COMPARISON OF LIGNIN AND CHROMIC OXIDE AS REFERENCE MATERIALS IN THE FLUX PATTERN OF NUTRIENTS THROUGH THE DIFFERENT SECTIONS OF THE GASTROINTESTINAL TRACT OF SHEEP

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ABSTRACT

COMPARISON OF LIGNIN AND CHROMIC OXIDE AS REFERENCE MATERIALS IN THE FLUX PATTERN OF NUTRIENTS THROUGH THE DIFFERENT SECTIONS OF THE GASTROINTESTINAL TRACT OF SHEEP

By

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Different kinds of markers have been used as reference materials in various studies. The use of markers are fairly common in investigation of digestibility coefficients, rate of passage, retention time, voluntary intake etc. In recent years markers have been used as reference materials of nutrients from the different sections of the gastrointestinal (G.I.) tract. However, few investigations have been performed in this area and the validity of the use of indicators should be further evaluated with more research in order to substantiate its use in such studies.

Lignin has been used as a nonabsorbable marker in this study to measure the indigestibility as well as the flux pattern of seven different nutrients (dry matter, acid detergent fiber, magnesium, potassium, sodium, calcium and zinc) from nine different sections of the G.I. tract of 16 sheep. Four different hays were used as rations. The mineral determinations, and the flux of these minerals by the chromic oxide method were determined in a previous M.S. study.

Lignin determinations for all the samples of the ingesta and the forages were done according to the method of Van Soest. The indigestibility of the different nutrients was determined by the lignin ratio technique. Also the flux patterns with this indicator were measured for all the different sections of the G.I. tract. The indigestibility of dry matter (D.M.) for the entire tract avaraged 39%. Analysis of variance indicated there was statistical difference in the indigestibility of dry matter among the sections of the gastrointestinal tract ($P < 0.0005$). The D.M. indigestibility in the rumen was 48%, indicating 52% absorption from the rumen. In the upper small intestine an endogenous secretion was observed, but absorption and/or reabsorption occurred in the middle S.I. and the lower sections of the G.I. tract.

About 48% indigestibility was observed for acid detergent fiber (ADF) for the entire tract and rumenal disappearance of this nutrient amounted to 42%.

The indigestibility of the minerals demonstrated a difference for the different sections ($P < 0.0005$). For certain minerals the indigestibility indicated a significant difference due to forage (grass vs legume). In general, the 6 hour and 12 hour postprandial did not show much differences in indigestibility for the flux pattern of different nutrients.

The flux pattern of minerals also indicated significant variation among the organs ($P < 0.0005$). An apparent absorption of Mg and K were observed from the rumen. For Na, Ca, and Zn the ruminal values were considered as the base values because of unmeasured dietary intake. A high endogenous secretion was common for all minerals in the upper S.I. In general, absorption occurred in the middle S.I. and in the following further sections of the G.I. tract.

Chromic oxide and lignin were compared as indicators by measuring their ratio values. The chromium lignin ratio indicated a highly significant difference ($P < 0.0005$) in their rate of passage through the different sections of the G.I. tract. The distribution of chromic oxide, lignin and dry matter in these sections showed that chromic oxide moved out of the rumen faster than did lignin or dry matter. Also in the lower sections of the G.I. tract chromic oxide as a percent of that in the entire tract was twice that of dry matter of lignin.

This work thus indicated that chromic oxide is not a suitable indicator for the flux pattern studies of nutrients from the rumen or omasum when given by capsule with a roughage diet.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES--continued

TABLE | Page

APPENDIX TABLES

LIST OF FIGURES

INTRODUCTION

Many studies have measured digestibility coefficients, rate of passage of digesta, retention time, absorption and secretion of nutrients in ruminants. Markers have been widely used in these studies with varying degrees of accuracy. There are certain characters which every indicator should possess. Few studies have been reported in the literature comparing the performances of markers with that of a standard. Results with markers are usually satisfactory and hence they have been widely used due to their simplicity and ease.

Markers also may be used to determine the flux pattern of nutrients in various sections of the digestive tract. This has been done in very few studies but interest in this subject and technique is increasing. Such influx-efflux studies provide information on the extent of absorption of dietary constituents and endogenous secretion in various organs in the gastrointestinal tract. Markers such as chromic oxide, polyethylene glycol, radioactive isotopes and lignin have been widely used as indicators in these studies. The use of two indicators simultaneously with similar dietary treatments might furnish information concerning the validity of results so obtained.

Indicators have shown satisfactory results in digestibility studies for the entire G.I. tract. However, when indicators have been used in sectional studies to measure digestibility or the flux pattern of nutrients, they sometimes showed variable results. Yang (1964) in a study with Dairy calves used both chromic oxide and lignin as indicators to measure the flux pattern in different sections. Flux patterns were similar for all organs except the rumen. However this difference in the flux pattern in the rumen due with the two indicators was very large for all nutrients. In the rumen one indicator showed a net absorption while the other showed a net secretion. The rumen is a very important organ and a true estimate of influx-efflux for this organ is of paramount importance.

This thesis compares two indicators, their distribution and their ratio in each section. Further, indigestibility absorption and secretion of different nutrients by the lignin ratio method were determined and are presented for comparison with those determined on the same samples where chromic oxide was used as the indicator. Values for chromic oxide were determined previously on the samples used in this study.

REVIEW OF LITERATURE

Various Techniques Used in Absorption, Secretion, Digestibility Coefficient, Retention Time, Rate of Passage etc.

The gastrointestinal (G.I.) tract of ruminants is very complicated in many respects and attempts to obtain more detailed information on the function of various portions has attracted the attention of many workers over the last several years. The digestion coefficients, absorption and secretion, retention time of particles of the digesta, nutrients and other materials have been used as measures of gastrointestinal tract function in ruminants. With the tremendous increase of knowledge of this field and need to solve problems and describe digestive process, adequate measurements are required using more sophisticated methods. This will involve individuals who are trained in nutrition, anatomy, physiology and as well as biochemistry.

In the past most of the studies have considered the digestive tract as a whole. But knowledge of the exact site of absorption, secretion and reabsorption of various nutrients has become more desirable and essential. The literature now contains studies comparing the absorption and secretion of nutrients from the different sections of the gastrointestinal tract. The rumen is a complicated organ and stores the ingested material with saliva and where microbes ferment carbohydrates and fibrous feeds, degrade feed protein and make microbial protein. Absorption of various nutrients also occurs from the rumen. Many workers have attempted to study the different dynamic functions which it performs one and at the same time.

Many techniques have been employed to study digestibility and absorption of nutrients etc. in ruminants. Following are some of these techniques.

1. Arterio-venous differences.
2. Perfussion of isolated organs.
3. Use of different types of cannulas in different sections of the G.I. tract and samples of digesta collected and/or materials put into the gut.
4. Everted sac technique
5. Use of radioactive isotopes.
6. Total collection of feaces for digestibility studies.
7. Markers fed to animals as reference materials--followed with total collection or grab samples of feaces.
8. Markers fed to anomals as reference materials followed with slaughter and collection of samples from different sections.

The techniques mentioned above have been used according to the nature of study under investigation. Almost all of these techniques have some limitations and one technique may generally be good only for a particular experiment.

Markers have however been employed in different types of studies for digestibility coefficients, absorption and secretion, rate of passage or retention time of particles in the different sections of the G.I. tract. The principle in using markers is based on the following set of characters.

1. The reference material which is used as an indicator should not be digestible to any significant level in the digestive tract and recovery of the fed indicator should be close to 100% in the feces.

2. The reference material used should be palatable and should not influence or interfere with intake digestion of nutrients or function of the digestive tract.

3. The analysis for the indicator should be simple and precise.

4. The reference material should be thoroughly mixed with the ingesta throughout the digestive tract and it must move through the G.I. tract at a rate equal to the nutrients of the digesta.

Eugene Wildt (1874) first used an indicator as a reference material to study the absorption of nutrients in sheep. Subsequently many different substances such as chemical compounds or inert materials have been used. Most of these are insoluble in water and thought to move along with solid portion of the digesta while a few substances are said to be water soluble and move with a liquid fraction. The different kinds of markers will now be discussed.

I. Chemical Compounds As Markers

A. Silica. Silica was first used as an indicator by Eugene Wildt in 1874 to study the absorption of nutrients in sheep. Silica has been used as an indicator to determine digestibility coefficients but the results obtained were questionable. Some believe that dust in the air or the contamination of feed with dirt interfere seriously with the determination of digestibility coefficients when silica is used as an indicator. Gallup et al. (1936) reported that approximately 15% of the silica was metabolized and thus is not a reliable indicator. Druce and Willcox (1949) reported that the amount of silica recovered in the feces was too variable and therefore not usable for digestibility studies. Gallup et al. (1945) studied digestion in steers under different conditions using silica as the reference material. They noted that silica excretion exceeded intake by 36% in the pasture situation and by 10% in steers on dry lot. This increase in excretion, they suggested, was due to the dirt ingested by the animal.

However, good agreements between digestibility coefficients determined by silica ratios and those obtained by the standard total collection procedure were reported by Skulmoswski in 1943. Pujszo et al. (1959) reported that silica can be used as an indicator for digestibility studies. In 1965, Jones et al. studied the relation between the silica content of the diet and the excretion of silica in sheep. They reported that the amount of silica excreted in the urine (metabolized) represented only small proportions of the amounts ingested, and recoveries of silica in feces was close to 100%, suggesting that silica can be used as an indicator in digestibility studies.

B. Iron Oxide As An Indicator. Bergium (1926), Heller *et al*. (1928), Mitchell *et al*. (1928) used iron oxide successfully as an indicator. In 1934 Moore and Winter used iron oxide as an indicator and demonstrated that it did not give an accurate estimate of total digestibility. Knott, Murer and Hodgson (1936) used iron oxide and reported that it was an unsatisfactory reference material in the determination of digestibility coefficients in cattle.

C. Chromic Oxide As An Indicator. Chromic oxide has been widely used as an indicator both in ruminants and non-ruminants. The use of chromic oxide as an index substance was first proposed by Edin in 1918.

Hamilton *et al*. (1927) reported good agreement between conventional fecal collection and the chromic oxide method with sheep. Satisfactory work with chromic oxide was also reported by some workers (Anderson *et al*. 1935; Barnicot 1945 etc). Schurch, Lloyd and Crampton (1950) demonstrated that chromic oxide can be used satisfactorily in digestibility studies. Kane *et al*. in 1950, and again in 1953, reported better results with chromic oxide than with other indicators. In 1951, Crampton and Lloyd demonstrated that chromic oxide was a good index material in digestion studies of human subjects. In the same year they reported that chromic oxide can be employed successfully as a marker in sheep, provided the ration includes ground feed with which chromic oxide was premixed.

Chromic oxide has been used often in recent years in many absorption studies. Miller and Cragle (1965), Yang and Thomas (1965), Horvath (1967), Miller et al. (1967), Heirs et al. (1968) and Perry et al. (1967) are some of those who have used this indicator for the measurement and movement of different nutrients in the G.I. tract.

However, there are reports in the literature which indicate that chromic oxide is not a very suitable indicator in the digestibility and absorption studies of ruminants. Kreula (1947) reported chromic oxide as an unsatisfactory indicator. Kane et al. (1952), Elam et al. (1961 and 1962) and Clanton (1962) have reported a diurnal variation in the excretion pattern of chromic oxide. Crampton et al. (1951) reported as follows:

1. When roughage comprised the whole ration for sheep, the chromic oxide method gave variable and low coefficients for total digestibility when compared to those by the conventional method; and

2. On a roughage ration, chromic oxide fed in a highly concentrated pellet was partially retained somewhere in the

digestive tract. This retention, they suggested, would account for the low dry matter digestion coefficients obtained when chromic oxide was used.

Balch (1957) reported that chromic oxide fed in capsule form to steers entered the anterior rumen and dissolved within five minutes. He indicated that there was a rapid transfer of chromic oxide to the omasum from the rumen, and in the first 30 to 60 minutes about 67% moved to the posterior portion of the rumen, leaving only 33% to pass with the solid digesta or the dry matter portion. In another study with this indicator, Bolin et al. (1960) observed that chromic oxide incorporated uniformly in a pelleted roughage ration was passing out of the rumen very rapidly. The premixed ground particles of chromic oxide in the feed were reported not to move with the roughage ration, especially the fiber portion. Corbett et al. 1959, employed a new method of feeding chromic oxide by incorporating it into paper. Langlands et al. (1963) reported that this product was better than when chromic oxide was fed in capsule to both grazing sheep and cattle. Johnson et al. (1964); McGuire et al (1966); Knapka et al. (1967) are among those who reported poor recovery of this indicator.

Yang and Thomas (1965) used chromic oxide and lignin as indicators in studying the flux pattern of nutrients in the different sections of the G.I. tract in dairy calves.

Both the indicators gave comparable results in all sections, except for the rumen. In the rumen, chromic oxide however indicated low digestion coefficients for all nutrients when compared to the values obtained by lignin as an indicator.

Erickson et al. (1970) reported that in digestibility studies using both chromic oxide and lignin gave comparable results for the feed/feces ratios, but not for the feed/rumen ratios.

D. Polyethylene Glycol As An Indicator. In recent years polyethylene glycol (PEG) has been used as a reference material in studying digestibility as well as absorption and secretion of various nutrients. This indicator is water soluble and theoretically is a better indicator for liquid fraction in the G.I. tract.

Smith et al. (1959) used this material as a reference substance in absorption and secretion studies of magnesium. Corbett et al. (1959) reported that PEG moved through the digestive tract at a faster rate than chromic oxide. In 1962 Weller et al. used PEG as an indicator and reported that it left the rumen more rapidly than lignin. Chandler et al. (1964) used this material as an index to measure the dry matter digestibility in dairy cows. They showed that 100% recovery was possible with this indicator, and suggested that due to its palatability, feed intake and other such properties, this material should serve as an acceptable reference substance for estimating digestion coefficient for any nutrient.

II. Radioactive Materials As Indicators

Radioactive rare earth materials and radioisotopes have been used as indicators in recent years mainly to study the absorption pattern of various nutrients from the G.I. tracts of both ruminants and nonruminants. Recovery of these water soluble materials in the feces is close to 100%, though some studies have shown lower recoveries than with other indicators. However, radioactive techniques have been welcomed by many workers due to their simplicity as well as accuracy. Radioactive contamination is a serious problem and hence use of this type of material is restricted.

Chandler and Cragle (1962) used radiocerium (Ce^{144}) as a non-absorbable marker in dairy calves to study absorption of certain nutrients from the G.I. tract. Cragle (1967) used radiocerium as a digestibility marker in calves to study the utilization of magnesium, calcium and phosphorous. In 1967 Knapka et al. used radiocerium in burros to study digestion coefficients.

Miller et al. (1967) used radiocerium as an indicator to determine the sites of absorption and secretion in the G.I. tract. They reported that recoveries were little lower than 100% and suggested that the lower recovery may be due to some adsorption of this material to the lining of the G.I. tract.

