurified diet containing three to four times the normal K levels had a net absorption of 40% in the rumen. This seems to support the work of Sperber and Hyden (144), which suggested that potassium could passively diffuse across the rumen epithelium.

Net absorption of potassium occurred in the omasum and abomasum of the sheep so that an average of 66% of the dietary potassium had been absorbed by the time the digesta had passed through the stomach (Table 14). The comparable value was 54% in the study by Perry and colleagues (119).

Table 14. Potassium ratio values in the gastrointestinal tract sections of sheep fed all forage diets

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	1.03	1.00	1.56	1.08	1.14	1.19
Omasum	0.55	0.44	0.70	0.66	0.53	0.65
Abomasum	0.30	0.30	0.42	0.33	0.31	0.37
SI-1	1.15	1.67	1.85	1.86	1.81	1.45
SI-2	0.56	0.73	1.51	0.99	0.97	0.92
SI-2	0.37	0.50	0.63	0.46	0.48	0.50
Cecum	0.17	0.16	0.23	0.19	0.19	0.18
LI-1	0.16	0.17	0.23	0.19	0.20	0.17
LI-2	0.10	0.08	0.19	0.09	0.13	0.10

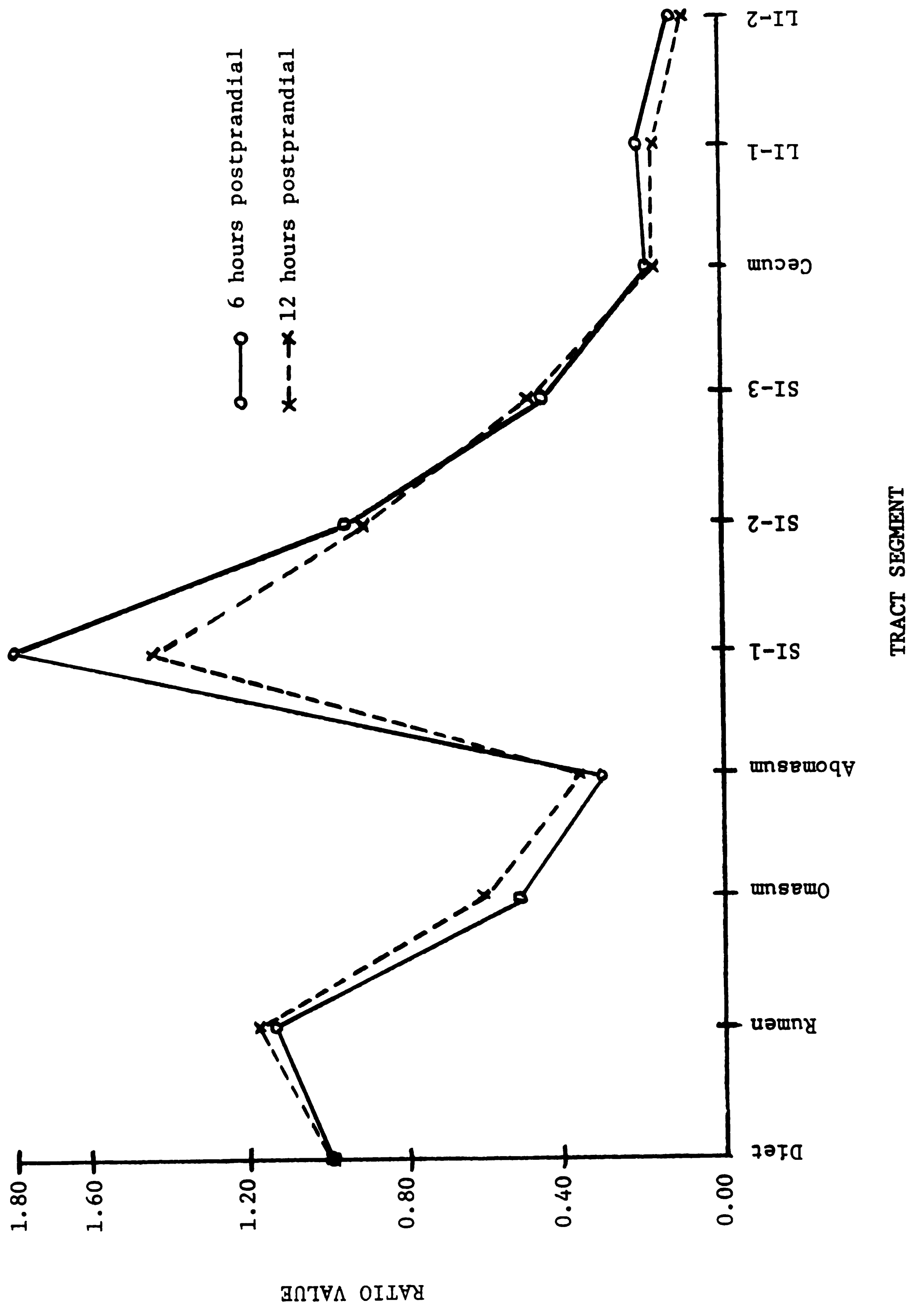
A large net secretion of potassium occurred in the first one-third of the small intestine resulting in the ratio value of this segment being 163% of the dietary ratio value. Extensive potassium absorption occurred as digesta passed through the remainder of the small intestine, in the present study. Perry _et al_. (119) also reported a large net secretion of K into the upper small intestine of older calves which resulted in ratio values of 280% greater than the diet, although Myrea (111) found no secretion of potassium into the small intestine of milk fed calves. The results of potassium absorption as digesta passed through the small intestine as shown in Table 14, corresponds to other investigators' research with ruminants (21, 25, 111, 119, 139).

Calculation of the minimal net secretion of potassium indicated an average net secretion into the upper small intestine of 27 grams of potassium per day. The comparable value was 36 grams per day for calves in a study reported by Perry _et al_. (119). Although the ratio values for the "Abomasum" and "Small Intestine-1" segments of the digestive tract varied for the different diets (Table 14), the minimal net secretions of potassium in this region were similar ranging from 24-29 grams per day for the four hay diets.

Investigations of the flux patterns for sodium and potassium as determined by cannulae in the digestive tract, have indicated that potassium was more extensively absorbed than sodium as digesta passed through the small intestine (21, 111, 139) while the large intestine absorbed sodium much more completely than potassium (21, 60, 139). Similar results were found in the present experiment. An average of 89% of the potassium and 71% of the sodium entering the small intestine was absorbed for the 16 sheep (Table 13 and Table 14). Furthermore, an average of 32% of the potassium and 76% of the sodium entering the large intestine was absorbed.

A graphic illustration of the data from sheep sacrificed at 6 hours and 12 hours postprandial is shown in Figure 4, and indicates a very similar flux pattern for the two periods. Therefore the reference material (inert Cr_2O_3) and potassium (water soluble) must

Figure 4. Potassium flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.


6 hours postprandial
12 hours postprandial
RATIO VALUE
0.00
0.40
0.80
1.20
1.60
1.80
TRACT SEGMENT
Diet
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2

have traversed the digestive tract at similar rates for both times concerned.

Absorption of dietary potassium averaged 88.5% with the apparent absorption for the different roughage diets ranging from 81-92% (Table 14). Literature values reported for the apparent absorption of potassium by ruminants range from 75-100% (119, 139).

Calcium Flux

The flux pattern for calcium was determined distally to the rumen since the ratio values for the rumen were set at 1.0 (Table 15). A small amount of Ca was absorbed from the omasum and a very large net absorption of calcium occurred from the abomasum. Net absorption of Ca as digesta passed through the stomachs of the sheep averaged 77% of the ruminal calcium for the 16 sheep.