Perry *et al.* (1967), Huston and Ellis (1968), have also used radiocerium as a reference material in experimental studies. In general, this material was a satisfactory marker.

III. Inert Materials As Reference Substances

Inert materials have been used as indicators to study the retention time and rate of passage of materials through the G.I. tract. Ewing and Smith (1917) used pieces of rubber hose as marker. Hoeizel *et al.* (1930) used substances like rubber, cotton thread, glass beads, pieces of aluminum, silver and gold as inert materials to measure the rate of passage in many nonruminants including man.

Moore and Winter (1934) used rubber ring with cattle to measure the rate of passage through the G.I. tract. Plastic particles have been used as indicators in human and cattle by King and Moore in 1957. Thomas *et al.* (1961) used tygon rings and reported that size and density of particles influenced rate of passage through the G.I. tract.

IV. Natural Constituents of Plants as Indicators

Many of the plant constituents have been used as indicators to determine rate of passage, digestibility coefficients and absorption and secretion relationships.

Stained particles as stained hay, stained straw, stained oats etc. were used as reference materials in digestibility and rate of passage studies. Early workers were Lenkeit _et al_. (1930), Falschani _et al_. (1933), Columbus (1936), Balch (1950), Castle (1956), Shellenberg _et al_. (1961). In many of these studies recoveries or excretion patterns were made by counting the coloured particles in the feces. Ellis _et al_. (1968) cautioned about use of the stained particle technique. In 1950 Forbes _et al_. used protein as an indicator. Reid _et al_. (1950) proposed a formula for the successful use of plant pigments as an indicator. Kane _et al_. (1953) used plant pigment ratio technique along with six other techniques to study the digestion coefficient of certain forages in dairy cows. The plant pigment ratio was found to be a satisfactory method, and it gave results, which were close to the total collection method. Cook _et al_. (1951), Schinder _et al_. (1953), and Soni _et al_. (1953) have used the plant pigment method in studying digestibility. Cook _et al_. (1951) reported lignin method was more satisfactory than the plant pigment method. Soni _et al_. (1953) however found plant pigments to be a satisfactory indicator.

Fecal nitrogen has been used as an indicator in digestibility studies as a reference material by Forbes _et al_. (1949), Schinder _et al_. (1953), Soni _et al_. (1954).

A formula to use this technique in practice has been described by Lancaster in 1949.

Lignin As An Indicator

Lignin a constituent of the fibrous portion of plants is not significantly digested in the G.I. tract. This characteristic of lignin may however be a "blessing in disguise" since it could easily be used as an indicator in studies with ruminants.

Hale (1940) proposed lignin as an indicator. Ellis *et al.* (1946) recommended lignin as a reference material in digestibility studies. They called this method the "Lignin ratio Technique", and prescribed the following formula for the calculation.

$$Y = 100 - 100 \frac{X}{Z} \cdot \frac{\text{n in feces}}{\text{n in feed}}$$

Where Y = percent digestibility of a specific nutrient,

n = percent of a specific nutrient in either feed or feces

X = percent lignin in feed, and

Z = percent lignin in feces.

Ellis *et al.* (1946) used the lignin ratio technique to determine the digestibility coefficients of various nutrients and compared the results with those of the conventional method. In the thirty trials compared only one was statistically different at 1 percent level and four at the 5 percent level.

In 1947 Gray _et al_. used the lignin ratio technique successfully for the digestion studies of cellulose at successive levels of alimentary tract with wheat straw and lucerne hay. This indicator was employed by Hale _et al_. (1947) to measure the digestion of nutrients in the rumen at 6 hours and 12 hours after feeding.

Forbes _et al_. (1948), Forbes _et al_. (1950), determined digestion coefficients with this indicator as a reference material using grazing animals. Cook _et al_. (1951) used lignin as the marker to measure the digestibility coefficient in grazing sheep. Kane _et al_. (1950) in a comparison study with lignin and chromic oxide reported that 100% recovery of both the indicators in the feces were possible.

Many other workers such as Gray _et al_. (1954), Weller _et al_. (1954), Makela _et al_. (1956), Balch (1957), Badawy (1958), Weller _et al_. (1958), Rogerson (1958), Smith (1961), Elam _et al_. (1961), Elam _et al_. (1962), Van Soest (1962), Johnson _et al_. (1964) have employed lignin as a reference material in digestibility coefficient studies. Most studies indicated that lignin was a satisfactory indicator, however, a few indicated that it was not a satisfactory reference material (Csonka (1929), Hale _et al_. (1947), Davis _et al_. (1947), Sullivan (1959), Elam _et al_. (1962)). In most of the cases the objection of using lignin as an indicator was due to its poor recovery, or its digestion or due to occasional high recoveries.

Van Soest (1962) reported drying, heating, and moisture removal from the sample are important factors influencing heat damage that can cause variation in the content of lignin.

A comparison study was made with lignin and chromic oxide as indicators with the total collection method for digestibility by Van Soest (1962 b). He used a pelleted ration for the cows in this study and conducted 22 trials. The lignin ratio showed a correlation of 0.96 to the total collection while the corresponding value of chromic oxide was 0.91. This work also showed that fecal recovery of both indicators were close to 100%.

Diurnal variation of lignin was reported by Kane *et al*. (1952) in a comparison study of chromic oxide and lignin. They reported that the diurnal variation with chromic oxide was significant, but that the diurnal variation in lignin was not significant. Elam *et al*. (1961) also studied the excretion pattern of lignin in cattle with pelleted rations. They concluded from the results of this work as well as considering the results of Kane *et al*. (1952), that there was not much diurnal variation with lignin and suggested that grab samples would not create significant variation from the results of the total collection.

Lignin also has been employed in absorption studies, and studies to measure the flux pattern of nutrients in the different organs of the G.I. tract of ruminants. Eldson et al. (1946) studied the absorption of volatile fatty acids by using lignin as an indicator. Hale et al. (1947) used lignin method to study the absorption of nutrients from the rumen. Yang (1964), and Yang and Thomas (1965), used lignin ratio technique to study the absorption as well as the influx-efflux pattern of different nutrients throughout the G.I. tract of young calves.

Rate of Passage of Digesta Through the G.I. Tract

Rate of passage of inert materials, markers, forages and other materials through the gastrointestinal tract have been studied by many workers. Castle (1956), cited references indicating that the rate of passage studies were done by Reaumer and Spallanzani in the eighteenth century. Ewing and Smith (1917), Mitchel et al. (1928), Useli (1930), Lenkeit and Habeck (1930), and Columbus (1936) were some of the workers who investigated rate of passage of food materials in the early years of the twentieth century. By the middle of this century more interest has been shown in this field since investigators have found rate of passage, food intake, retention time, digestibility, particle size, and specific gravity etc. to be interrelated.

Inert materials like rubber rings have been used to measure the rate of passage of digesta (Ewing and Smith, 1917; Moore and Winter 1934). Thomas et al. (1961) used tygon ring and lucite particles in dairy heifers to measure the rate of passage of the forages through the G.I. tract. Iron oxide has been used as a reference material by Mitchel et al. (1928), Moore and Winter (1934).

Balch (1950) suggested that studies of the rate of passage of food in ruminants is greatly complicated by the peculiar arrangements of the stomach compartments which leads to greater mixing and shifting of their contents, and reported that the conventional method of measuring rate of passage by using markers ingested as a loose mixture with the food was not satisfactory since the marker tended to become separated from the food with which they were consumed.

A more physiological method has been recommended by Lenkeit and Habeck (1930). They introduced stained particles such as stained straw, stained hay etc. in the diet and determined their recovery in the feces. Many workers have employed stained particle to study rate of passage of forages etc. (Useli (1930), Balch (1950), Blaxter (1955), Castle (1956, a,b,c), Blaxter (1961), Rodrigue et al. (1960), Campling et al. (1963) etc.).

Lignin has been used as an indicator for the last few years. However the rate of passage of this material through the G.I. tract was studied by only a few workers. Most of the studies were done to measure the digestion co-efficients of various nutrients, and in such studies lignin's rate of passage was not directly measured. In recent years this indicator has been used to measure the absorption-secretion pattern of various nutrients in different sections, and in these cases the rate of passage of this indicator can be measured from the samples collected and analysed.

Stallcup _et_ _al_. (1956) measured the influence of lignin in the passage of nutrients through the G.I. tract of fistulated steers which were fed different levels of lignin by using different varieties of lespedeza hay. The results of this study indicated that in most cases the removal of nutritive materials (crude protein and ash) was inversely proportion to the percentage of lignin in the hay diet. They observed highly significant correlations between the percentage of lignin in hays and the removal of lignin, ash and protein from the rumen in 12 hours. They also showed that lignin retarded the passage of nutrients from the rumen.

Weller _et_ _al_. (1962) showed that PEG moved out from the rumen faster than did lignin in sheep.

Different digestibility studies were conducted with sheep by Crampton et al. (1951) using chromic oxide as an indicator. He concluded that in certain cases chromic oxide was not adequately excreted and recommended that it should be fed 9 days with concentrate ration and 5 days with roughage ration in order to have equilibrium established.

Balch et al. (1957) administered chromic oxide in steers (10 g finely ground chromic oxide in capsule, and placed in the cardia). They reported that capsule of chromic oxide entered the anterior rumen or the reticulam and dissolved in about 5 minutes, releasing chromic oxide and allowing its admixture with the contents of those regions. During the first 30-60 minutes after administration they indicated that there was a rapid transfer of chromic oxide to the omasum. Of the chromic oxide given at the beginning of feeding less than 33% remained in the rumen when the meal had been completed.

Different rates of passage for chromic oxide fed in different forms have been reported in the literature. Corbett et aI. (1959) and Langlands et al. (1963) observed different passage rates for chromic oxide when fed as capsule, powder form, or when incorporated into paper. Johnson (1964), compared the rate of passage of chromic oxide in powder and compared this with this excretion of different nutrients of the digesta. Erickson et al. (1970)

used chromic oxide (powder) and lignin as indicators to measure digestibility of feed in sheep. Chromic oxide apparently was passed out of the rumen faster than lignin or the bulk of the rumen ingesta. Indigestibilities and levels of lignin and crude fiber in the entire tract showed a high degree of association in their rate of flow through the tract. Many workers have discussed the factors which influence the rate of passage of materials through the G.I. tract such as size, specific gravity, the nature of feed, voluntary intake, retention time, etc. Most of the studies report that in general small or finely ground particles move through the digestive tract much faster than coarsely ground or that not ground (Balch 1950, Blaxter _et al_. (1956), Rodrigue _et al_. (1960), Thomas _et al_. (1961), Campling _et al_. (1962) etc.).

Thomas _et al_. (1961) studied the rate of passage of different forages through the G.I. tract of heifers by using tygon rings and lucite as markers. They demonstrated that both size and density of particle influenced the rate of passage through the G.I. tract. Campling and Freer (1962), in study with inert material (methyl methocrylate), demonstrated that rate of passage was affected by size and specific gravity. Shalk and Amaden (1928) studied the effect of specific gravity of individual particles in the reticulo-rumen. Shalk and Amaden concluded that low specific gravity of hay and concentrates in the reticulo-rumen resulted in the accumulation of the majority of fibrous digesta in the dorsal sac of the rumen. They believed that as the particles of the digesta become saturated and partly decomposed, the specific gravity of particles increased and they tended to sink into the ventral regions of the reticulo-rumen and then increased their chances of passage to the omasum and abomasum. King and Moore (1957) reported a relationship between the rate of passage and the specific gravity of particles. The relationship between voluntary intake and rate of passage was studied by several investigators (Balch (1950), Blaxter (1955), Castle (1956 b), Makela _et al_. (1956), Campling _et al_. (1961), Campling _et al_. (1963), Freer _et al_. (1963) etc.).

Balch (1950) indicated the rate of passage of the roughage and the concentrate fraction of the ration was not the same. Eng _et al_. (1964) demonstrated that as the amount of hay in the ration increased then the rate of passage increased. It appeared that the rate of passage of hay was controlled by the amount of hay entering the digestive tract. The movement of corn was hastened by an increase in rate of passage of hay portion of the ration (Eng _et al_. (1964)). Campling _et al_. (1961) showed that there was a slower rate of passage of straw than that of hay. Digestibility of the forage can also cause variation in the rate of passage (Rodrigue _et al_. (1960)).

Dry Matter: Its Digestion, Absorption, and Secretion in the Gastrointestinal Tract

Dry matter (D.M.) includes everything except water. Van Soest (1965) has divided forage dry matter on a nutritive basis into cellular and cell wall portions. According to him the cellular contents included lipids, most of the proteins, soluble carbohydrates, and most of the water soluble materials. The cell wall portion includes cellulose, hemicellulose and lignin that are insoluble in detergent solutions.

Once the food is ingested into the mouth it passes to the rumen. A large quantity of saliva is secreted which is later thoroughly mixed with the stored materials in the rumen. Fermentation of the fibrous portion of the roughage occurs in the rumen, some carbohydrates undergo digestion, and some end products are absorbed from the epithelial layers of the rumen. The residues of the fermented portion together with the portion of the digesta which escaped digestion in the rumen move to other portions of the G.I. tract where they are acted on by different enzymes in different sections and may be thus digested and absorbed. Secretion of some of these absorbed materials and reabsorption of the nutrients occur in the different sections of the G.I. tract. Rogerson (1958) thus described "Digestion is in every sense a dynamic process, many actions and reactions occurring simultaneously. Thus there may be food intake, food passage, nutrient absorption, fermentation secretion, and synthesis, all going side by side in the same organ".

Different types of carbohydrates have been studied to determine their digestibility and utilization. Philipson et al. (1942) studied the digestion pattern of different types of carbohydrates in the rumen of sheep. They observed that glucose, fructose, and cane-sugar underwent rapid fermentation while maltose, lactose and galactose were fermented less rapidly. Bondi and Meyer (1943) studied the chemical nature and digestibility of roughages and observed that digestibility ranged from 64.0% to 66.2% for soluble pentosans and from 74.0% to 76.5% for the insoluble hexosans. Weller et al. (1954) studied the passage rate of starch through the omasum of the sheep. He showed that destruction of starch occurred in rumen as well as the omasum.

The extent of digestion in the reticulo-rumen of cows was studied by Balch in 1957. The animals received 58% of the dry matter from the nitrogen free extract (NFE) fraction, 20% from the crude fiber fraction and total carbohydrates constituted about 80% of the intake. The result of this study suggested that on the average almost half (43%) of the dietary dry matter was digested in the reticulo-rumen and that some 80% of the apparently digested dry matter was in the form of NFE, and 13% was crude fiber representing 81 and 54% of the total digestion of these fractions. In these studies the portion of dry matter digested in the reticulo-rumen was much higher with diets high in concentrates than with those containing mainly or entirely roughage. For a roughage ration, the apparent digestion of crude protein in the reticulo-rumen was low, thus little or no absorption of nitrogen occurred from the reticulo-rumen. A range of 12 to 54% of dietary nitrogen disappeared from the rumen with high concentrations. The range of apparent ruminal digestibility of dry matter was 26 to 62% and the apparent digestibility of dry matter of the hind gut was 12 to 34%.

Rogerson (1958) studied the digestion of different kinds of rations along the G.I. tract of sheep. He used Rhode grass hay, Rhode grass hay plus Cassava meal, and Maize-meal as rations in three different groups. He observed that 40% of the dietary dry matter was digested in the sheep rumen on the hay diet, 50% on the mixed diet and 75% on the concentrate diet.

In a total digestibility study conducted in sheep, Elam _et al_. (1962) used 60% ground hay and 40% barley as the ration. The digestibility coefficient of dry matter determined by the total collection method was 65.4%. They observed highly significant decrease in dry matter digestibility with increasing planes of nutrition.

Wright and Grainger (1966) conducted a trial to observe the extent of post-ruminal digestion absorption of carbohydrates in mature sheep. A concentrate ration was used. The results indicated that the ruminant possess an adequate capacity to digest carbohydrate post-ruminantly. They also indicated that starch was completely digested and absorbed from the intestine.

Cellulose digestion throughout the gastrointestinal tract was studied by Philipson _et al_. (1942), Gray _et al_. (1947), Hale _et al_. (1947), Gray _et al_. (1958), etc. Philipson _et al_. (1942) reported cellulose was fermented very slowly when compared to sugars. In another study sheep were fed a constant amount of wheat straw or lucerne hay and later slaughtered. Samples were taken from different sections of the G.I. tract. The results showed that 40 to 45% of the cellulose present in the fodder was digested before the food passed into the abomasum and an additional 15 to 20% was digested in the large intestine. During the second fermentation 7 to 11% disappeared in the cecum and 4 to 9% in the colon. Approximately 70% of cellulose that was digested was broken down in the rumen, 17% in the cecum, and 13% in the colon (Gray _et al_. (1947).

Hale _et al_. (1947) studied the D.M. digestibility by periods in the rumen. They demonstrated that soluble nutrients disappeared predominately in the first 6 hours of a 12 hour period. Cellulose was only slightly digested during the first 6 hours. They noted a more rapid degeneration of cellulose during the second 6 hours than during the first 6 hours.

Gray et al. (1958) reported that the rumenal digestion of cellulose of sheep fed on wheat straw and lucerne hay was 30% and 50% of the total respectively.

Yang and Thomas (1965) observed that D.M., organic matter and fiber were digested to a different extent in the rumen when rations consisted of two different levels of fiber in young dairy calves. The D.M. and organic matter of the high fiber rations were less digestible in the rumen than those of the low fiber ration.

In a study with different kinds of forages, Van Soest (1965) observed that as acid detergent fiber (ADF) values increased from 24.8 to 54.8% digestibility decreased, A similar relationship also has been shown with the detergent lignin which ranged from 11.6 to 20%. In another study Van Soest reported that a fraction of carbohydrate contained substances which could be digested only by micro-organisms. He has shown that these types of carbohydrates were not completely available because of lignification. In general he suggested increasing maturity of plants lead to greater lignification and decrease in digestibility. Further he reported that alfalfa has relatively low cell wall content, which is highly lignified, while cell walls of grasses and straw form a greater proportion of the dry matter.

A study was conducted by Ingalls et al. (1965) to measure the digestibility and nutritive value index in whethers using different types of legumes and grasses. They found a positive correlation between lignin and D.M. intake, and a significant negative correlation between lignin or fiber content of the forages and percentage of digestible dry matter. In another study Ingalls _et al._ (1966) showed that rumen retention time of D.M. was 0.65 days for legumes and 1 day for grasses. As intake of D.M., fiber, and lignin increased, retention time of each constituent decreased.

Campling _et al._ (1966) conducted two experiments with cows fed artificially dried grass (highly digestible) and oat straw (poorly digestible) at restricted and at ad libitum rates of feeding. Cows were fed with long grass in the first trial and ground grass in the second. The results indicated that the rumen digestibility of organic matter of long dried grass was 74% and of ground dried grass was 67.7%. They reported that the digestibility of ground dried grass was much less than that of long dried grass when fed ad libitum. In this study the digestibility of crude fiber was 48.6% in cows fed dried grass, 43.2% for oat straw (long) and 54% for ground oat straw.

Sectional studies of the G.I. tract in respect to dry matter absorption were made by few investigators using ruminants. Hale _et al._ (1947 b) reported that the average ruminal digestion coefficient as a percentage of total was 48.4% for D.M., 59.6% for protein, 27.2% for crude fiber, 43.4% for cellulose, 83% for other carbohydrates and 3.1% for lignin. Similarly cecal coefficients were 11.6% for cellulose and 9.5% for protein. Weller et al. (1954) reported extensive destruction of starch in the omasum. Wright and Grainger (1966) reported that starch was digested and absorbed from the intestine. Boyne et al. (1956) observed that dry matter in the rumen decreased from 75% of the total in the tract just after feeding to about 60% 12 hours after feeding. They noticed that in the omasum the D.M., ash and energy concentrations of the contents were 50% higher than in the reticulo-rumen, and the nitrogen concentration was about 90% higher. In the small intestine they found that the D.M. content was 20% higher than in the abomasum and in cecal contents the concentration of D.M. was 40% greater than in the small intestine. Dry matter concentration was 60% higher in the colon than in the small intestine.

Rogerson (1958) reported that absorption took place from the rumen. Badawy et al. (1958) demonstrated that the reticulo-rumen of sheep contained 74% of the total G.I. tract dry matter some four hours after feeding. They suggested that the dry matter percentage in the omasum was considerably higher in the omasum and the colon than in other parts of the G.I. tract due to water absorption. In another experiment they indicated that there was a decrease in the dry matter percentage in the abomasum and suggested that this could be attributed to the dilution by gastric juice added (Badawy et al. (1958).

Hogan and Philipson (1960) in an investigation with sheep demonstrated that the dry matter content of duodenal digesta varied from 3.3 to 7.1% with a mean of 5.2%. Of the 66.2% that disappeared, 70% left the digestive tract between the mouth and pylorous, 11% in the small intestine and 19% in the large intestine.

Yang and Thomas (1965) reported that absorption from rumen ranged from 51 to 86% for dry matter, 54 to 87% for organic matter, and 29 to 68% for fiber in the high fiber ration. They found no absorption for these materials from the omasum, abomasum, and upper small intestine. However, they observed absorption in the lower portions of the G.I. tract.

Calves and goats fed milk replacer plus starter were used in a study by Heir et al. (1968) to measure the absorption in different sections of the G.I. tract. They observed that there was some net absorptiom in the reticulorumen and variable but moderate changes in the omasum and abomasum. They indicated that a large amount of dry matter were secreted in the upper S.I. but re-absorbed in the remainder of the gut. Only little changes were noted in the cecum and large intestine in this study.

Topps et al. (1968) reported that 69% of the digestible dry matter disappeared in the stomach (reticulo-rumen, omasum and abomasum), 17% in the small intestine, and 4% in the large intestine when fed concentrate and 67% of the digestible dry matter disappeared in the stomach, 22% in the small intestine and 11% in the large intestine when fed hay.

Summary

In many respects the gastrointestinal (G.I.) tract of ruminants is very complicated. In the G.I. tract of the ruminants, the rumen is the most complicated organ and its various functions are difficult to measure. Studies like digestion coefficients, absorption-secretion, retention time of particle of digesta, voluntary intake, rate of passage etc. have been made by many workers.

Markers have been used for many years in measurements of digestion coefficients, rate of passage, retention time of particles of digesta etc. In recent years indicators have also been used to study flux pattern of various nutrients in different sections of the G.I. tract. The reference materials used in these studies include chemical compounds, radioactive materials, inert materials and natural constituents of plants etc. Most of these studies have been done using chromic oxide or lignin as the reference material. Digestibility comparisons made with both indicators were satisfactory. However in a few sectional studies performed with ruminants there is the suggestion that chromic oxide might move out of the rumen at a more rapid rate than lignin or dry matter. Diurnal variations in excretion pattern have been noticed with both these indicators. Chromic oxide tended to have a highly significantly different diurnal pattern, while lignin showed only slight differences.

Flux patterns of dry matter throughout sections of the G.I. tract have been reported by a few workers. Most workers reported that dry matter was mainly digested in rumen and about 25 to 80% was absorbed from this organ. Further digestion and absorption occurred in the cecum and large intestine. An endogenous secretion of dry matter has been reported for the proximal portion of the small intestine.

Absorption and Secretion of Some Elements Through the G.I. Tract

Sodium and Potassium

Parthasarathy (1952) noted absorption of certain elements from the sheep alimentary tract. He showed that rumen sodium was absorbed against a concentration gradient while potassium was absorbed on account of its high concentration in the rumen. In the other regions of the alimentary tract sodium and potassium absorption from the small intestine and cecum were demonstrated.

Field et al. (1954) demonstrated that sodium was absorbed from the intestinal tract against a concentration gradient in humans. Visher et al. (1945) reported that the lower part of the small intestine absorbed sodium against a concentration gradient.

Absorption of sodium from the rumen was found by Dobson (1959) in sheep. He indicated that there existed a mechanism for active transport of sodium in rumen epithelium. He suggested that this inducing mechanism could drive the sodium into the plasma against a higher concentration and electrical gradient of this ion.

Van Weerden (1961) in an experiment with cows observed the absorption and secretion of sodium. He reported that sodium in the abomasum was much less than in blood, but he found an increase in the duodenum. Distally in the small intestine they observed that the concentration of sodium reached that of the blood in the distal end of the small intestine they noted that sodium concentration again declined and that it was much lower than that in the blood. This study suggested that in the lower part of the S.I., sodium was absorbed against a concentration gradient. Also they indicated that sodium can be absorbed from the large intestine against a concentration gradient.

Van Weerden (1961) demonstrated that the concentration of potassium along the intestinal tract was greater than that in the blood serum, so that absorption was not hindered by a concentration gradient.

Yang and Thomas (1965) demonstrated that sodium was absorbed from the rumen and omasum and secreted into abomasum and upper section of the small intestine. They observed that reabsorption took place in lower sections of the small intestine.

In calves Perry et al. (1967) studied the absorption pattern of sodium and potassium using different types of rations. They reported that there was no significant difference in the concentration of sodium in the rumen of the calves fed different rations (semi-purified, concentrate, and concentrate plus hay). Nevertheless they observed a high load of sodium in the rumen of calves fed concentrate and hay ration. The concentrate ration moved out of the rumen at a rapid rate and hence the sodium load for this ration was lowest. Also they reported a large secretion of sodium into the upper S.I. and absorption of sodium throughout the remainder of the gut. Thus only 13% was absorbed from the cecum and large intestine. In the same way, Perry et al. (1967) indicated that 40% of the ingested potassium was absorbed from the rumen of calves that received the semi-purified ration and they suggested that this absorption was due to a high concentration gradient resulting from the high potassium concentration in the feed. The percent of potassium intake absorbed in the rumen was 98, 75, and 80 for the semi-purified, concentrate, and the concentrate plus hay diet respectively.

Calcium

Wallace et al. (1951) studied the extent of excretion of calcium from the G.I. tract in rats. He reported that most of the excretion of calcium occurred in the small intestine.

Smith (1961) observed that absorption of calcium decreased with age in calves. Storry (1961) using sheep studied the distribution of calcium in contents of the reticulo-rumen, omasum, abomasum, S.I., cecum and colon. He observed that a considerable portion of calcium existed in a non-ultrafilterable form in all organs except the abomasum. He concluded from this study that the concentration of non-ultrafilterable calcium was the main determinant for absorption. Storry (1961) reported that in the sheep rumen ultrafilterable calcium amounted to 20 to 60% of the total while in the abomasum it was close to 100%. Thus he concluded that calcium could be absorbed from abomasum at a greater rate than from any other sections of the G.I. tract.

In calves, Chandler and Cragle (1962) studied the calcium and phosphorous absorption-secretion pattern.

They observed endogenous secretion of calcium into the omasum with a large net absorption from the abomasum. They further showed that calcium was absorbed in the first part of the S.I., then secreted in the middle S.I. and stayed fairly constant thereafter.

Philipson and Storry (1965), using isolated sections of the small intestine, reported that losses of calcium occurred from the upper jejunum and middle of the S.I. Cragle (1962) concluded that the major region for calcium absorption was the small intestine in calves.

Perry et al. (1967) reported similar results to those of Chandler and Cragle (1962) for endogenous secretion and absorption of calcium in calves. No net secretion was found in the omasum. Absorption of calcium was found in the abomasum. Also they reported some secretion in a few calves and suggested this could be due to the nature of the ration used. The major site of absorption however was the small intestine. They reported little change in the flux pattern of calcium in the cecum and large intestine.

Magnesium

Field (1961) studied the distribution of Mg in the G.I. tract and tissues of sheep. He demonstrated that the main site of absorption for Mg was in the middle third of the small intestine. Mg was secreted in this study in the first section of the small intestine and was approximately all reabsorbed from the lower segments of the S.I. tract.

In sheep, Storry _et_ _al_. (1961) reported that the principal site of absorption was the abomasum and the duodenum. Storry (1961 b) observed that ultrafilterable Mg in the rumen was about 20 to 60% of the total while that of the abomasum was around 100%. The proportion varied with pH.

Ross (1962), by using an everted sac technique with rat's small intestine, reported that there was either a saturation process or a facilitated diffusion involved in the transport of Mg. Smith (1962) in a study with milk fed calves reported that in the G.I. tract the apparent absorption of Mg ranged from 30 to 40%.

Perry _et_ _al_. (1967) observed an apparent net secretion of Mg in the upper small intestine in all calves. However they reported that net absorption occurred in the lower sections of the S.I. with little change thereafter. The average apparent absorption of Mg with all the rations in this study was 35%.

Cragle (1967) demonstrated that there was no change in the ruminal concentration of Mg, while he indicated an apparent secretion of Mg in the upper S.I. in all calves used.

Zinc

Miller and Cragle (1965) used cows and older calves which were fed both hay and concentrate with ZN^{65} administered orally and showed that approximately 35% of the daily administered ZN was absorbed from the abomasum. They observed that the secretion of Zn occurred in the first segment of S.I. but that absorption took place through the rest of the S.I. They indicated that little absorption or secretion occurred below the cecum.

In another study Miller (1967) determined the absorption, excretion, and retention of orally administered ZN^{65} in various tissues of Zn deficient goats and calves. They noticed that the apparent absorption of Zn^{65} was 77.5% in the control calves and 83.2% for the Zn deficient ones by the end of 6 days. Absorption was 64.4% for control goats and 78% for deficient goats.