Table 15. Calcium ratio values in the gastrointestinal sections of sheep fed all forage diets.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.98	0.86	0.73	0.97	0.82	0.95
Abomasum	0.26	0.23	0.18	0.25	0.21	0.25
SI-1	0.57	0.58	0.48	0.51	0.52	0.55
SI-2	0.67	0.75	0.61	0.61	0.70	0.62
SI-3	0.75	0.75	0.61	0.64	0.72	0.65
Cecum	0.66	0.66	0.62	0.69	0.74	0.57
LI-1	0.71	0.69	0.62	0.70	0.78	0.58
LI-2	0.68	0.64	0.58	0.75	0.75	0.57

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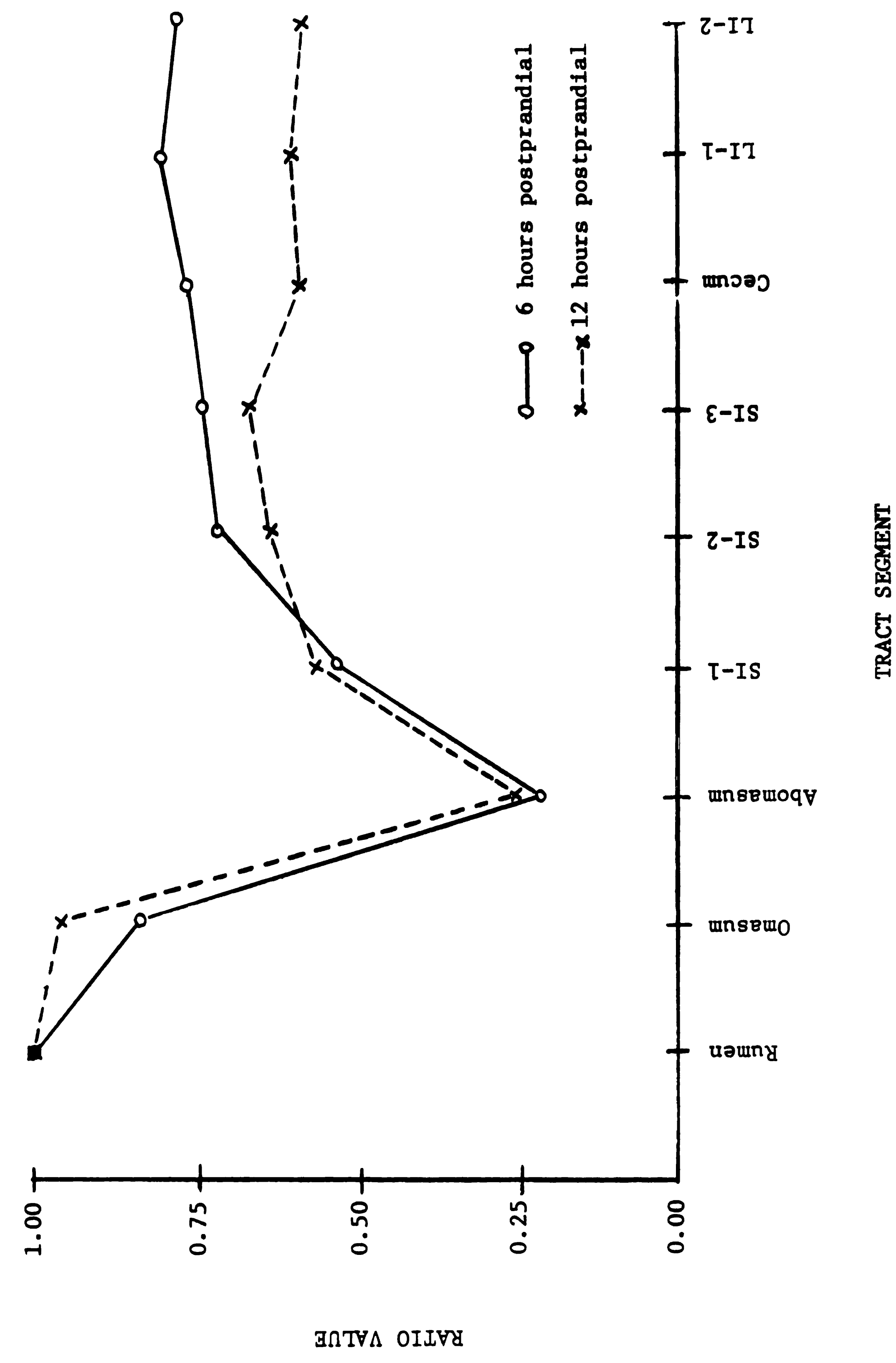
No research has been reported on calcium flux patterns in the digestive tract of mature ruminants, however flux patterns of calcium in calves have been studied. Calcium was reported to be both secreted and absorbed in the omasum (27, 139, 171). Similarily, the abomasum was indicated to have a net secretion of calcium in some experiments (139, 171), while a net absorption of Ca was indicated to occur in other research reports (37, 139, 171). Yang and Thomas (171) reported that in 14 out of 24 calves, more calcium was absorbed than secreted into the abomasum. Cragle et al. (37) reported an average of 66% net absorption of dietary calcium by the time the digesta had passed through the abomasum for a group of calves ranging from 12-20 weeks of age. Data indicate that practically all of the calcium in the abomasal contents was ultrafiltrable because of the low pH and therefore the best possible milieu would exist for absorption of Ca (151, 152). Out of the 16 sheep (Table 15), 12 had a net absorption of calcium in the omasum while all 16 sheep had a net absorption of calcium in the abomasum.

In the present study the net secretion of calcium in the proximal one-third of the small intestine amounted to a two to three fold increase over abomasal ratio values (Table 15). There was also a small gradual secretion of Ca as digesta passed through the remainder of the small intestine, with no net absorption or secretion of calcium occurring in the cecum or large intestine. Other research has also reported a large influx of calcium into the upper small intestine (27, 37, 119, 121, 171), but most of this research has indicated a gradual net absorption of calcium as digesta passed through the remainder of the small intestine. The secretion of Ca into the proximal small intestine probably came from the bile and pancreatic juices since Storry (150) reported that these secretions contained appreciable quantities of both calcium and magnesium. The reason why the sheep had relatively little change in Ca flux from the middle of the small intestine to end of the digestive tract in the present experiment remains unknown. Cragle *et al*. (37) reported a similar pattern where little or no changes in net flux of calcium in passage from the middle small intestine on through the hind gut in older calves (12-20 weeks). However, these same authors reported that in young calves (4 weeks) calcium was absorbed throughout the small intestine. Perhaps the calcium of the small intestine digesta was in a form unavailable for absorption, in the diets of older animals. Smith (143) indicated that ileal effluent of calves fed concentrate or pasture diets contained 63-93% of the calcium in a non-ultrafiltrable form while the same value for calves fed a milk diet was 9%.

The lack of calcium absorption in the large intestine found in this trial (Table 15) is in agreement with other research which indicates no net absorption or secretion of calcium from the large intestine (37, 119).

Figure 5 is a graphic illustration of the calcium flux patterns for sheep sacrificed at 6 hours or 12 hours postprandial. The two groups of sheep had the same relative flux pattern for calcium with the ratio values being very similar for the stomach and the small intestine. In the cecum and large intestine, the 6 hour values were slightly greater suggesting the possibility of differential rate of passage between Cr_2O_3 and calcium in this region of the digestive tract.

Figure 5. Calcium flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.



6 hours postprandial
12 hours postprandial
RATIO VALUE
1.00
0.75
0.50
0.25
0.00
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2
TRACT SEGMENT

A larger 6 hour ratio value would result if the calcium was moving faster than the chromium oxide in the digestive tract.

The apparent absorption of calcium from the diet was 34% of all sheep when the digesta from "Large Intestine-2" was considered as if it was feces (Table 15). The range of apparent absorption for the different roughage diets was from 25-42%. This falls within the literature range of 8-50% calcium absorption reported for mature ruminants (44, 68, 69, 97).

Magnesium Flux

Ratio values for magnesium in successive segments of the gastrointestinal tract are given in Table 16. A large net absorption of Mg occurred in the rumen averaging 44% of dietary magnesium for all sheep. The omasum and abomasum further absorbed magnesium so that net absorption of dietary Mg was 86% in the sheep stomach. The stomach of the ruminant has been shown to be permeable to Mg (23, 148), but no significant uptake of magnesium by the reticulo-rumen has been demonstrated (23, 119, 121,136). However, Care and Van't Klooster (26) reported that the rumen may play an important role in magnesium absorption of a diet supplemented with magnesium. Perry et al. (119) reported that net absorption of dietary magnesium was 38% in the omasum of calves fed either a concentrate or hay plus concentrate diet.

In contrast to the data of Table 16, other research has indicated that no significant magnesium absorption occurs from the abomasum of the ruminant (26, 119), although Stewart and Moodie (148) found the abomasum was permeable to Mg. It has been generally accepted that in order to be absorbed magnesium needs to be in the ionic form. One important condition which governs the release of dietary magnesium into a soluble or ultrafiltrable form is the low pH in the abomasum (57, 59, 151, 152). Analysis of abomasal contents revealed that almost all the Mg was present in an ultrafiltrable form for sheep, whether they were fed hay or spring grass (152). Smith (143) found that 100% of the magnesium in digesta was ultrafiltrable at pH two to three, but this decreased progressively as the pH increased so that the percentage of ionic magnesium was 75% at pH 6.0.

In the present study a net secretion of magnesium occurred in the upper small intestine of all sheep amounting to approximately three-fold the abomasum Mg level. Perry and colleagues (119) reported

Table 16. Magnesium ratio values in the gastrointestinal tract sections of sheep fed all forage diets.