Heirs jr. et al. (1968) studied the endogenous secretion and absorption of Zn in various sections of the G.I. tract of the Zn deficient and normal goats using chromic oxide as an inert indicator. In this study they observed that Zn was secreted into the rumen followed by a variable amount of reabsorption in the abomasum. Also they have reported that a large proportion of Zn was secreted into the upper small intestine and absorbed in the lower portions of the S.I.

Heirs jr. et al. (1968) measured the endogenous secretion of Zn in Holstein calves and in goats and observed that absorption took place in the omasum with a large secretion in the upper S.I. Reabsorption occurred in the lower sections of the small intestine.

Summary

In ruminants it has been reported that sodium could be absorbed against a concentration gradient from the rumen (Parthasarathy 1952; Dobson 1959; and Yang and Thomas 1965). Absorption of sodium has been reported in the lower S.I. by Vischer et al. (1945), Van Weerden (1961), Yang and Thomas (1965), and Perry et al. (1967). Few studies indicated an endogenous secretion of sodium in the upper S.I. (Van Weerden 1961; Yang and Thomas 1965; and Perry et al. 1967). Absorption of sodium was also reported to occur from large intestine and cecum by these workers.

Parthasarathy (1952) reported that potassium was absorbed from the rumen due to its high concentration. Also he indicated that absorption of this mineral was possible from the small intestine and cecum. Perry et al. (1967) reported a 40% absorption of potassium from the rumen of calves fed a semi-purified ration. Van Weerden (1961) showed that potassium absorption took place from the small intestinal area.

Smith (1961) reported that calcium absorption decreased with age. Storry (1961) reported that calcium absorption could be maximum in the abomasum since calcium existed completely in an ultrafilterable form in this organ. Chandler and Cragle (1962) reported a secretion of calcium in the omasum but an absorption in the abomasum and upper S.I. in calves.

Field (1961) indicated that the principal site of magnesium absorption was in the middle S.I., while Storry (1961) suggested that this was in the abomasum and in the upper S.I. Perry et al. (1967) and Cragle (1967) reported an apparent net secretion of magnesium in the upper small intestine.

Few studies with Zinc in the gastrointestinal tract of ruminants indicated that some absorption of zinc occurred in the abomasum. Most of these studies also reported a high endogenous secretion of zinc in the upper S.I., and indicated reabsorption in the lower sections of the small intestine (Miller and Cragle 1965; Miller et al. 1967; and Heirs jr. et al. 1968).

EXPERIMENTAL PROCEDURES

In previous work at this station sixteen sheep were used in a digestion trial (Bauman, M. S. Thesis, 1968). Rations used were siberian reed grass, reed canary grass, alfalfa early cut (June 25th 1965) and alfalfa late cut (July 16th 1965). The sheep were fed the hay for a period of 20 days and then sacrificed. Eight were slaughtered at 6 hours and the remaining eight were slaughtered at 12 hours post prandial. These sheep were fed chromic oxide twice a day in a capsule. Both chromic oxide and lignin were then used as an indicator in measuring the absorption and or secretion of various nutrients (Miller and Cragle, 1965; Yang, 1964; Yang and Thomas, 1965; Perry et al. 1967; Cragle, 1967 etc.).

The digestive tracts of sheep were removed soon after sacrificing the animals, and separated into nine different sections (rumen, omasum, abomasum, small intestine (1), small intestine (2), small intestine (3), cecum, large intestine (1) and large intestine (2). The contents of digesta from each of the above sections were removed, collected and weighed separately and dried. A portion of each sample from every section were used for analysis of different nutrients and for chromium. The diet samples were also taken and a portion analysed. The samples were then stored at room temperature for future studies.

This experiment was designed to use the above mentioned samples for forages as well as the samples from the different sections to study several parameters. The parameters measured in this experiment were

1. The indigestibility of different nutrients in different sections of the gastrointestinal (G.I.) tract of sheep by using the lignin ratio technique.

2. To measure the flux pattern of different nutrients in the different sections of the G.I. tract by using lignin as the indicator.

3. To examine whether chromic oxide and lignin behave in a similar fashion in the different sections of the gastrointestinal tract or to evaluate the suitability of both compounds as indicators for studying the flux pattern of nutrients in sectional studies of the G.I. tract in ruminants.

Methods and Materials

All the forage samples, and samples of digesta from the nine different sections already mentioned were analysed in duplicate for acid detergent fiber (ADF), and acid detergent lignin (lignin) by the method of Van Soest (1963). Analytical values for minerals and dry matter were taken directly from the thesis of Bauman (1968).

Indigestibility of the following nutrients was determined by the lignin ratio technique (Ellis et al. 1946). The nutrients studied were Dry Matter (D.M.), Acid detergent fiber (ADF), Magnesium (Mg), Potassium (K), Sodium (Na), Calcium (Ca), and Zinc (Zn). The flux pattern for the same nutrients was calculated for the different sections of the G.I. tract. The digestibility of the nutrients and flux pattern for D.M., ADF, Mg, and K were calculated for the forages fed. On the other hand the total Na, Ca, and Zn ingested by the animals represented not only the feed but other sources (mineral supplement and licking of galvanized pans). For this reason the feed equalled 100% for nutrients in the first category but rumen equalled 100% for nutrients in the second category.

Calculation of Indigestibility

Indigestibility of any ration can be defined as the portion which is not digested but is excreted through the feces. In sequential sectional studies however this would be the portion that entered into the next consecutive section of the G.I. tract. This indigestibility can be calculated by the lignin ratio technique by the following equation.

Equation 1

$$\text{Indigestibility} = \begin{matrix}\text{Ratio}\\ \text{Value}\end{matrix} = \frac{\dfrac{(\%\text{ of nutrient in section})}{(\%\text{ of lignin in section})}}{\dfrac{(\%\text{ of nitrient in "Diet"})}{(\%\text{ of lignin in "Diet"})}}$$

"Diet" used in the formula represented either "Feed" or the "Rumen", depending upon the nutrient measured. For D.M,, ADF, Mg, and K the "Diet" represented the "Feed" value, while for Zn, Na, and Ca the "Diet" represented the "Rumen" value.

The percentage of indigestibility can be obtained by multiplying the ratio value by 100.

The digestibility value can be calculated from the indigestibility value given in figures and tables. For instance, digestibility of diet at the rumen would be 100 - (0.48 x 100) = 52%; at the S.I. (1) = 100 - (2.29 x 100) = -12.9% and at large intestine (2) = 100 - (0.39 x 100) = 61%.

Flux Pattern of Nutrients Through the Different Sections of the G.I. Tract

The absorption/secretion pattern of any nutrient could be studied by measuring the nutrients in the various sections of the G.I. tract and expressing one in relation to the diet or to any previous organ by using Equation 1 (Yang 1964).

Absorption or secretion can be expressed as the "Net Flux", which would either indicate a net absorption or a net secretion from the diet to the organ. The net flux does not indicate the flux of a single section, but would show the net result of all fluxes in the previous sections. The measurement would help in finding how much of a nutrient is present in any particular section compared to the diet or shows the quantity of nutrient absorbed to the organ in question.

Calculation of the "Apparent Flux"

This term was used to compare the amount of nutrient in a designated section to that in the immediately preceding section. Whenever the value for "Apparent Flux" has a negative sign (-), it means an "apparent secretion" into that organ and whenever values have a positive sign (+) it indicates an "apparent absorption". In the presentation the + sign will be omitted. The calculation for net and apparent flux values are as presented below.

Equation 2

$$\text{Apparent Flux} = (\text{R.V of A} - \text{R.V of B})$$

where R.V = ratio value obtained as per the first equation

A = the previous section in reference to section designated as B

B = the section in which the flux is measured.

These values were not presented for each nutrient but can be calculated from indigestibility values given in Tables 1 through 7. For instance in Table 1 the apparent flux from small intestine (1) to small intestine (2) would be 2.29 - 1.05 = 1.24 or from abomasum to small intestine (1) would be 0.45 - 2.29 = -1.81.

Calculation of the Net Flux

Equation 3

$$\text{Net Flux} = \underset{\text{Ratio Value}}{\text{"Diet"}} - \underset{\text{Ratio Value.}}{\text{Section}}$$

Where "Diet" Ratio Value is taken as 1 (Diet would mean either "Feed" or "Rumen" as defined previously).

The value obtained for the net flux would show a net secretion whenever the value has a negative sign, and would show a net absorption whenever the value is expressed without any sign (omitted for this presentation).

The Apparent Flux and the Net Flux can be expressed in percentage by multiplying those values by 100.

Evaluation of Chromic Oxide and Lignin as Indicators Used in the Flux Pattern of Nutrients in Different Sections of the Gastrointestinal Tract of Sheep

The flux patterns (apparent and net) of nutrients in different sections of the G.I. tract was compared using both indicator. All nutrients and indicators were expressed on a dry matter basis. If both the indicators behaved in a similar manner, then the fluxes by the two indicators would show similar values. If there happened to be a difference in these fluxes, then it would indicate that the indicators are not moving together.

If the flux patterns show that there is a difference in fluxes, then the ratio between the two indicators would be different. A similar chromium/lignin ratio in the diet and in the different sections would indicate that both indicators travelled at a similar rate. Also in such cases the ratio values among the sections should be the same. The data were analysed statistically by the analysis of variance to find whether there was any significant difference in the chromium-lignin ratio. The chromium lignin ratio was calculated for any section or for diet by using the following equation.

Equation 4

Chromium/lignin ratio = chromium in ppm/lignin percent.

A difference in chromium lignin ratios would indicate whether there existed a difference in the rate of passage of the two indicators used. However different chromium lignin ratios would not indicate which of the indicators moved differentially than the dry matter or water. In this study the rate of passage of these materials can be estimated by calculating the proportion of dry matter, lignin and chromium present in each section of the tract or the distribution throughout the tract. Since the feeds and markers were given at the same time, this distribution should be related to the rate of passage of these materials. Hence a comparison of the distribution of lignin, dry matter and chromic oxide would give some information on the comparative movement of these three ingredients.

The comparison of fluxes in different sections, the chromium lignin ratio, and the distribution of dry matter, lignin and chromium were used to indicate whether both the indicators are suitable for different sectional studies of the G.I. tract.

RESULTS AND DISCUSSIONS

Dry Matter

The indigestibility of dry matter (D.M.) is given in Table 1. The base value for the D.M. has been taken as 1.00. The total D.M. indigestibility for the whole gastro-intestinal (G.I.) tract (feces) can be assumed to be the same as the lower portion of the large intestine. This averaged 39%. There was considerable variation in indigestibility of this nutrient for the different sections. Analysis of variance indicated a highly significant difference for the different organs at ($P < 0.0005$).

The indigestibility of D.M. at 6 hour and 12 hour after feeding is also given in Figure 1. On the whole the results show little difference but in certain sections rather large differences were noted. However, this difference was not statistically significant.

Some variations in indigestibility were noted among forages for the whole tract. The grasses showed 66.5% digestibility while alfalfa showed only 41% (Table 1). This difference for D.M. was not significant. Indigestibility was larger for the late cut than for the early cut alfalfa (45 vs 37%).

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

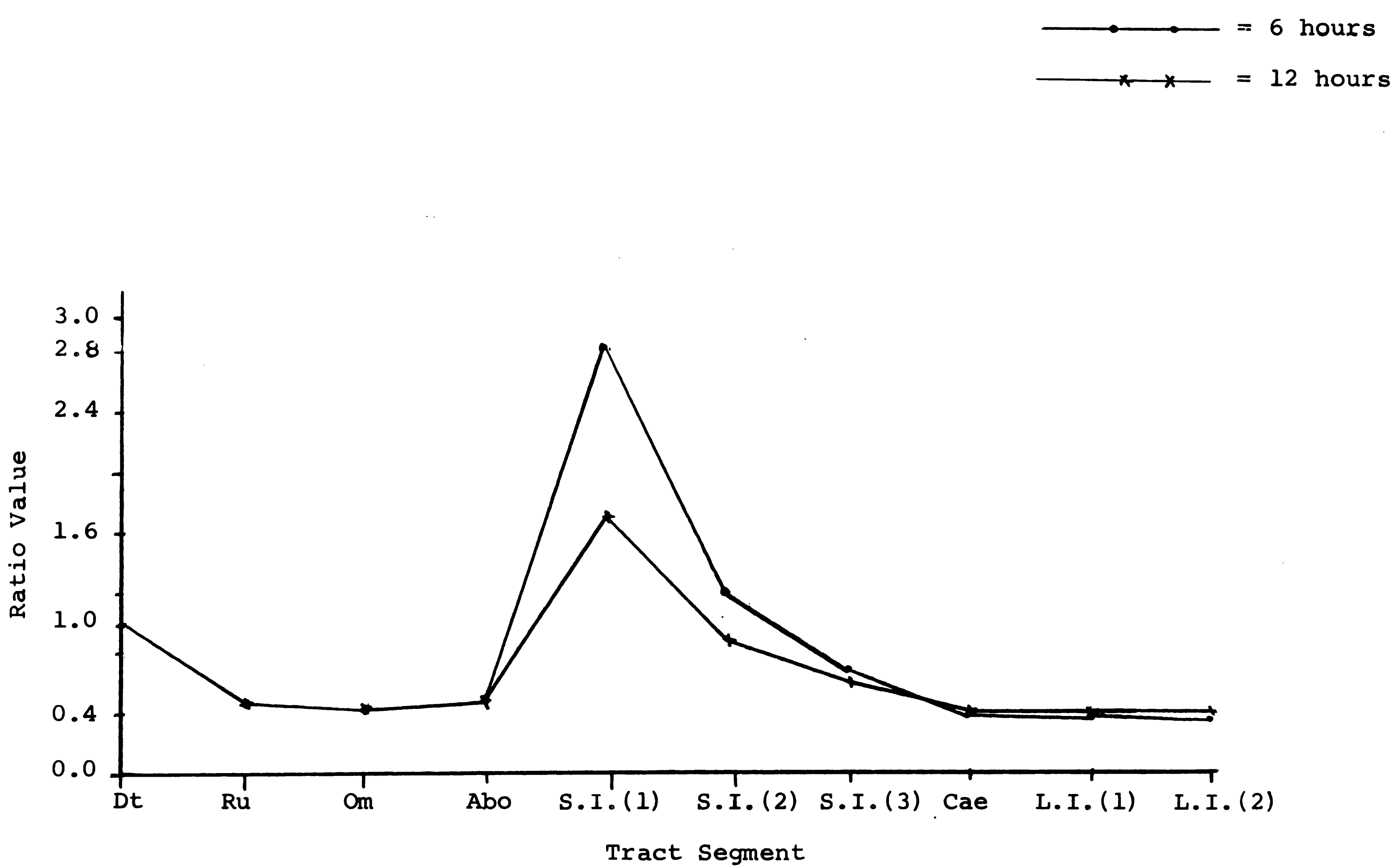

= 6 hours
= 12 hours
Ratio Value
3.0
2.8
2.4
1.6
1.0
0.4
0.0
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 1

Table 1.--Indigestibility of dry matter for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary grass	Siberian Reed Canary grass	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	0.44	0.51	0.51	0.47	0.48	0.48	0.48
Omasum	0.37	0.42	0.49	0.47	0.44	0.44	0.44
Abomasum	0.43	0.48	0.52	0.50	0.48	0.48	0.48
Small intestine(1)	1.60	2.56	1.55	10.87	2.29	2.85	1.73
Small intestine(2)	0.71	0.97	1.32	1.22	1.05	1.19	0.92
Small intestine(3)	0.52	0.68	0.89	0.67	0.69	0.72	0.66
Caecum	0.35	0.41	0.49	0.43	0.42	0.42	0.42
Large intestine(1)	0.33	0.42	0.48	0.43	0.41	0.43	0.40
Large intestine(2)	0.31	0.36	0.45	0.37	0.39	0.39	0.38
Digestibility percent	69	64	55	63	61	61	62
Grasses vs legume	66.5		59.0				

The indigestibility of D.M. in the rumen averaged 48%. This amounted to 85.2% of the total D.M. digestibility. There was not any difference observed in the indigestibility between the rumen values for the 6 hour period and 12 hour period (48% vs 48%). The rumen digestibility of grasses was 52.5% and 50.5% for the legume. Lignin content or structure may be a factor which makes the legumes more indigestible in this organ. Van Soest (1965) noted that alfalfa contained more lignin than the grasses. Increased maturity can also cause more indigestibility.