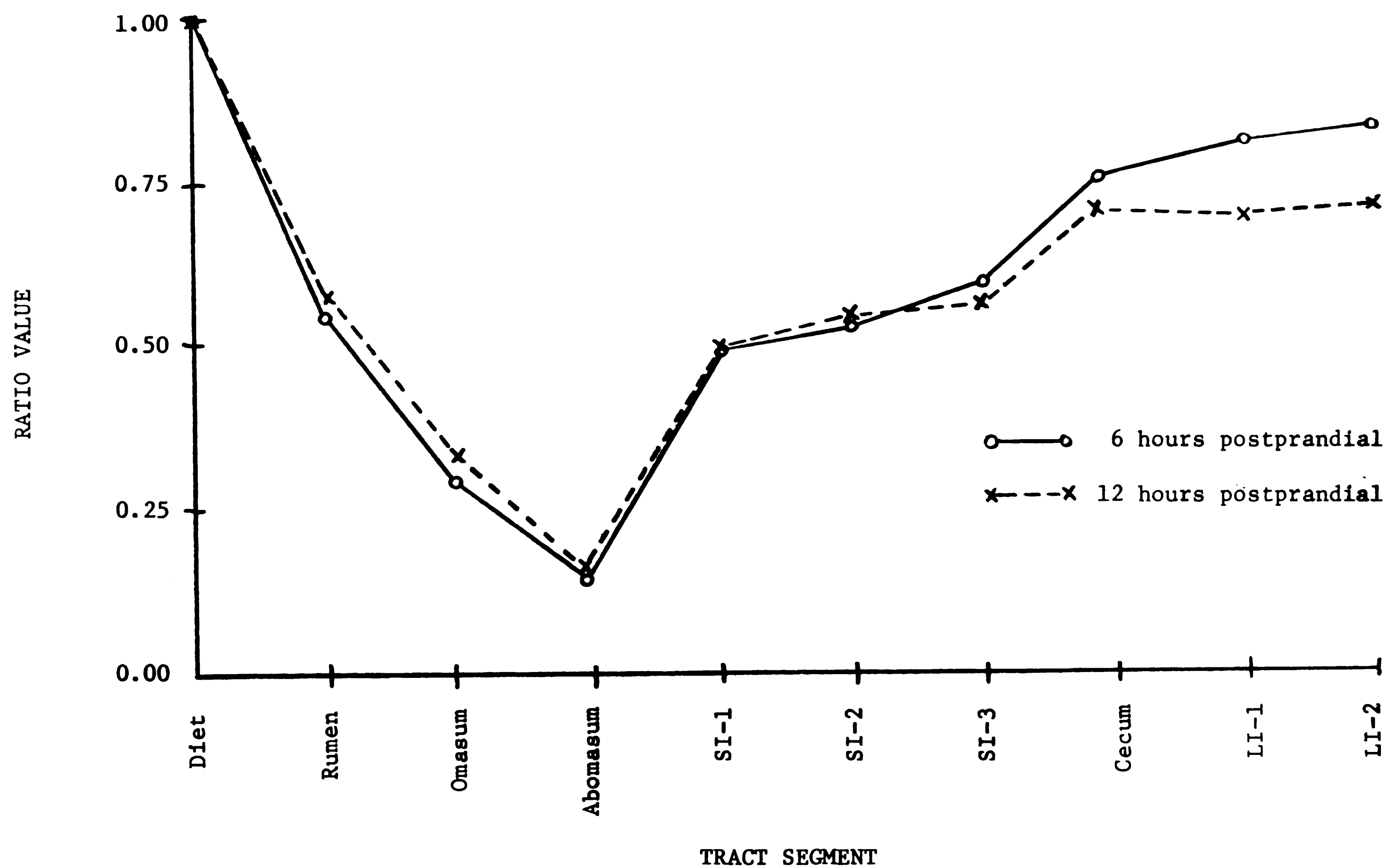
Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	0.58	0.48	0.71	0.46	0.54	0.58
Omasum	0.40	0.27	0.31	0.26	0.29	0.33
Abomasum	0.19	0.16	0.13	0.12	0.14	0.15
SI-1	0.63	0.49	0.47	0.37	0.49	0.49
SI-2	0.54	0.42	0.62	0.58	0.53	0.54
SI-3	0.42	0.49	0.78	0.61	0.59	0.56
Cecum	0.51	0.61	0.87	0.94	0.76	0.70
LI-1	0.49	0.61	0.94	0.96	0.81	0.69
LI-2	0.53	0.56	0.87	1.11	0.83	0.71

that a large secretion of magnesium into the proximal small intestine also occurred in calves. Presumably this endogenous Mg came from bile and pancreatic juices since these secretions contain appreciably amounts of magnesium (150).

The flux pattern for magnesium in passage through the "lower" tract was very similar to calcium. The results indicated that no net absorption of magnesium occurred in the small intestine or large intestine. In fact, there was a small net secretion of Mg as digesta passed through the lower small intestine and cecum, with no change in magnesium levels in the large intestine. These findings concerning Mg flux in the small intestine are in contrast to some other reported data which indicates that the small intestine is the major region of magnesium absorption (26, 119, 121, 148). Perry et al. (119) reported a gradual absorption of magnesium as digesta passed through the small intestine of calves. However other research by these same authors (38), involving calves fed a diet of grain and milk, indicated a magnesium flux pattern in the "lower" gut almost exactly the same as was found in the present trial.

One explanation for the observed differences in the magnesium flux patterns in the small intestine may be the different diets fed. Smith (140, 141) found the greater the transit time of the diet, the greater the percent of magnesium absorbed. Smith (143) also established that the Mg in the ileal effulent was 34-74% non-ultrafiltrable. If magnesium must be in the ionic form to be absorbed, then the amount of Mg absorbed may well depend on the amount of ionic magnesium in the digesta at the site of absorption. In this respect, diets may differ in the amount of available magnesium. Smith (143) indicated the extent

Figure 6. Magnesium flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.


1.00
0.75
0.50
0.25
0.00
RATIO VALUE
Diet
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2
TRACT SEGMENT
6 hours postprandial
12 hours postprandial

of the magnesium bound in small intestinal digesta was unrelated to pH, but was dependent upon at least two processes, one of which was the amount of phosphate present.

A difference in magnesium absorption dependent upon diets seems to be clearly indicated from data in Table 16. The grass diets had an apparent magnesium absorption of 45.5% of the dietary magnesium (using the LI-2 digesta as feces). Although the alfalfa diets had nearly twice the concentration of Mg (Appendix Table 17), the apparent absorption of magnesium for the two alfalfa rations averaged only 1.0%. In fact, out of eight sheep receiving the alfalfa diets, four had no apparent absorption of Mg while another two sheep had an apparent absorption of less than 5%.

Figure 6 depicts the flux patterns of magnesium for the sheep sacrificed at 6 and 12 hours postprandial. The flux patterns were very similar thereby strongly indicating that the indicator and Mg were traversing the digestive tract at similar rates. There were some differences in the 6 hour and 12 hour ratio values in the large intestine but the relative patterns were similar. Calcium and magnesium are both divalent ions and the flux pattern for magnesium in passage through the alimentary tract was very similar to that found for calcium (Figure 5).

Zinc Flux

Average data by diet and slaughter time on the net flux pattern of the zinc is shown in Table 17 where the rumen ratio values are adjusted to equal 1.0. These results indicate that zinc was absorbed in the omasum and abomasum resulting in an average net absorption of 67% of the rumen zinc levels in passage through the ruminant stomach. The only other research on the sites of gastrointestinal zinc absorption and secretion was done by Miller and Cragle (37, 107), with the same research being reported in both papers. These authors followed the flux of zinc-65 which may or may not approximate dietary zinc, by the use of Ce-144 as the reference material. The results of Miller and Cragle indicated a small net secretion of zinc into the rumen with Zn absorption occurring in the omasum and abomasum. This resulted in an average of 35% of the dietary zinc being absorbed as digesta passed through these organs or a 47% absorption of the zinc present in the rumen digesta.

A large secretion of zinc occurred in the proximal small intestine of the sheep (Table 17), resulting in an increase in the ratio value to 151% of the rumen ratio value. This large secretion of zinc was reabsorbed in the passage of digesta through the remainder of the small intestine. The amount of zinc secreted in the proximal small intestine was estimated to be 107 mg per day. Presumably the secretion of zinc came from bile, pancreatic secretions, intestinal secretions, and cell desquamation. This would tend to be an underestimation since absorption probably was occurring simultaneously with secretion and the estimate was based on net secretion. Little or no net absorption of zinc was found to occur in the large intestine (Table 17).