In the omasum the average indigestibility of D.M. was found to be 44%. This decrease in the indigestibility might be due to the absorption of volatile fatty acids (VFA) and other nutrients in the omasum. There was no difference noted for the different hours. Digestibility to this organ of grass hay was 60.5% and 52% for the legume hay.

Indigestibility in the abomasum was 48% on an overall basis. There was no difference noticed between the 6 hour and 12 hour period in this organ. The higher indigestibility in this organ than the omasum could be a result of "net secretion" into the abomasum. Digestibility for the grasses was 54.5% and 49.1% for the alfalfa rations.

In the upper small intestine the indigestibility averaged 229%. There was much individual variation in this section. The difference between the 6 and 12 hour period was not statistically significant (285% vs 173%; $P < 0.10$). The grass hay was 228% indigestible while the legume was 621% in this organ. This high D.M. indigestibility in this organ was surely from other sources than the diet and could be assumed to be due to high amount of endogenous secretion into this organ. The indigestibility decreased considerably in the middle section of the small intestine indicating much absorption in this area of the small intestine. Both forages showed a similar trend. The average indigestibility in the middle S.I. was found to be 105%. The 6 hour period averaged 119% indigestibility, while the 12 hour period was only 92%. Little dry matter disappeared from the 6th to 12th hour. Legumes had greater indigestibility values in this section than the grasses (127 vs 84%). Digestion continued in the lower S.I. Indigestibility of D.M. in this organ averaged only 69% being 60% for the grasses and 78% for the legumes. Indigestibility was less at 12 hour than at 6 hour (66% vs 72%).

In the cecum, indigestibility was found to be 42%. This could have been due to further digestion of D.M. by microorganisms. In this section there was no difference between the 6 hour and the 12 hour values. Indigestibility of grass hay was 38% and the legume hay 46%. The difference between the forages was not statistically significant.

There was little digestion in the large intestine. The overall indigestibility in the upper portion of the L.I. was 41%. The indigestibility for the 6 hour period was 43%, and the corresponding value for 12 hour was 40%. Only 33.5% indigestibility was noted for the grasses while the legumes was 42%. Total indigestibility at the lower portion of the large intestine showed 39% for the dry matter.

In every section of the G.I. tract which was studied the 6 hour value indicated similar or more indigestibility than the 12 hour value. Alfalfa was more indigestible than grasses at all sections. The greater indigestibility value for the 6 hours can be explained by more digestion of fibrous material at 12 hours. However all the digestion for these nutrients could not be credited for the second 6 hour since these materials are digested to a certain extent within this first 6 hour period. Extent and rate of passage also influenced these values.

Dry Matter Flux

In the rumen the apparent flux showed 52% apparent absorption of the dietary dry matter (D.D.M.) which amounted to 85.2% of the total D.M. absorbed.

In the omasum further absorption was observed. This apparent absorption on the basis of the dietary dry matter was 4% and on the basis of the previous section (rumen), the absorption was 8.3%. The VFAs are probably absorbed in the omasum. Apparent secretion occurred in the abomasum. This amounted to 9.1% of the D.M. in the omasum.

A large secretion was noticed in the upper portion of S.I. This amounted to 181% (apparent secretion) of the D.D.M. and 377% of abomasal D.M. This large secretion in the upper portion of S.I. must be due to a high secretion of D.M. from the endogenous sources. This endogenous source could be due to the high chloride ions, enzymes, and also from sloughing epithelial layers of cells etc. Considerable absorption or reabsorption occurred in the middle portion of the S.I. This absorption in the middle section of the small intestine amounted to 124% (2.29-1.05 x 100) on the basis of the D.D.M. Also this absorption amounted to 203% (124/61 x 100) of the total D.M. absorbed for the entire tract. In this section most of the enzymes, pancreatic juise, bile etc. would have had time to act on indigest D.M. and these absorption of the nutrients in this organ would appear likely. Further absorption continued in the lower S.I. This amounted to 34% of the D.M. present in the middle S.I.

In the cecum and large intestine further absorption took place. Absorption in the cecum amounted to 27% of the D.D.M., 39.2% of the D.M. in the lower S.I. and 40.3% (27/61 x 100) of the total absorption of the entire tract. Absorption in the upper portion of the L.I. was 4.9%.

Acid Detergent Fiber (ADF)

The indigestibility of acid detergent fiber is given in Table 2. The overall indigestibility of the ADF (ligno-cellulose) in the rumen was 58%. There was little difference in the indigestibility of this nutrient in the rumen for the two time periods involved (6 hour = 59% vs 12 hour = 57%). No statistical analysis was calculated for this nutrient. The grass hay ADF was 49.5% digestible while the alfalfa was 35%.

In the omasum indigestibility was further decreased for this nutrient. The overall, the 6 hour, and the 12 hour indigestibility were all 48%, indicating some further removal of ADF in this organ. Digestibility of grass hay at the omasum was 61% and the legume was 44%.

As in the case of dry matter, ADF in the omasum also showed a higher indigestibility than in the previous section. The average indigestibility found in this organ was 53%. The 6 hour period averaged 54% and the 12 hour period 51% indigestibility. The legume showed 40% digestibility while the grasses 45.5%. The reason for digestion of ADF from grasses and not legumes in this organ may be related to differences in carbohydrate composition of these forages.

In the entire small intestine the indigestibility averaged 52%. There was no difference found between the 6 hour and 12 hour periods. By the end of the lower S.I.

Table 2. Indigestibility of ligno-cellulose (ADF) for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	0.49	0.52	0.67	0.63	0.58	0.59	0.57
Omasum	0.39	0.39	0.60	0.54	0.48	0.48	0.48
Abomasum	0.43	0.48	0.63	0.57	0.53	0.54	0.51
Small intestine(1)	0.38	0.39	0.62	0.55	0.49	0.46	0.52
Small intestine(2)	0.40	0.44	0.61	0.58	0.50	0.51	0.49
Small intestine(3)	0.42	0.46	0.64	0.57	0.52	0.52	0.52
Caecum	0.39	0.42	0.55	0.51	0.47	0.48	0.46
Large intestine(1)	0.36	0.42	0.57	0.52	0.47	0.48	0.46
Large intestine(2)	0.38	0.40	0.59	0.54	0.48	0.48	0.48
Digestibility percent	62	60	41	46	52	52	52
Grasses vs legumes percent	61		43.5				

the digestibility of ADF in grasses was 56%, and of the alfalfa ADF 39.5%.

Further digestion of ADF occurred in the cecum. The overall indigestibility in this section was reduced to 47%. Values for the large intestine however did not indicate any further digestion of ligno-cellulose. In this organ the upper portion showed 47% indigestibility, while the lower portion showed 48% indigestibility.

The digestibility of ADF in the rumen of these sheep averaged 42%. In the cecum further digestion by bacteria probably occurred as indicated by an additional 11% digestion of ADF. The overall indigestibility of ADF for the entire tract was 48%. At this point the two time periods did not show any differences in the indigestibility of this nutrient (6 hour = 48%, 12 hour = 48%). The differences in ADF digestibility of grasses for the whole tract was 61% and the corresponding value for alfalfa was 43.5%.

Flux Pattern of ADF

In the rumen the lignin indicator method showed that there was 42% disappearance of this nutrient. From rumen to the omasum a further disappearance occurred which amounted to 10% of the dietary ADF, and 17.3% of this nutrient present in the previous section. In the abomasum a 5% secretion occurred which reduced the net absorption to 47% in this organ.

Some apparent absorption was found in the upper portion of the small intestine. Absorption in this section was due to the value found for the 6 hour period. The net absorption was found to be 50% for ADF in the small intestine.

In the cecum disappearance occurred. The net disappearance in this section changed to 53% from 50% in S.I. In the large intestine there was no further change in the flux pattern. The net disappearance of ADF for the entire G.I. tract amounted to 52%.

Magnesium

Data in Table 3 indicate that on an average the total indigestibility of magnesium (Mg) for the entire tract was 62%, being 63% for the 6 hour period and 61% for the 12 hour period. Statistical analysis indicated some difference between the time periods ($P < 0.10$).

For the entire tract grass hay showed 40.5% indigestibility, while alfalfa showed 75.5%. The analysis of variance indicated a highly significant difference between the grasses and legumes ($P < 0.0005$).

Indigestibility of magnesium in the rumen was 15% with little difference between the 6 hour and 12 hour period. Grass hay had 16% indigestibility while alfalfa hay had 14.5%.

In the abomasum the 6 hour period had 16% indigestibility but the 12 hour period had 12%. Grass hay indicated a higher indigestibility (15.5%) than legume (13%). However in the hind gut the indigestibility of grass was much lower

Table 3. Indigestibility of magnesium for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	0.16	0.16	0.16	0.13	0.15	0.16	0.15
Omasum	0.14	0.14	0.17	0.13	0.15	0.15	0.15
Abomasum	0.18	0.13	0.12	0.14	0.14	0.16	0.12
Small intestine(1)	0.50	0.51	0.45	1.05	0.57	0.68	0.45
Small intestine(2)	0.31	0.31	0.58	0.58	0.44	0.50	0.39
Small intestine(3)	0.28	0.35	0.82	0.61	0.52	0.42	0.62
Caecum	0.40	0.53	0.71	0.90	0.64	0.62	0.66
Large intestine(1)	0.54	0.51	0.75	0.90	0.63	0.62	0.63
Large intestine(2)	0.37	0.44	0.67	0.84	0.62	0.63	0.61
Digestibility percent	63	56	33	16	38	37	39
Grasses vs legumes percent	59.5		24.5				

than the indigestibility of the legumes (grasses = 40.5%, legumes = 75%). Statistical analysis indicated that the forage (grass and legume) differed significantly ($P < 0.01$) in the indigestibility of Mg in the S.I., cecum, and large intestine.

Flux Pattern of Magnesium

In the rumen Mg appeared to be highly absorbed. The apparent absorption of Mg in this section amounted to 85% of the mineral present in the diet. Storry (1961) indicated that 20-60% of total Mg can be found in the rumen in the ultrafilterable form and hence can be absorbed from this section. In the omasum no change occurred in the flux pattern.

In the abomasum the net flux showed 86% net absorption but only 1% compared to that present in the omasum. Storry (1966) demonstrated that in the abomasum Mg existed almost 100% in an ultrafilterable form and hence would be available for maxium absorption. In this study net absorption in this section was also high.

The apparent flux in the upper S.I. showed a large apparent secretion while the net flux showed 43% net absorption. There was a 13% apparent absorption in the middle S.I. while the net flux for the lower S.I. showed a 48% net absorption.

An apparent secretion of Mg has been reported in the upper S.I. in sheep (Field 1961) and in calves (Perry et al.

1967; Cragle 1967). The middle portion of the S.I. was found to be the major site of Mg absorption. A similar result has been reported by Field (1961). Mg absorption may involve both active and passive transport. Ross (1962) using everted S.I. sac technique with rats reported that there is either a saturated active process or a facilitated diffusion involved in the transport. Apparent flux in the cecum showed a 20% apparent secretion, while the large intestine showed little apparent absorption. The apparent absorption in both the sections of the L.I. amounted to 1% each. On the whole the net absorption of Mg in the G.I. tract was 38%. Smith (1962) demonstrated a similar result. He showed an apparent absorption of Mg for the entire G.I. tract of milk fed calves ranging from 30 to 40%. Perry et al. (1967) reported 35% apparent absorption of Mg in calves.

Potassium

Table 4 shows the indigestibility of potassium (k) for the different sections of the G.I. tract. Analysis of variance indicated a highly significant difference for the different organs ($P < 0.0005$).

On the whole, the result showed little difference between the 6 and 12 hour period (6 hour = 9%, 12 hour = 8%).

Some variations in digestibility were noted among forages for the whole tract. The lignin indicator technique

Table 4. Indigestibility of potassium for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	0.27	0.34	0.36	0.32	0.32	0.34	0.31
Omasum	0.20	0.23	0.38	0.33	0.29	0.29	0.29
Abomasum	0.31	0.24	0.38	0.36	0.32	0.34	0.31
Small intestine(1)	0.92	1.70	1.77	7.25	2.41	3.43	1.39
Small intestine(2)	0.31	0.54	1.39	1.04	0.82	0.96	0.68
Small intestine(3)	0.25	0.35	0.64	0.45	0.42	0.42	0.43
Caecum	0.12	0.14	0.19	0.18	0.16	0.15	0.17
Large intestine(1)	0.10	0.14	0.19	0.17	0.15	0.15	0.16
Large intestine(2)	0.06	0.06	0.14	0.07	0.09	0.09	0.09
Digestibility percent	94	94	86	93	91	91	91
Grass vs legumes percent	94		89.5				

showed a significant difference in the indigestibility of potassium in the upper S.I. ($P < 0.05$) due to forage difference (grasses vs legumes).

The indigestibility of potassium in the rumen averaged 32%. Rumen digestibility amounted to 35% of the total potassium digestibility. There was slight difference in the indigestibility between the values for the 6 hour period and 12 hour period (34% vs 31%). The digestibility of K in grass was 70% and 66% in the legume. In the omasum the indigestibility was reduced little (29%) and there was no difference between the time periods (29% vs 29%). In the abomasum the indigestibility increased slightly and reached the value previously shown in the rumen (32%).

In the upper portion of the small intestine secretion of K was found (241%) and this value was greater in this section than all other sections of the G.I. tract. Also at this point the two time periods demonstrated a higher variation in indigestibility than other sections of the G.I. tract. This amounted to 343%, and 139% respectively for the 6 and 12 hour periods. On the whole the indigestibility of potassium for the entire small intestine was only 42%.