Miller and Cragle (37, 107) reported a similar large zinc influx into the proximal small intestine (this proximal small intestine ratio value averaged 284% of dietary value). These authors further found that this zinc secretion was absorbed gradually as digesta passed

Table

Tract Segmen
Rumen
Omas
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SI-1
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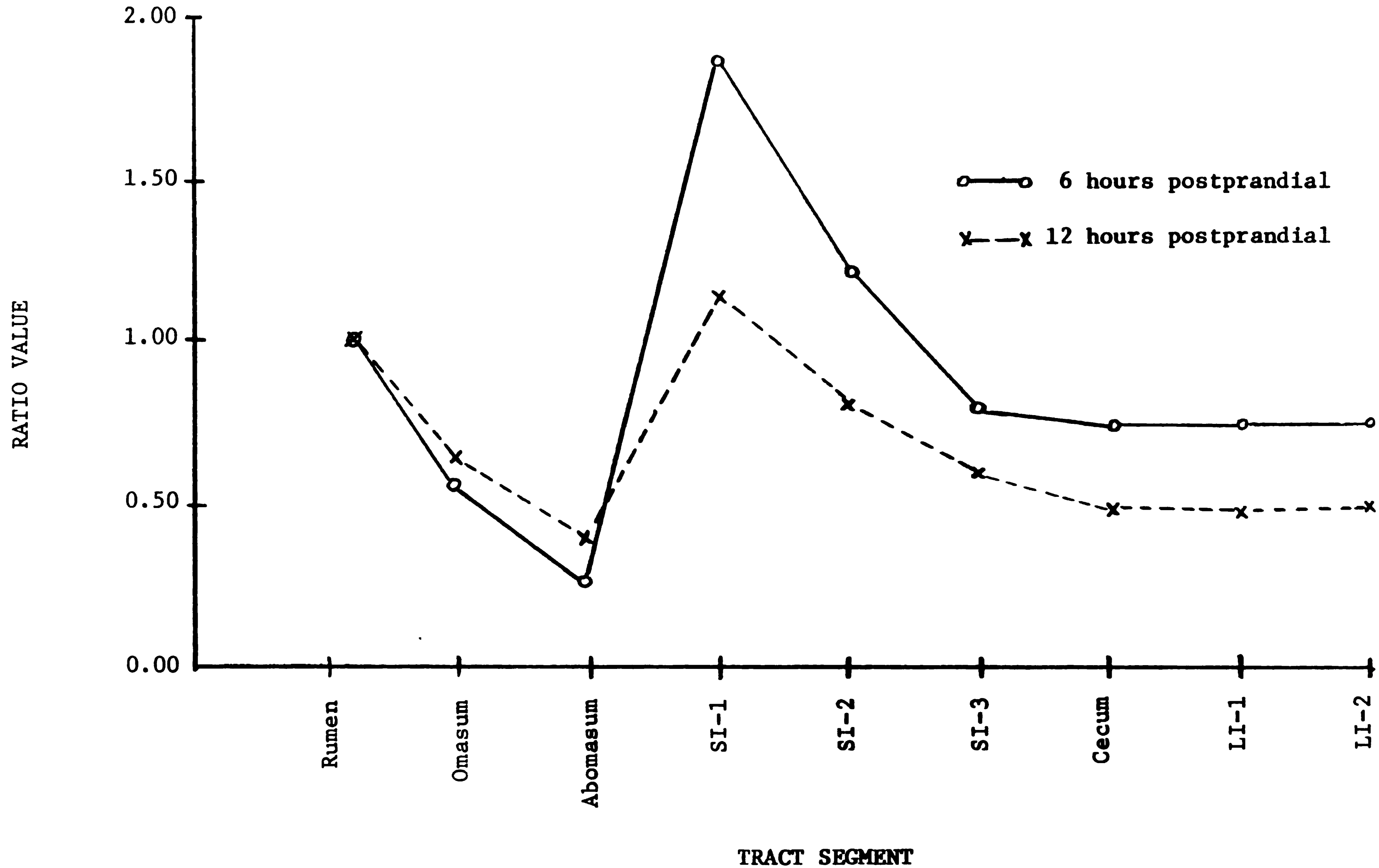
Table 17. Zinc ratio values in the gastrointestinal tract sections of sheep fed all forage diets.

Tract Segment	Reed Canary	Siberian Reed	Alfalfa (late cut)	Alfalfa (early cut)	Postprandial 6 hours	Postprandial 12 hours
Rumen	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.74	0.61	0.45	0.64	0.56	0.67
Abomasum	0.30	0.46	0.29	0.56	0.26	0.40
SI-1	1.44	2.00	1.15	1.45	1.87	1.15
SI-2	0.91	1.10	1.15	1.22	1.22	0.81
SI-3	0.69	1.01	0.56	0.53	0.80	0.60
Cecum	0.60	0.72	0.67	0.49	0.76	0.49
LI-1	0.58	0.71	0.71	0.47	0.75	0.48
LI-2	0.56	0.74	0.64	0.61	0.77	0.51

through the remainder of the small intestine. Similarily to the present study, Miller and Cragle (37, 107) found no net absorption or secretion of zinc in the large intestine.

Results of 6 hour and 12 hour data of Table 17 are shown graphically in Figure 7. As with sodium, these results indicated large differences between the two times for the ratio values in the upper two-thirds of the small intestine and smaller differences throughout the remainder of the digestive tract. This may mean there was some difference in rate of passage in this area between zinc and chromium oxide. Greater ratio values in the 6 hour sheep would result if Zn was moving through the digestive tract at a faster rate than Cr_2O_3. However, the overall trend remained the same for

Figure 7. Zinc flux along the gastrointestinal tract of sheep. Sheep were sacrificed at 6 hours or 12 hours postprandial and ratio values determined with Cr_2O_3 as reference substance.


2.00
1.50
1.00
0.50
0.00
RATIO VALUE
6 hours postprandial
12 hours postprandial
Rumen
Omasum
Abomasum
SI-1
SI-2
SI-3
Cecum
LI-1
LI-2
TRACT SEGMENT

sheep

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3-28%

(49,

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sheep sacrificed at 6 hours or 12 hours postprandial, therefore the difference in rate of passage could not have been great.

Using the digesta of LI-2 as fecal material, the apparent absorption of zinc averaged 36% with a range of 26-44% for the different roughage diets. Other research has indicated that from 3-28% of the dietary zinc was absorbed in older calves and cows (49, 107), while the corresponding value was 55% in young calves (107).

In both this study and that of Miller and Cragle (37, 107), the net dietary zinc absorption was greater in the abomasum than at the end of the digestive tract. The small intestine absorbed the greatest quantity of zinc but never absorbed a sufficient amount to attain the ratio value found in the abomasum because of the large zinc secretions into the proximal small intestine.

INTEGRATED RESULTS AND DISCUSSION

The data for dry matter flux pattern indicated that Cr_2O_3 was not being mixed adequately with the digesta in the rumen. Therefore the method of administration of the indicator (gelatin capsule) was found to be unsatisfactory for determining the flux pattern for a nutrient in the first part of the digestive tract. However, the mixing appeared to be complete by the time the digesta had passed to the abomasum. Future research should indicate whether adequate mixing would be obtained for animals fed other types of diets.

The sites of absorption and secretion were studied by the use of a marker technique. This method is limited by the degree to which the reference marker meets the four requirements stated in the Review of Literature. Of the four requirements, the most difficult one to test is whether the reference material moves through the digestive tract at the same rate as the nutrient under study. Horvath (80) reasoned that at least two indicators were needed to accomplish these objectives; one for the fluid phase and another for the solid phase of the ingesta.

One technique used to determine if the particular nutrient and the marker have the same rate of passage is to compare flux patterns obtained at different times postprandial. If the nutrient is moving faster or slower than the marker, a difference in the flux patterns for the two time periods will be obtained. The longer the time interval between flux pattern compared, the greater will be the magnitude of difference in rate of passage between marker and nutrient. However, it is recognized that other factors can also give rise to different results in flux patterns. If the secretion rate of the nutrient into the tract varies at the two time periods in which the flux patterns were investigated, then this phenomena would cause different flux patterns. This variation in secretion rate could be either in amount of secretion or in concentration of nutrient in the secretion. Also if the absorption rate of the nutrient under study varied in a given segment, then one would find a difference between flux patterns measured at two different times.

Although these phenomena may cause variation in flux patterns at two different times, it would seem likely that any difference in flux patterns would be the result of a difference in rate of passage between nutrient and indicator. This would seem to be especially true in the ruminant where the rumen acts as a food reservoir and digesta passes through the tract at a relatively constant rate. A uniform rate of absorption and secretion would be more likely to exist if the rate of passage of the digesta was fairly constant as is found in the ruminant.

In the present study, the sheep were sacrificed at 6 hours and 12 hours postprandial and flux patterns compared. The data indicated that Cr_2O_3 gave similar overall flux patterns for sheep sacrificed at 6 hours or 12 hours after eating for every nutrient studied. Flux patterns for the two periods were in excellent agreement for dry matter, water, and potassium. Therefore one must assume that Cr_2O_3 was moving through the digestive tract at the same rate as for each nutrient studied. Since Cr_2O_3 is water insoluble, it seems likely that from the abomasum on through the hind gut, the digesta was moving as a water-digesta-slurry complex.

In the case of every mineral studied, there was a marked absorption of the mineral in the ruminant stomach. Due to the inadequate mixing of indicator and diet in the rumen, and possibly in the omasum, it could not be determined which segment or segments of the stomach were responsible for the absorption. However, the abomasum appeared to be the logical choice as the organ where the major portion of this absorption occurred. In the abomasum the pH is the lowest in the tract. Other research has indicated that a lower pH results in a greater percent of the mineral (divalent minerals) being ultrafiltrable (57, 59, 151) and in the abomasum the minerals are almost completely ionic (143, 152). Therefore the best possible milieu for mineral absorption from the gastrointestinal tract may exist in the abomasum.

Further proof of the absorption capacity of the abomasum is some unpublished results of Cragle referred to in a talk by the same author at a recent symposium (36). He ligated the abomasum from the remainder of the digestive tract in 12 calves. The absorption of Ca-45 averaged 15% in 24 minutes.

Research using the nonabsorbable marker technique has shown that not all minerals are absorbed in the abomasum. Barua et al. (14) showed that a large net secretion of iodine occurred in the abomasum. Myrea (111) by another method, has also shown a large net secretion of Cl into the abomasum.

A marked secretion of every nutrient studied occurred in the proximal portion of the small intestine in the present study. Presumably, this nutrient secretion was due to bile, pancreatic juice, and intestinal secretions. For most nutrients the amount of each nutrient secreted per day in this region was greater than the amount of that nutrient consumed each day in the diet. Reabsorption of this secretion occurred in the lower two-thirds of the small intestine and in some cases continued reabsorption occurred in the large intestine.

It was established in this study for the ruminant animal the major portion of the dietary mineral was absorbed in the stomach for every mineral studied. The small intestine absorbed the greatest quantity of most minerals studied, but was merely reabsorbing the large secretion which occurred in the upper portion of the small intestine.

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SUMMARY

A nonabsorbed marker technique (Cr_2O_3) was used to determine net absorption and secretion of nutrients in the gastrointestinal tract. Sixteen mature sheep were fed one of four different hay diets. The diets consisted of siberian reed grass, reed canary grass, alfalfa early cut (cut 6/25/65), and alfalfa late cut (cut 7/16/65). The individually penned sheep were trained to consume one-half of their daily diet in a one-hour period. All sheep were fed a constant amount of their respective diet at 12 hour intervals.

At the end of the one-hour feeding period, a gelatin capsule containing 1.0 gram of Cr_2O_3 was given and this time was considered to be zero time. The twice-daily dosing with chromium oxide was initiated ten days before sacrificing.

In order to evaluate whether the indicator traversed the digestive tract with the nutrient in question, the sheep were sacrificed at two different periods postprandial. One-half were sacrificed 6 hours after feeding and the remainder at 12 hours. Therefore, two sheep eating each hay diet were sacrificed at each time period. The gastrointestinal tracts were removed, divided into nine segments by ligation, and the digesta sampled from each segment for subsequent analysis.

Daily dry matter consumption averaged 16.3, 22.5, 28.5, and 21.7 grams per kilogram body weight for sheep fed the siberian reed grass,

reed canary grass, alfalfa early cut, and alfalfa late cut respectively. No differences were apparent in the pH of the digesta from the same segment of the tract between the sheep sacrificed at 6 hours and 12 hours postprandial. The average pH values for all sheep were 6.45, 6.46, 4.19, 6.36, 7.14, 7.53, 7.09, and 7.23 for the digesta from the rumen, omasum, abomasum, SI-1, SI-2, SI-3, cecum, and LI-1 respectively.

The gastrointestinal digesta accounted for 18.7% and 17.4% of the body weight of the sheep sacrificed at 6 hours and 12 hours postprandial respectively. The rumen digesta amounted to 13.8% of body weight for the 6 hour sheep and 12.0% for the 12 hour sheep.

The distribution of dry matter in the digestive tract for sheep sacrificed 6 hours after eating was 75.0% in the rumen, 2.1% in the omasum, 3.0% in the abomasum, 1.5% in the SI-1, 2.0% in the SI-2, 2.9% in the SI-3, 4.5% in the cecum, 7.1% in the LI-1, and 1.9% in the LI-2. Corresponding percentage values for the sheep sacrificed 12 hours postprandial were 69.5, 3.2, 3.7, 1.7, 3.0, 3.3, 5.1, 7.3, and 3.2.

The rate of passage of the digesta through the tract when the different roughage diets were fed was found to be 1.11 days for the grass diets while the corresponding value for the alfalfa diets was 0.89 days. The difference observed was attributed to a faster rate of passage from the reticulo-rumen when the alfalfa diets were fed. Sheep fed the reed canary grass diets averaged 57.4% of the daily Cr_2O_3 intake in the rumen when sacrificed while the corresponding value was 38.2% for sheep fed alfalfa diets.

Data on dry matter and chromium oxide distribution in the digestive tract, coupled with the flux pattern of dry matter, indicated the method of dosing with Cr_2O_3 in a gelatin capsule did not give adequate mixing of Cr_2O_3 and hay diet in the rumen. Therefore, flux patterns found in the rumen were of limited value. However, mixing appeared to be complete by the time the digesta had reached the abomasum.

The flux patterns between sheep sacrificed at 6 hours and 12 hours were in excellent agreement for dry matter, water, and potassium. Although the overall flux patterns were in very good agreement for the other nutrients studied, there were small differences between the 6 hour and 12 hour flux patterns in the small intestine for Na and Zn and in the large intestine for Ca, Mg, and Zn. Therefore, we can assume that Cr_2O_3 was traversing the digestive tract at the same rate as the nutrients studied. Since Cr_2O_3 is water insoluble, it seems likely that from the abomasum on through the hind gut, the digesta must be moving as a water-digesta-slurry complex.

Fifty percent of the dry matter was absorbed in the sheep stomach. A large net secretion of dry matter occurred in the proximal portion of the small intestine with a gradual absorption of the dry matter as digesta passed through the remainder of the small intestine. The overall dry matter digestibility averaged 50% for the four diets.

Water was absorbed from the omasum and secreted in proximal portion of the small intestine. A minimal estimate of H_2O secretion in this region was 12.0 liters per day. Water absorption occurred throughout the remainder of the small intestine and large intestine. Apparent absorption from the entire alimentary tract averaged 87.5% of the water present in the rumen.

Sodium and potassium were both absorbed as digesta passed through the stomach (rumen, reticulium, omasum, and abomasum). This absorption amounted to 74.5% and 66% of the ruminal Na levels and the dietary K concentrations respectively. A net secretion of both sodium and potassium occurred in the proximal one-third of the small intestine with minimal estimates of the daily secretion in this segment being 26.5 g Na and 27 g K.

Results indicated that 89% of the potassium and 71% of the sodium entering the lower two-thirds of the small intestine was absorbed. Conversely, Na was more extensively absorbed in the large intestine with 76% of the Na and 32% of the K entering the large intestine being absorbed. For the entire tract, apparent absorption of Na averaged 90% of the ruminal Na level while the apparent absorption of potassium averaged 88.5% of dietary potassium.

Similar flux patterns were found for Ca and Mg. The abomasum was the site of net absorption of calcium and magnesium with the absorption of these minerals being 77% and 85.5% complete as digesta passed through the ruminant's stomach. A net secretion of Ca and Mg occurred in the upper two-thirds of the small intestine with little net flux occurring as digesta passed through the remainder of the tract. Apparent absorption of calcium for all diets averaged 34% of ruminal Ca levels while the corresponding value for magnesium was 23% of the dietary Mg.

Zinc was absorbed from the stomach of the sheep to the extent of 67% of the dietary Zn. A net secretion of Zn occurred in the anterior portion of the small intestine with the minimal estimate of this secretion being 107 mg per day. Absorption of zinc occurred in the remainder of the small intestine but no net absorption or secretion of Zn occurred in the large intestine.