In the cecum the average indigestibility was found to be only 16% indicating that 84% of the dietary potassium disappeared prior to entering the large secretion. In the lower L.I. the value for the indigestibility was further reduced. At this point the average indigestibility was 9%.

The Flux Pattern of Potassium

In the rumen the flux pattern of potassium showed 68% absorption. Parthasarathy (1952) and Parthasarathy and Philipson (1953) have reported absorption of K from the rumen. They suggested that potassium is absorbed from rumen on account of its high ruminal concentration compared to its concentration in blood. Sperber and Hyden (1952) suggested that potassium could passively diffuse across the rumen epithelium.

In the omasum and the abomasum the flux changed little. The net absorption for abomasum amounted to 68%.

The apparent flux for the upper S.I. showed 209% apparent secretion and the net flux 141% net secretion. In the middle portion of the S.I. the apparent reabsorption amounted to 159%. The net flux at the end of the large intestine showed that 91% of dietary potassium was absorbed. Perry *et al*. (1967) also reported similar results for potassium absorption in calves. After a large endogenous secretion in the upper S.I. absorption continued throughout the remainder of the tract.

Sodium

The indigestibility of sodium (Na) is given in Table 5. The sectional studies indicated that there was considerable variation in the indigestibility of Na in different organs of the G.I. tract. Analysis of variance indicated a highly

Table 5. Indigestibility of sodium for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.47	0.49	0.54	0.57	0.52	0.53	0.50
Abomasum	0.99	0.72	0.95	0.95	0.91	1.05	0.76
Small intestine(1)	4.67	6.30	4.54	16.26	6.85	9.62	4.08
Small intestine(2)	2.94	3.68	4.21	3.71	3.64	4.49	2.79
Small intestine(3)	2.85	2.96	3.77	2.45	3.02	3.33	2.71
Caecum	1.24	1.34	1.26	1.01	1.22	1.33	1.11
Large intestine(1)	0.96	1.10	1.07	0.90	1.01	1.11	0.90
Large intestine(2)	0.27	0.21	0.38	0.23	0.28	0.34	0.23
Digestibility percent	73	79	62	77	72	66	77
Grass vs legumes percent	76		69.5				

significant difference for the different sections ($P < 0.0005$).

The total indigestibility of Na for the entire G.I. tract (up to L.I. (2)) averaged 28%. The indigestibility of Na at 6 hours exceeded the 12 hour value (34 vs 23%, $P < 0.10$).

The overall digestibility of Na from the two forages did not show any significant differences. The digestibility of Na from grass hay showed on an average of 76% while the same for legume was 69.5%.

In the omasum the average indigestibility of sodium was 52%. In the abomasum the indigestibility was 91% for sodium. The 6 hour period indicated 105% and 12 hour period indicated 76%. The digestibility of Na in the abomasum was 14.5% for grass hay and 5% for legume.

The average indigestibility of sodium in the upper small intestine was 685% due to high endogenous secretion. The two time periods also showed much variation in the indigestibility. The 6 hour value was 962% indigestibility while the 12 hour value was 408%. The average indigestibility of Na decreased considerably throughout the remainder of the intestine. The average indigestibility in the cecum was 122% and this was reduced further to 28% by the time it reached the lower L.I. Values for each forage as well as the two time periods followed a similar decrease in the indigestibility of sodium.

Flux Pattern of Sodium

The flux pattern of sodium has been measured in the different sections of the G.I. tract after the rumen. In this calculation the rumen value represented the base value.

The apparent flux of sodium in the omasum showed a 48% apparent absorption, while value in the abomasum showed a 39% apparent secretion. The net flux at the end of the abomasum was a 9% net absorption of sodium.

In the small intestine, the magnitude of apparent flux was much greater than any other section. An apparent sodium secretion of 594% was calculated for this section. In the middle S.I. an apparent absorption of 321%, and in the lower S.I. 62% apparent absorption were calculated. Yang and Thomas (1965) by using lignin ratio technique demonstrated an absorption of Na in the rumen and omasum and secretion in abomasum and in upper S.I. In their study also the secretion obtained in the upper S.I. was of a higher magnitude than the values shown in any other section. In the lower S.I. these authors showed a large reabsorption of Na. In the present study the small intestine was divided into 3 sections and hence the flux was measured more accurately. The middle portion showed greater absorption of Na than any other section. Reabsorption continued, in the lower S.I., cecum and large intestine. This is different than the study of Yang and Thomas (1965). However they indicated that their observed secretion into the large intestine and cecum might have been due to other reasons (experimental errors). Perry _et al_. (1967) showed similar results as found in this study in dairy calves. They showed that a large secretion occurred in the upper S.I. and absorption of sodium occurred throughout the remainder of the gut. They also indicated that 13% of sodium was absorbed from the cecum. In this study the net absorption of sodium on the basis of rumen value was found to be 78%. Yang and Thomas (1965) reported that total absorption of sodium ion was 69 to 89% for the entire tract.

Calcium

Data in Table 6 indicate that the average total indigestibility of ruminal calcium (Ca) for the total G.I. tract was 182%. Analysis of variance indicated a highly significant difference for the different organs ($P < 0.0005$).

The two time periods on an average indicated very similar indigestibility for the entire tract (6 hour = 183% and 12 hours = 182%). The average indigestibility of grasses was 152%, and the corresponding value for alfalfa was 198%. Statistical analysis by the analysis of variance indicated this difference was significant at ($P < 0.10$).

The indigestibility of calcium in the omasum averaged 153% being 152% for the 6 hour and 155% for the 12 hour time period. In the abomasum the indigestibility value

Table 6. Indigestibility of calcium for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	1.31	1.34	1.83	1.67	1.53	1.52	1.55
Abomasum	0.89	0.56	0.74	1.04	0.81	0.77	0.85
Small intestine(1)	1.71	1.81	2.11	5.43	2.41	2.90	1.93
Small intestine(2)	1.40	1.65	2.48	2.13	1.92	2.15	1.69
Small intestine(3)	1.78	1.64	2.86	2.14	2.11	2.13	2.09
Caecum	1.77	1.67	2.23	2.17	1.98	1.99	1.97
Large intestine(1)	1.78	1.69	2.17	2.17	1.96	1.98	1.93
Large intestine(2)	1.61	1.44	1.99	1.97	1.82	1.83	1.82
Digestibility percent	-61	-44	-99	-97	-82	-83	-82
Grass vs legume	-52.5		-98				

decreased on the average as well as for different hours (averaged = 81%, 6 hour = 77% and 12 hour = 85%) indicating some absorption occurred in the abomasum.

In the upper S.I. the indigestibility reached the maximum (241%) when compared to other sections. This was probably due to endogenous secretion of calcium. The indigestibility was reduced to some extent in the middle S.I. (192% from 241%). However by the lower value for indigestibility had again increased to 211%. A similar trend of decreasing and increasing the indigestibility value was noted for both time periods. In the cecum and large intestine the indigestibility values decreased slightly. On the average, the cecum showed 198% indigestibility for calcium while the two sections of the large intestine had values of 196% and 182% respectively.

Flux Pattern of Calcium

The rumen value represents the base value for calcium. In the omasum the flux pattern showed that a net secretion occurred and in the abomasum a net absorption was noticed. Chandler and Cragle (1962) observed an endogenous secretion of calcium in the omasum with a large net absorption from the abomasum. In this study the endogenous secretion in the omasum was 53% (net secretion). Abomasal absorption amounted to 52.9% of omasal calcium. Smith (1961) reported that calcium existed in the abomasum in an ultrafilterable form and hence could easily be absorbed. Perry et al. (1967) could not find a net secretion of calcium in the omasum, but did show that calcium was being absorbed from the abomasum.

In the upper S.I. calcium was found to be further secreted. The apparent flux indicated an apparent calcium secretion of 160% and a net secretion of 141%. Reabsorption occurred in the middle S.I. This absorption amounted to 79.6% of the calcium present in the S.I.(1). In the lower S.I. further apparent secretion was noticed (19%). This is similar to the observed apparent secretion of Mg for this organ (Table 3). Apparent flux for the cecum, L.I.(1), and L.I.(2) were 13%, 2% and 6% respectively. The net flux at the end of the small intestine showed 111% secretion. By the end of the large intestine the net flux indicated 82% net secretion of ruminal calcium.

Perry et al. (1967) showed that major site of absorption of calcium was the S.I. They also indicated that very little change occurred in the flux pattern of calcium in the cecum and large intestine.

Zinc

The indigestibility of Zinc (Zn) is given in Table 7. The base value for Zn has been taken as 1.00 for the rumen. The ruminal Zn indigestibility for the whole G.I. tract

Table 7. Indigestibility of zinc for the four different rations and nine different sections of the gastrointestinal tract of sheep--average is given for both 6 and 12 hours as well as overall. Lignin used as indigestible indicator.

Organ	Reed Canary	Siberian Reed Canary	Alfalfa (late)	Alfalfa (early)	Total ave.	6 hr. ave.	12 hr. ave.
Rumen	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Omasum	0.97	0.96	1.30	1.07	1.08	1.10	1.05
Abomasum	1.02	1.13	1.16	1.25	1.14	0.91	1.36
Small intestine(1)	4.47	6.07	5.51	20.21	7.70	11.38	4.02
Small intestine(2)	2.00	2.42	5.42	3.19	3.26	4.34	2.19
Small intestine(3)	1.76	2.03	3.24	1.80	2.21	2.55	1.89
Caecum	1.70	1.82	2.55	1.54	1.92	2.19	1.64
Large intestine(1)	1.55	1.76	2.54	1.48	1.81	2.08	1.55
Large intestine(2)	1.46	1.68	2.13	1.54	1.78	1.99	1.56
Digestibility percent	-46	-68	-113	-54	-78	-99	-56
Grass vs legume	-57		-83.5				

averaged 178%. Analysis of variance indicated a highly significant difference for the different organs ($P < 0.0005$).

The average indigestibility of Zn by the 6 hour and 12 hour time periods showed some differences for the different sections. In certain cases these values varied widely. Statistical analysis for the two time periods were not calculated. On an average the 6 hour period showdd 199% indigestibility for Zn for the entire tract while the 12 hour value was 156%. On the whole, legume was more indigestible than grasses (legume = 183.5%, grasses = 144%).

Indigestibility of Zn in the omasum was 108% and 114% in the abomasum. The indigestibility of Zn for the abomasum as indicated by the 6 hour and the 12 hour time periods was 91% and 136%, respectively. The 6 hour period showed some absorption of Zn, while after the second 6 hour period the value indicated secretion.

Maximum indigestibility of Zn was noticed in the upper S.I. Both time periods indicated increases in this section. The increased indigestibility of Zn was found to be more pronounced for the 6 hour time period (1138%) than the 12 hour period (401%). In the later sections of the small intestine indigestibility of Zn decreased. In the cecum and large intestine Zn indigestibility was further reduced. A similar pattern was noticed for both time periods and for all four forages. However the indigestibility value found indicated that Zn excretion was greater than ruminal Zn, even though most of the endogenous Zn was absorbed. Since fecal Ca and Zn exceeded ruminal amounts these must have been ruminal absorption of dietary Ca and Zn.

Flux Pattern of Zinc

The rumen value represented the base value in this study. The apparent flux of Zn in the omasum showed an 8% apparent secretion. It has been reported that Zn absorption occurred in the omasum and the abomasum (Miller and Cragle, 1965; Heirs jr. *et al.* (1968).

In the upper portion of the small intestine the apparent flux amounted to a 656% secretion. Large secretions of Zn in this section have been reported by several workers (Miller and Cragle, 1965; Miller *et al.* 1967; Heirs jr. *et al.* 1968; etc.). However secretions of this magnitude have not been reported. In most reports the indicators used were either chromic oxide or radioisotopes. Probably the difference showed could be due to the indicator (lignin) used in this study. More research with both types of these indicators would be necessary for substantiation.

Most of the endogenous Zn which was secreted in the upper S.I. was absorbed in the lower portions of the small intestine. Only slight amount of absorption occurred in the cecum and large intestine. Of the 656% of apparent secretion in the upper S.I., 67% was absorbed in the middle S.I. and 16% absorbed in the lower S.I., 4.3% absorbed in the cecum and only 1.7% and 0.2% absorbed in L.I.(1) and

L.I.(2), respectively. Thus the middle S.I. was the major site of zinc absorption.

In general there appeared to be a trend in showing some difference between the forages with respect to the indigestibility in the sections of the G.I. tract (legume vs grasses). The difference was more pronounced with minerals such as magnesium, calcium, potassium and zinc and generally this great difference in indigestibility was shown in the small intestine. Concentration of these different minerals vary in grasses and legumes. In legumes calcium concentration and magnesium concentration are generally higher than grasses, while Zn and K are generally lower than grasses. However the difference shown in indigestibility between sections could not be due to the difference in concentration but could be due to some other factors. Some organic compounds in the G.I. tract could combine with these minerals and make their digestion or absorption difficult. Mineral absorption of legumes are often affected in this way and many inorganic compounds formed in the small intestine can associate with those organic compounds to influence their absorption. It has been reported that inorganic phosphates, iron, stronium, Berillium etc. influence indigestibility of calcium. Ca, K, and Mg are interrelated.

Flux Pattern of Nutrients as Shown by Lignin and Chromic Oxide Method for the Different Sections of the G.I. Tract of Sheep

The net fluxes of 6 different nutrients were compared by the lignin and chromic oxide method and the results were plotted graphically (Figures 2 through 7). For the dry matter the apparent fluxes were also calculated as shown in Table 8. These values were not tested for the statistical significance.

Using the lignin indicator the rumen showed a 52% apparent absorption of D.M. The Cr_2O_3, however, showed a 76% secretion of D.M. into the rumen.

In the rumen the indicators showed a divergent result of a high magnitude. Over the years many people have shown that dry matter is digested and absorbed in the rumen (Hale et al. (1947); Gray et al. (1947); Kane et al. (1950); Bolin et al. (1956); Rogerson (1958); Badawy (1958); Hogan and Philipson (1960); Yang and Thomas (1956); Topps et al. (1968); Erickson et al. (1970); etc.). The range of dry matter absorbed or digested in these studies was from 20 to 75% and for this section alone the dry matter absorbed might be up to 85%. In this study the values indicated by the lignin method were found to be in agreement with those reported in the literature. The high secretion suggested by chromic oxide for dry matter in the rumen is questionable since a high endogenous secretion of dry matter into the rumen is

Figure 2. The flux pattern of dry matter in the different organs of the G.I. tract of sheep as measured by using chromic oxide and lignin as indicators.