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APPENDIX

Table 1. Sheep #1: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	5965	12.02	5.91	7320	1.500	13.5	20.3	10.5	0.625	0.065
					1.600	13.0	21.3	10.5	0.625	0.045
Omasum	136	17.54	5.86	4700	3.075	8.0	16.7	19.5	0.625	0.065
					3.075	7.5	16.7	20.0	0.625	0.060
Abomasum	272	11.30	3.20	7850	4.725	9.0	13.3	5.0	0.500	0.045
					4.500	9.0	13.0	5.0	0.475	0.085
SI-1	59	11.95	6.39	7370	0.600	15.3	20.7	3.0	0.250	0.075
					0.600	15.2	21.0	3.0	0.325	0.070
SI-2	231	10.83	7.08	8230	1.450	17.0	17.3	8.5	0.550	0.070
					1.500	17.0	19.0	8.5	0.600	0.070
SI-3	186	9.12	7.46	9960	2.150	21.0	15.0	12.5	0.925	0.085
					2.100	20.0	15.3	13.0	0.925	0.090
Cecum	191	11.15	7.32	7970	4.275	21.0	9.4	25.0	2.100	0.180
					4.275	21.0	10.3	24.5	2.100	0.130
LI-1	422	12.24	7.63	7170	4.050	19.0	9.2	23.5	1.950	0.125
					4.275	19.0	9.2	24.5	2.050	0.135
L2-1	68	27.24	—	2600	5.025	4.5	5.4	24.0	2.000	0.120
					5.025	4.5	5.0	22.5	1.800	0.120

*Mineral concentrations determined in duplicate samples

Tract 2. Sheep #2: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	6772	11.73	6.28	7530	0.600	13.5	19.0	5.5	0.400	0.045
					0.600	15.0	20.0	5.5	0.500	0.055
Omasum	122	16.08	6.12	5220	0.875	7.0	15.7	9.0	0.575	0.080
					1.025	8.0	15.7	9.0	0.525	0.060
Abomasum	318	10.05	4.57	8950	2.950	14.0	15.3	3.5	0.600	0.060
					2.850	13.0	15.3	4.0	0.600	0.055
SI-1	136	10.93	6.18	8150	0.475	17.0	17.7	2.0	0.450	0.065
					0.525	16.0	17.0	2.0	0.400	0.065
SI-2	281	9.49	7.30	9540	0.850	26.0	15.7	4.0	0.575	0.080
					0.875	24.0	16.0	4.0	0.450	0.090
SI-3	413	7.44	7.34	12440	1.300	34.5	17.0	6.5	0.700	0.080
					1.450	36.0	17.5	7.0	0.700	0.090
Cecum	417	10.93	7.17	8150	2.650	22.0	10.4	10.5	1.200	0.130
					2.500	24.0	10.4	11.0	1.250	0.125
LI-1	567	13.53	6.98	6390	2.800	18.0	9.4	12.0	1.250	0.130
					2.600	19.0	9.2	12.0	1.300	0.125
LI-2	45	24.59	—	3070	3.700	6.0	5.2	11.5	1.275	0.125
					2.800	7.0	5.2	11.0	1.425	0.110

*Mineral concentrations determined in duplicate samples

Table 3. Sheep #3: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (%)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	8369	12.88	6.32	6760	0.950	8.5	21.0	11.0	0.500	0.060
					1.000	9.5	21.0	11.0	0.500	0.040
Omasum	146	16.44	5.92	5080	2.350	7.0	18.7	17.5	0.525	0.060
					2.200	7.0	18.3	17.0	0.575	0.055
Abomasum	463	11.72	4.02	7530	2.350	7.5	16.0	7.0	0.475	0.060
					2.400	6.5	15.3	7.0	0.425	0.060
SI-1	91	11.18	6.27	7940	0.625	15.0	20.3	3.5	0.350	0.070
					0.625	15.0	21.5	4.0	0.400	0.070
SI-2	227	10.55	7.22	8480	0.925	23.0	17.0	9.5	0.475	0.070
					0.950	21.0	17.3	9.0	0.450	0.075
SI-3	327	8.59	7.51	10640	1.400	24.0	17.0	15.0	1.000	0.100
					1.100	25.0	16.7	15.0	1.100	0.105
Cecum	626	11.69	7.17	7550	2.650	16.0	13.7	23.5	2.000	0.130
					2.600	18.0	13.3	24.5	2.200	0.120
LI-1	476	14.22	7.20	6030	2.600	13.0	14.3	24.5	1.900	0.115
					2.500	12.5	14.3	24.5	1.950	0.130
LI-2	113	27.72	—	2610	2.550	3.0	7.6	23.5	2.000	0.135
					2.550	3.0	8.3	24.5	2.000	0.150

*Mineral concentrations determined in duplicate samples

Table 4. Sheep #4: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	7076	12.41	6.30	7060	1.025	10.0	21.3	5.5	0.500	0.115
					1.050	10.5	21.7	5.5	0.525	0.050
Omasum	100	16.65	6.05	5010	2.200	6.5	18.0	9.5	0.450	0.070
					2.100	7.0	18.0	9.5	0.550	0.065
Abomasum	449	5.27	3.98	17980	3.700	18.0	37.4	8.0	0.800	0.070
					3.800	19.0	36.6	7.5	0.650	0.065
SI-1	154	11.15	6.08	7970	1.025	17.0	15.0	2.5	0.350	0.100
					1.000	19.0	16.5	2.5	0.350	0.090
SI-2	236	9.64	7.68	9370	1.400	33.0	12.0	7.5	0.625	0.080
					1.250	30.0	12.0	7.0	0.625	0.075
SI-3	231	8.91	7.58	10220	1.800	33.0	9.6	10.0	0.750	0.100
					1.850	33.0	10.2	10.0	0.750	0.090
Cecum	327	11.77	6.93	7500	2.600	22.0	7.2	13.5	1.375	0.160
					2.750	24.0	7.2	14.0	1.050	0.110
LI-1	454	14.09	7.18	6100	2.600	20.0	7.0	15.0	1.275	0.105
					2.700	19.0	7.0	14.5	1.325	0.105
LI-2	54	25.47	—	2930	2.700	6.5	5.0	15.0	1.475	0.120
					2.700	6.5	5.0	15.0	1.475	0.120

*Mineral concentrations determined in duplicate samples

Table 5. Sheep #5: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	8079	13.93	6.23	6180	0.600	12.5	13.3	14.5	0.800	0.080
					0.625	13.5	13.0	15.0	0.850	0.030
Omasum	204	18.95	6.52	4280	1.250	6.5	13.0	27.0	0.950	0.055
					1.350	6.5	13.0	28.0	1.000	0.040
Abomasum	186	10.78	5.22	8280	2.800	15.0	11.7	11.5	0.550	0.035
					2.500	15.0	11.7	10.5	0.700	0.040
SI-1	200	10.76	6.18	8290	0.725	15.0	15.5	8.0	0.550	0.055
					0.700	16.0	16.0	7.5	0.600	0.055
SI-2	181	11.81	7.18	7470	0.800	19.0	15.0	13.0	1.100	0.125
					0.825	19.0	15.3	13.0	1.000	0.060
SI-3	544	11.54	7.42	7670	1.350	23.0	9.2	24.5	2.350	0.055
					1.325	23.0	9.6	23.5	2.100	0.055
Cecum	508	14.56	7.04	5870	1.575	17.0	5.0	33.0	3.500	0.060
					1.625	18.0	5.2	33.0	3.400	0.060
LI-1	685	14.72	7.08	5790	1.575	16.0	5.8	33.0	4.300	0.105
					1.550	17.0	5.6	32.0	3.500	0.055
LI-2	73	24.56	—	3070	1.525	9.2	3.6	30.0	2.950	0.115
					1.750	10.0	4.4	36.0	3.600	0.065

*Mineral concentrations determined in duplicate samples

Table 6. Sheep #6: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	4060	15.02	7.06	5660	0.675	15.0	10.0	21.5	0.625	0.065
					0.725	14.5	10.7	22.0	0.600	0.060
Omasum	138	20.30	6.77	3930	1.075	8.0	12.7	32.0	0.750	0.070
					0.925	8.0	12.0	31.0	0.667	0.065
Abomasum	531	8.31	3.54	11030	2.000	11.5	13.7	19.0	0.767	0.040
					2.150	12.5	14.3	19.0	0.675	0.045
SI-1	109	13.30	6.32	6520	0.275	13.0	17.5	6.0	0.325	0.070
					0.275	11.0	16.0	4.5	0.250	0.068
SI-2	191	11.60	7.08	7620	0.800	17.0	15.3	16.5	1.050	0.095
					0.800	18.0	15.7	16.0	1.050	0.095
SI-3	340	10.63	7.68	8410	1.700	24.0	11.7	29.0	2.000	0.080
					1.634	24.0	11.3	29.0	1.900	0.070
Cecum	227	13.38	6.86	6470	2.450	16.0	7.0	51.0	5.800	0.100
					2.450	16.0	7.2	51.0	6.000	0.095
LI-1	640	14.50	7.08	5900	2.200	12.0	6.8	48.0	5.800	0.100
					2.200	13.5	6.8	48.0	5.800	0.095
LI-2	436	27.81	—	2600	1.775	4.5	3.4	51.0	5.800	0.105
					1.800	3.5	3.4	52.0	6.200	0.115