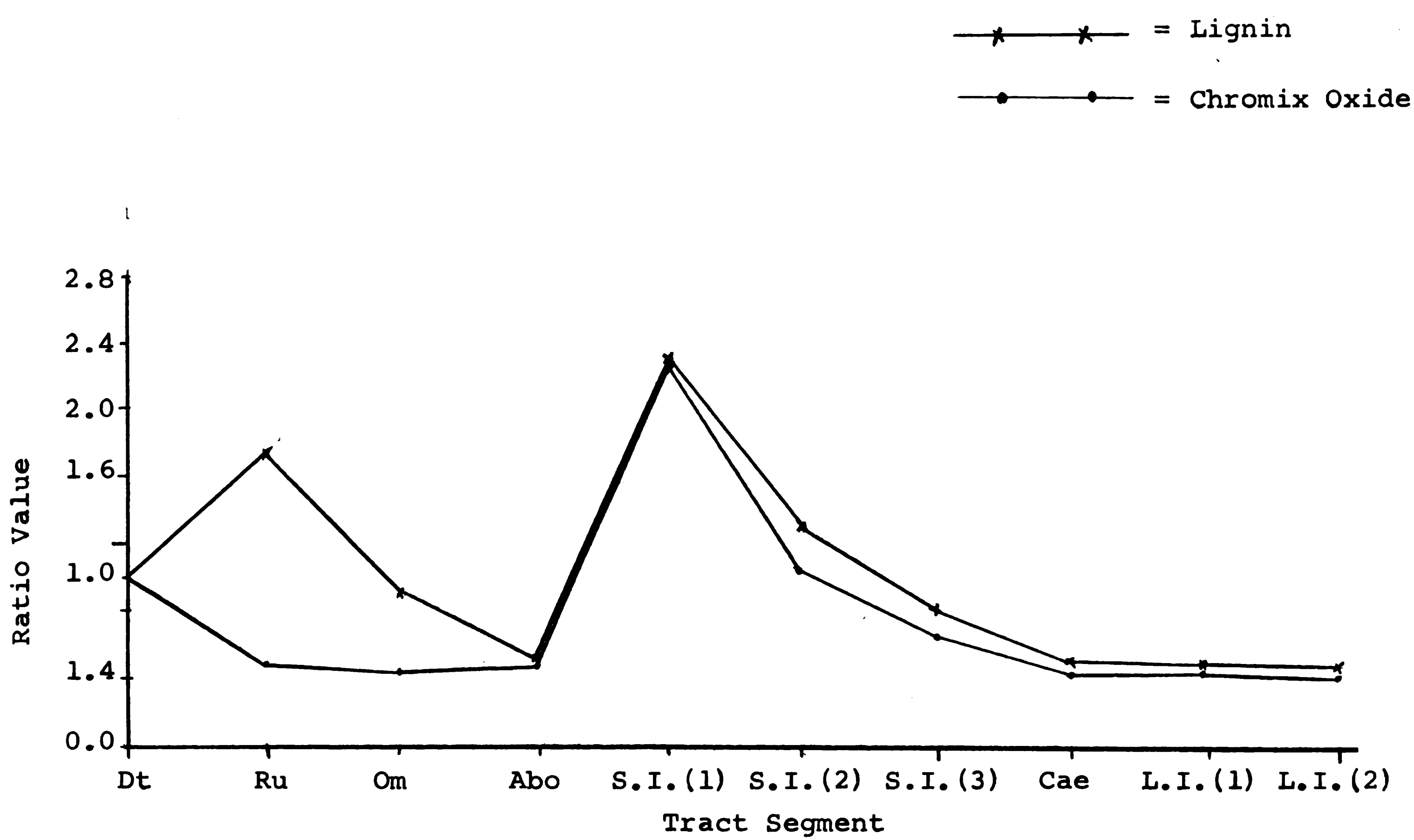

= Lignin
= Chromix Oxide
Ratio Value
2.8
2.4
2.0
1.6
1.0
1.4
0.0
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 2

Figure 3. The flux pattern of magnesium in the different organs of the G.I. tract of sheep as measured by using chromic oxide and lignin as indicators.

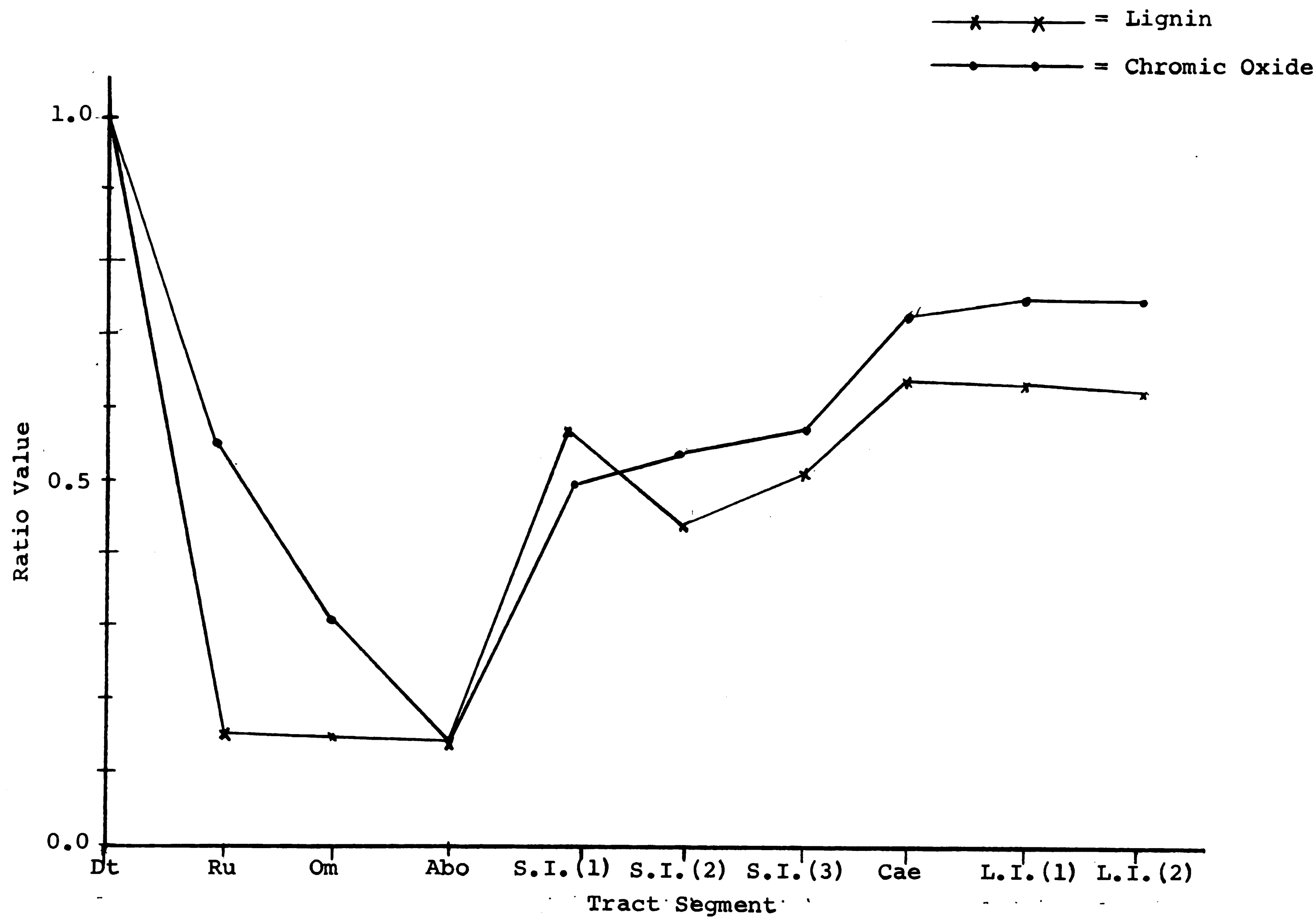
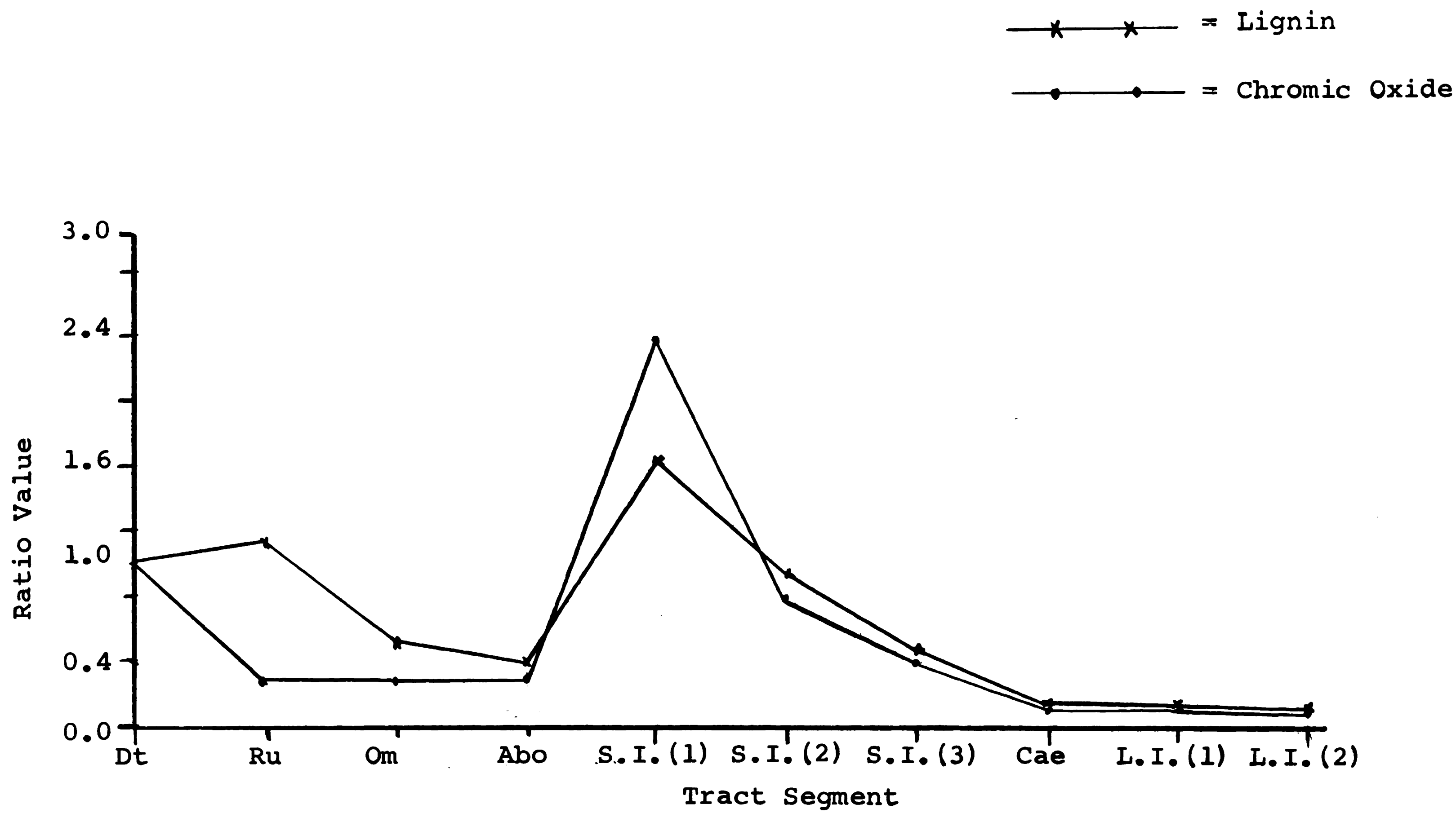

= Lignin
= Chromic Oxide
1.0
0.5
0.0
Ratio Value
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 3

Figure 4. The flux pattern of potassium in the different organs of the G.I. tract of sheep as measured by using chromic oxide and lignin as indicators.



= Lignin
= Chromic Oxide
Ratio Value
3.0
2.4
1.6
1.0
0.4
0.0
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 4

Figure 5. The flux pattern of sodium in the different organs of the G.I. tract of sheep as measured by using chromic oxide and lignin as the indicators.

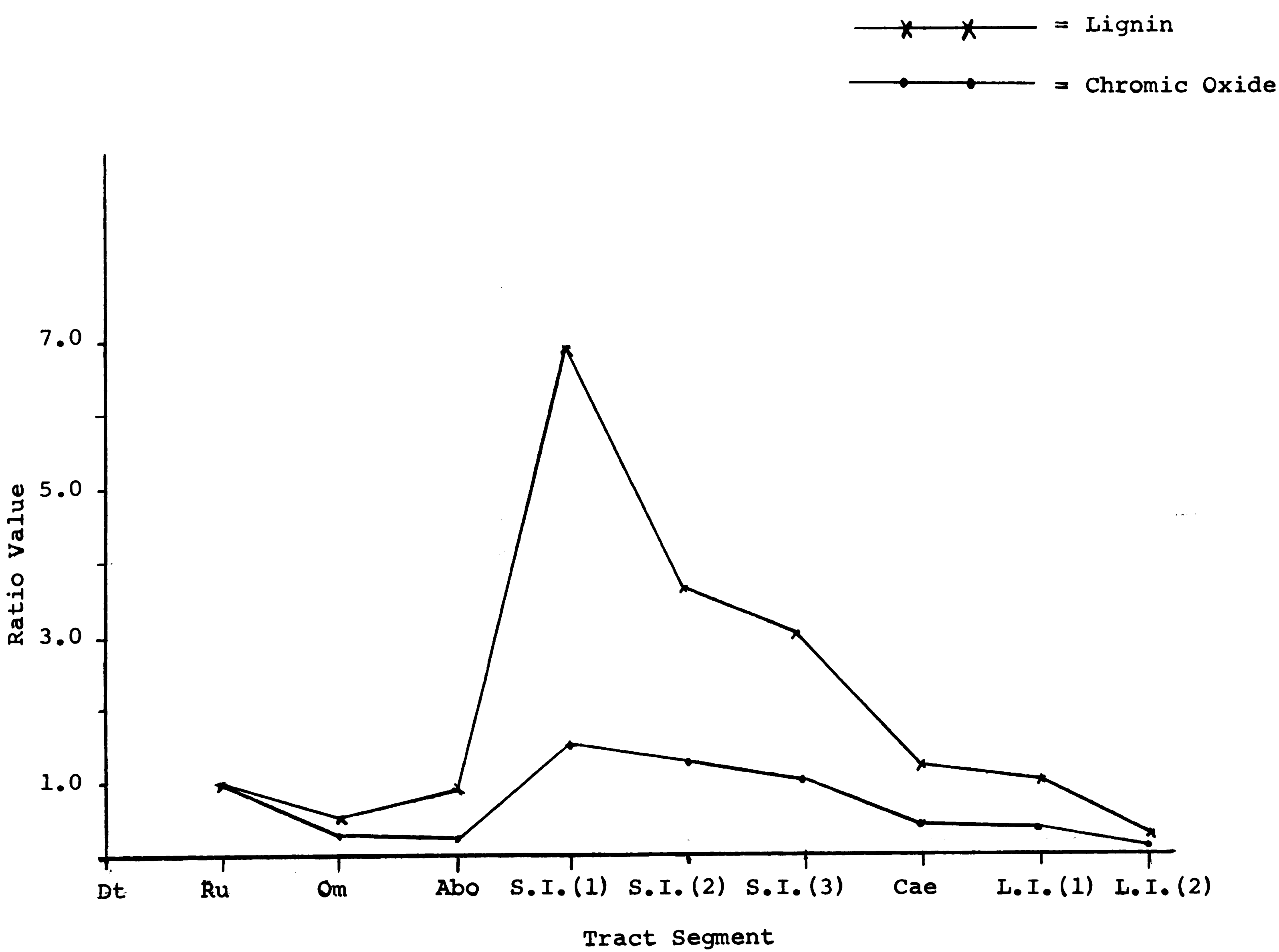

= Lignin
= Chromic Oxide
7.0
5.0
3.0
1.0
Ratio Value
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 5

Figure 6. The flux pattern of calcium in the different organs of the G.I. tract as measured by chromic oxide and lignin as the indicators.