*Mineral concentrations determined in duplicate samples

Table 7. **Sheep #7: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.**

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	4740	10.94	6.00	8140	1.350	17.0	18.3	11.0	0.650	0.085
					1.050	17.0	18.5	11.0	0.475	0.055
Omasum	154	18.53	5.90	4400	2.025	8.0	16.0	17.5	0.625	0.115
					2.250	8.0	16.3	17.5	0.550	0.100
Abomasum	227	13.06	3.87	6660	3.300	8.4	13.0	6.5	0.425	0.060
					3.300	7.6	12.7	6.5	0.475	0.055
SI-1	95	11.29	6.34	7860	1.200	15.0	16.0	5.0	0.400	0.085
					1.200	15.0	17.0	5.5	0.375	0.085
SI-2	222	11.16	7.23	7960	1.900	23.4	13.3	10.0	0.600	0.095
					2.000	23.4	13.7	10.0	0.600	0.095
SI-3	95	9.69	7.40	9320	2.400	27.0	13.7	11.5	0.750	0.105
					2.475	26.0	15.3	12.5	0.775	0.095
Cecum	404	10.40	7.06	8620	5.175	24.6	8.2	20.5	2.700	0.135
					5.325	23.6	8.0	20.5	2.700	0.135
LI-1	381	11.41	7.18	7760	4.900	22.0	8.2	19.5	2.550	0.135
					4.900	22.0	8.2	20.5	2.550	0.140
LI-2	136	24.83	___	3030	4.575	4.5	3.4	20.5	2.500	0.195
					4.875	4.0	3.4	20.5	2.600	0.135

*Mineral concentrations determined in duplicate samples

Table 8. Sheep #8: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	4717	14.47	6.92	5910	3.300	15.0	8.0	21.5	0.600	0.040
					3.300	15.0	8.0	23.0	0.650	0.035
Omasum	50	24.04	7.67	3160	15.000	8.0	10.7	37.0	0.800	0.075
					14.000	8.0	10.7	36.0	0.800	0.070
Abomasum	181	12.06	3.75	7290	13.500	15.0	6.8	8.0	0.250	0.300
					14.250	15.0	6.8	8.0	0.400	0.300
SI-1	100	9.26	7.68	9800	4.500	26.0	17.7	15.0	0.700	0.110
					4.500	26.0	17.3	15.0	0.700	0.105
SI-2	14	11.00	7.20	8090	5.300	26.5	16.5	17.5	1.120	0.106
					5.300	26.5	16.5	17.5	1.120	0.106
SI-3	100	14.14	6.29	6070	8.730	31.8	9.9	28.9	2.260	0.080
					8.730	31.8	9.9	28.9	2.260	0.080
Cecum	327	15.05	7.33	5640	12.250	17.0	5.4	39.0	3.700	0.175
					10.000	17.0	5.4	38.0	3.200	0.175
LI-1	422	18.01	7.50	4550	10.000	13.5	4.8	39.0	3.600	0.200
					9.500	13.0	4.8	37.0	3.600	0.150
LI-2	77	33.29	—	2000	9.625	3.0	5.4	34.0	3.400	0.125
					9.750	3.0	5.4	34.0	3.400	0.150

*Mineral concentrations determined in duplicate samples

Table 9. Sheep #9: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	7575	11.83	6.23	7450	0.700	14.5	16.0	6.0	0.475	0.075
					0.775	14.5	16.7	6.0	0.450	0.040
Omasum	172	17.09	6.10	4850	1.025	8.5	14.7	8.5	0.525	0.075
					1.200	8.0	14.7	9.0	0.450	0.070
Abomasum	771	8.75	4.02	10430	3.000	11.0	18.5	5.0	0.433	0.095
					3.300	10.5	17.5	5.5	0.525	0.055
SI-1	136	9.72	6.27	9290	0.575	16.0	17.0	2.5	0.500	0.070
					0.575	16.0	18.0	3.0	0.450	0.070
SI-2	272	11.07	7.11	8030	0.975	22.0	14.0	4.5	0.575	0.070
					1.075	22.0	14.0	4.0	0.500	0.065
SI-3	386	9.14	7.77	9940	1.800	28.0	11.0	10.0	0.800	0.095
					1.700	30.0	10.8	9.5	0.725	0.085
Cecum	553	12.20	7.03	7200	3.600	19.0	6.6	13.0	1.850	0.115
					3.700	20.0	6.4	13.0	1.933	0.105
LI-1	612	13.14	7.47	6610	3.700	19.0	6.8	14.0	1.500	0.125
					3.700	17.0	6.8	13.5	1.725	0.115
LI-2	109	28.89	—	2460	3.400	4.5	2.0	13.0	1.825	0.130
					3.400	4.5	1.8	12.0	2.000	0.120

*Mineral concentrations determined in duplicate samples

Table 10. Sheep #10: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	6364	14.55	6.48	5870	0.625	12.5	13.7	19.0	0.975	0.060
					0.550	11.0	13.3	20.0	0.925	0.050
Omasum	154	18.34	6.53	4450	1.300	6.0	12.8	33.0	0.825	0.055
					1.250	7.0	12.8	33.0	0.850	0.060
Abomasum	372	9.49	4.90	9540	3.250	13.0	14.0	16.0	0.900	0.045
					2.300	11.5	14.7	16.0	1.033	0.045
SI-1	372	10.80	6.30	8260	0.800	15.6	16.0	12.0	0.875	0.060
					0.800	15.6	16.0	11.5	0.825	0.075
SI-2	390	10.39	7.06	8620	1.025	21.0	15.0	17.0	1.600	0.055
					0.975	20.0	15.7	17.0	1.500	0.065
SI-3	653	10.38	7.48	8630	1.400	22.0	10.3	26.0	2.200	0.060
					1.500	22.0	11.7	26.5	2.100	0.060
Cecum	594	14.24	6.99	6020	1.650	13.5	5.4	45.0	5.200	0.095
					1.650	12.0	5.4	45.0	5.200	0.110
LI-1	748	14.33	6.93	5980	1.750	14.0	6.6	47.0	5.200	0.080
					1.650	13.0	6.4	45.0	5.200	0.085
LI-2	18	27.50	—	2640	1.490	3.9	3.5	28.0	5.800	0.113
					1.490	3.9	3.5	28.0	5.800	0.113

*Mineral concentrations determined in duplicate samples

Table 11. Sheep #11: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	4060	14.65	6.45	5830	0.725	16.0	9.6	12.5	0.650	0.055
					0.575	15.0	9.8	12.5	0.650	0.035
Omasum	154	19.03	6.69	4250	1.375	9.0	11.7	23.5	0.650	0.045
					1.350	9.0	11.3	23.0	0.650	0.045
Abomasum	172	11.64	4.11	7590	2.450	10.4	11.3	11.0	0.450	0.105
					2.650	10.4	11.0	10.5	0.300	0.025
SI-1	159	7.87	6.18	11710	1.025	19.0	17.7	9.5	0.675	0.060
					1.025	19.0	17.7	9.5	0.700	0.055
SI-2	281	11.26	6.85	7880	1.100	20.0	15.7	11.5	0.650	0.060
					1.150	19.0	16.0	12.0	0.750	0.060
SI-3	395	9.68	7.46	9330	2.200	27.0	13.7	23.0	1.450	0.065
					2.250	26.0	13.7	22.5	1.550	0.065
Cecum	272	13.36	6.96	6490	4.200	18.0	5.6	34.0	3.300	0.095
					4.275	17.0	5.4	35.0	2.450	0.095
LI-1	544	14.95	7.17	5690	4.425	16.0	5.6	34.0	3.400	0.080
					4.425	16.0	6.2	35.0	3.800	0.080
LI-2	82	28.16	—	2550	4.275	5.0	3.4	33.0	3.400	0.105
					4.050	5.0	3.4	33.0	3.300	0.075

*Mineral concentrations determined in duplicate samples

Table 12. Sheep #12: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	4228	12.22	6.86	7180	0.775	17.0	13.3	21.0	0.725	0.040
					0.775	15.0	14.0	20.5	0.700	0.065
Omasum	136	19.59	6.69	4100	1.050	8.5	12.3	35.0	0.725	0.065
					1.100	8.0	13.0	35.0	0.750	0.070
Abomasum	168	10.00	5.18	9000	2.250	19.0	17.0	26.0	0.900	0.065
					2.350	19.0	17.7	26.0	0.825	0.075
SI-1	145	9.12	6.22	9960	0.650	15.2	16.0	10.5	0.625	0.065
					0.675	16.0	16.0	11.0	0.675	0.065
SI-2	277	13.80	7.02	6250	0.900	17.0	12.3	18.5	1.433	0.055
					0.975	17.0	13.7	18.5	1.500	0.060
SI-3	290	9.97	7.69	9030	1.900	23.0	14.3	31.0	2.500	0.075
					1.850	24.0	13.7	32.0	2.600	0.075
Cecum	431	12.66	6.97	6900	3.250	13.5	11.0	47.0	5.200	0.085
					3.300	14.0	12.0	47.0	5.400	0.085
LI-1	590	15.17	7.08	5590	3.250	9.5	10.0	49.0	5.600	0.110
					3.500	9.5	11.0	49.0	5.400	0.095
LI-2	231	29.08	___	2440	3.150	1.5	3.0	54.0	5.800	0.115
					3.300	1.0	3.2	53.0	5.600	0.095

*Mineral concentrations determined in duplicate samples

Table 13. Sheep #13: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	3239	12.78	7.02	6820	1.750	13.0	17.0	11.5	0.500	0.105
					1.800	14.5	17.7	11.5	0.550	0.055
Omasum	80	18.93	7.10	4280	3.075	8.0	15.0	18.0	0.550	0.070
					2.925	7.5	15.0	18.0	0.600	0.070
Abomasum	426	7.62	3.95	12120	4.200	14.0	18.0	7.5	0.450	0.130
					4.200	15.0	17.3	7.5	0.500	0.110
SI-1	154	10.01	6.51	8990	1.150	15.0	20.0	4.5	0.400	0.065
					1.200	15.0	18.5	4.5	0.375	0.065
SI-2	245	8.93	7.42	10200	2.250	30.0	16.0	10.0	0.625	0.075
					2.200	29.0	16.0	10.5	0.625	0.070
SI-3	386	7.11	7.63	13060	3.675	40.5	15.0	14.5	0.875	0.090
					3.525	40.5	15.3	14.5	0.850	0.090
Cecum	381	10.64	7.64	8400	5.800	22.0	8.0	20.5	2.250	0.135
					5.850	23.0	7.8	21.0	2.100	0.135
LI-1	336	13.04	7.56	6670	5.400	17.0	7.8	22.0	2.100	0.140
					5.600	17.0	7.6	21.5	2.200	0.140
LI-2	109	27.80	—	2600	5.900	3.0	4.0	22.0	1.900	0.180
					5.900	3.0	4.0	22.0	2.150	0.140

*Mineral concentrations determined in duplicate samples

Table 14. Sheep #14: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	5851	11.22	6.72	7910	0.850	16.0	18.5	5.5	0.400	0.060
					1.000	16.0	18.5	5.5	0.525	0.040
Omasum	197	16.15	6.77	5190	1.250	7.0	16.0	8.0	0.500	0.065
					1.200	8.0	16.3	8.0	0.450	0.050
Abomasum	349	11.71	3.43	7540	1.950	7.0	14.3	3.5	0.400	0.045
					2.050	7.0	13.7	3.5	0.400	0.050
SI-1	181	9.52	6.28	9500	0.700	19.0	19.5	3.5	0.450	0.060
					0.750	19.0	20.0	3.5	0.350	0.060
SI-2	177	12.88	6.92	6760	1.125	17.0	12.0	4.0	0.625	0.055
					1.100	17.0	12.5	4.5	0.700	0.055
SI-3	549	8.05	7.77	11420	1.900	34.0	18.5	8.0	0.700	0.075
					1.800	34.5	19.0	8.0	0.625	0.075
Cecum	408	10.60	6.87	8430	2.800	16.4	19.5	13.0	1.825	0.125
					2.500	16.4	19.0	12.0	1.625	0.110
LI-1	481	12.79	7.46	6820	2.600	11.5	18.5	13.5	1.567	0.115
					2.700	11.5	18.0	13.5	1.533	0.125
LI-2	27	23.15	—	3320	2.700	2.5	13.3	13.0	1.750	0.110
					2.500	2.5	13.0	12.5	1.600	0.110

*Mineral concentrations determined in duplicate samples

Table 15. Sheep #15: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	5761	16.23	5.97	5160	0.775	10.8	11.7	21.0	0.875	0.060
					0.700	10.8	11.7	21.5	0.900	0.070
Omasum	154	19.44	6.21	4140	1.550	7.0	13.0	38.0	0.800	0.060
					1.500	7.0	12.7	38.0	0.725	0.050
Abomasum	417	12.50	5.35	7000	6.000	4.5	5.6	17.5	0.325	0.120
					5.000	4.0	5.2	17.5	0.275	0.115
SI-1	249	10.51	6.08	8510	1.025	15.0	18.3	11.0	0.550	0.060
					1.075	15.0	18.0	11.0	0.550	0.060
SI-2	295	11.40	6.79	7770	1.000	17.0	16.7	16.0	1.133	0.060
					1.025	18.0	16.7	16.0	1.200	0.065
SI-3	254	10.69	7.41	8350	1.600	20.0	12.0	36.0	3.100	0.080
					1.500	20.0	12.7	36.0	3.100	0.080
Cecum	363	14.96	7.07	5680	2.350	14.0	5.4	50.0	6.000	0.100
					2.450	14.0	5.4	50.0	6.000	0.105
LI-1	644	14.97	6.98	5680	2.450	13.5	5.4	51.0	5.800	0.080
					2.350	14.0	5.4	50.0	6.200	0.090
LI-2	68	26.85	—	2720	2.250	4.0	3.0	47.0	5.800	0.105
					2.450	4.5	3.0	47.0	5.600	0.090

*Mineral concentrations determined in duplicate samples

Table 16. Sheep #16: digesta weight, percent dry matter, pH, water, and mineral concentrations of gastrointestinal digesta.

Tract Segment	Digesta Weight (g)	Dry Matter (%)	Digesta pH	mg/g Dry Matter*						
				Water	Cr	Na	K	Ca	Mg	Zn
Rumen	5230	14.70	6.34	5800	0.675	12.4	10.3	14.0	0.800	0.060
					0.775	12.8	10.3	14.0	0.850	0.030
Omasum	236	20.04	6.44	3990	1.850	7.0	11.0	29.0	0.850	0.065
					1.950	7.5	10.7	29.0	0.850	0.050
Abomasum	236	10.22	3.84	8780	2.600	11.0	13.7	13.5	0.650	0.095
					2.650	11.5	13.0	13.0	0.750	0.050
SI-1	186	9.91	6.39	9090	1.050	19.0	16.3	10.0	0.800	0.055
					1.075	18.0	17.0	10.0	0.700	0.055
SI-2	159	10.41	7.08	8610	1.200	20.0	15.8	18.0	1.250	0.065
					1.255	20.0	14.2	17.0	1.200	0.060
SI-3	308	10.06	7.70	8940	1.850	27.0	11.3	24.5	2.700	0.065
					1.750	27.0	10.5	24.0	2.350	0.060
Cecum	277	12.74	7.02	6850	2.550	19.0	6.4	34.0	3.100	0.120
					2.650	20.0	6.6	35.0	4.100	0.060
LI-1	376	14.51	7.13	5890	2.925	17.0	6.6	34.0	3.500	0.100
					3.050	17.0	6.6	37.0	3.400	0.650
LI-2	45	26.42	—	2790	3.375	6.5	5.8	36.0	3.900	0.075
					3.225	6.5	5.8	36.0	3.700	0.080

*Mineral concentrations determined in duplicate samples

Table 17. Water and mineral concentrations of the roughage diets.

Diet	mg/g Dry Matter*					
	Water	Na	K	Ca	Mg	Zn
Reed Canary Grass	157	0.06	30.6	5.3	1.333	0.040
		0.06	30.6	4.5	1.333	0.040
Siberian Reed Canary Grass	150	0.06	30.0	10.5	1.700	0.055
		0.06	29.4	10.5	1.833	0.060
Alfalfa (late cut)	152	0.35	15.0	15.0	2.250	0.030
		0.35	14.7	15.5	2.400	0.035
Alfalfa (early cut)	162	0.40	18.0	18.0	2.750	0.030
		0.40	18.0	18.0	2.650	0.030

*Mineral concentrations determined in duplicate samples

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