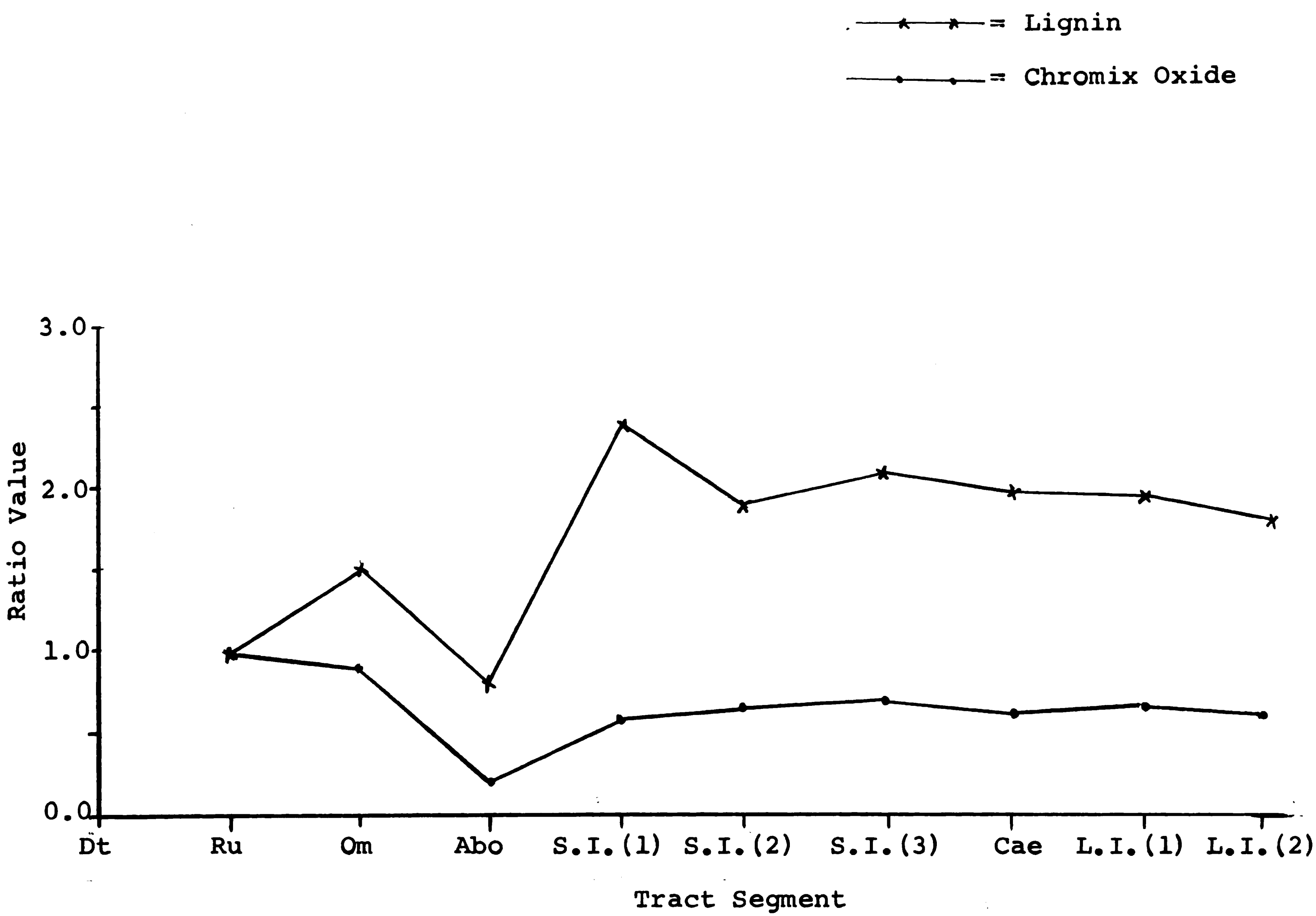

= Lignin
= Chromix Oxide
3.0
2.0
1.0
0.0
Ratio Value
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 6

Figure 7. The flux pattern of zinc in the different organs of the G.I. tract of sheep as measured by chromic oxide and lignin as the indicators.

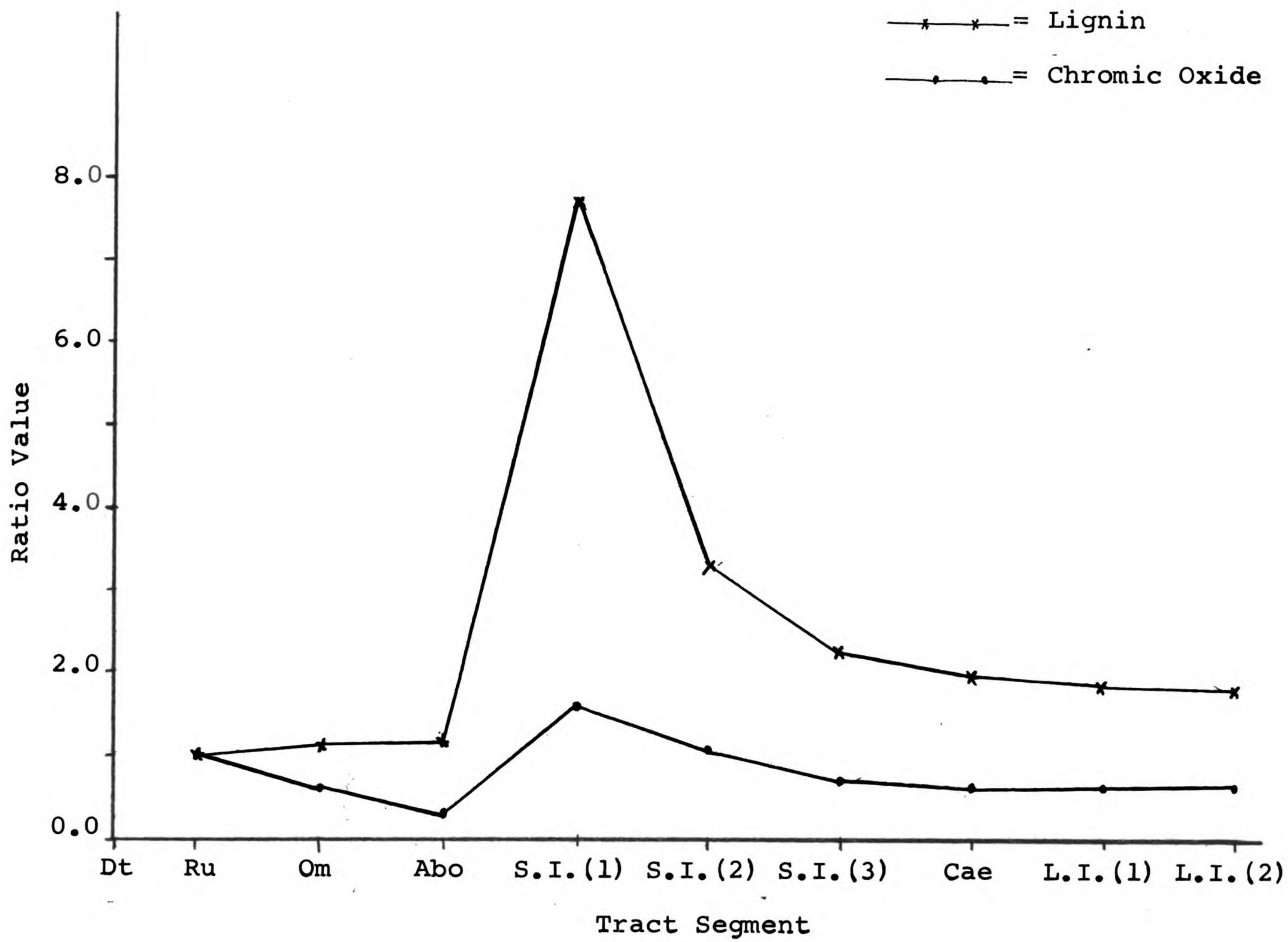

= Lignin
= Chromic Oxide
Ratio Value
8.0
6.0
4.0
2.0
0.0
Dt
Ru
Om
Abo
S.I.(1)
S.I.(2)
S.I.(3)
Cae
L.I.(1)
L.I.(2)
Tract Segment

Figure 7

Table 8. The flux pattern of dry matter in the different organs of the G.I. tract of sheep as measured by using chromic oxide and lignin as indicators.

Organ	Apparent Flux		Net Flux (digestibility)	
	Cr	Lignin	Cr.	Lignin
Rumen	-0.76	0.52	-0.76	0.52
Omasum	0.80	0.04	0.08	0.56
Abomasum	0.41	-0.04	0.49	0.52
S.I.(1)	-1.81	-1.81	-1.32	-1.29
S.I.(2)	1.03	1.24	-0.29	-0.05
S.I.(3)	0.48	0.39	0.19	0.34
Cecum	0.31	0.24	0.50	0.58
L.I.(1)	0.00	0.01	0.50	0.59
L.I.(2)	0.01	0.02	0.51	0.61

not likely. Yang (1964) indicated that when chromic oxide was used as an indicator in absorption/secretion studies of different nutrients, in the rumen dry matter flux showed a similar secretion as in the present study. Lignin, however, indicated a considerable absorption of dry matter in the rumen. This difference must be due to some differential passage between the two indicators.

In the omasum the apparent flux by lignin indicated 4% absorption while the flux using chromic oxide indicated 80% absorption. In general, absorption of dry matter has been reported in the omasum, this however is usually a fraction of what has been shown for the rumen. The value shown by chromic oxide in this section is unlikely to occur in the omasum. The absorption indicated by the lignin method appears reasonable as well as close to what has been reported in the literature.

A slight secretion of 4% was demonstrated for abomasum by the lignin method. In the abomasum chromic oxide indicated an apparent absorption of 41%. The net flux nevertheless did not show much variation (49 vs 52%) between the values indicated by both the indicators. Therefore either of these indicators could be used to study net effect from diet in the abomasum.

In the small intestine, the apparent flux shown by both lignin and chromic oxide amounted to a secretion of 181%. Also a very similar pattern occurred throughout the remaining sections of the S.I., cecum, and large intestine.

A more or less similar pattern of flux could be seen between the two indicators for the other nutrients (Figures 3 through 7) also. The difference shown by the two indicators in the flux of nutrients, especially in rumen and omasum strongly suggested that the variation was mainly due to the indicators used. Differences in the rate of passage of these indicators could account for the different ratio values in each section.

Chromium/Lignin Ratio

The average ratio for chromium to lignin in the dry matter for the 16 sheep are given in Table 9. The flux comparison of different nutrients in different sections of the G.I. tract by lignin and chromic oxide methods suggested that the difference found could be due to differences between the two indicators. Many indicators have been used to study different parameters in digestion trials, rate of passage, retention, etc. The comparisons of markers in such studies were done to evaluate the dependability of these markers as well as their accuracy for that purpose. Recoveries of markers in feces, and comparison with total collection methods generally indicated the merit of the marker used in such studies. However in studies for observing the flux pattern of nutrients through the G.I. tract recovery of markers in the feces is not a valid basis for comparing indicators.

Table 9. Average chromium/lignin ratio of 16 sheep in the different sections of the G.I. tract.

Location	Ratio
Diet	4.14
Rumen	1.19
Omasum	2.25
Abomasum	3.93
S.I.(1)	4.25
S.I.(2)	3.31
S.I.(3)	3.32
Cecum	3.48
L.I.(1)	3.39
L.I.(2)	3.13

The chromium/lignin ratios could be used as one of the best estimates of the differential rate of movement of these indicators throughout the G.I. tract. The data indicated that there existed some difference in this ratio between the diet and the various sections. Further, it also pointed out that there was a difference among the ratio values among various sections. Statistical analysis by the analysis of variance indicated that these differences in the sections were highly significant ($P < 0.0005$).

In this study it was expected that both lignin and chromic oxide would move together in a similar fashion with the digesta in different sections. In such case similar chromium/lignin ratios in diet and in all the different sections would have been obtained. However the data demonstrated that this was not true.

The chromium/lignin ratio in the diet was 4.14 but in the rumen it was only 1.19 (Table 9). This suggests that the indicators varied in their rate of passage out of the rumen.

Also, in the omasum the ratio value was considerably lower (2.25) than found in the diet or only 54.3% of that observed in the diet. In the abomasum the chromium/lignin ratio was 3.93 or 94.9% of the dietary value.

In the upper S.I. the ratio value was found to be a little above than that of the diet (4.25). In the lower two sections of the small intestine the ratio value was slightly lower than that of the diet. Corresponding ratio values for the cecum, L.I.(1), and L.I.(2) were 3.48, 3.39 and 3.13 respectively. These values were 84% to 74% of the diet value. The chromium/lignin ratio was also compared for a series of consecutive sections by dividing the subsequent section into the previous section. For the rumen this value was 2.95 and for the subsequent sections it was: omasum = -1.06, abomasum = -1.68, S.I.(1) = -0.31, S.I.(2) = 0.93, S.I.(3) = -0.51, cecum = 0.34, L.I.(1) 0.09, L.I.(2) = 0.26.

Chromium-lignin ratio with respect to the diet showed large differences for the rumen, and omasum only. However when the consecutive sections were compared the chromium/lignin ratio indicated high values for the rumen, omasum, and abomasum and S.I.(2). This study indicated that there were large variations in the rate of passage between the two indicators.

To find the variation in the rate of passage these markers were compared with dry matter, which constituted the major portion of the ingesta. This was done by comparing the concentration of the markers with dry matter throughout the tract (Table 9) and the distribution of dry matter, lignin and chromic oxide throughout the tract (Table 10).

The data indicated that the rumen contained 72.3% of the dry matter, 72.4% of the lignin, but only 47.7% of the chromic oxide in the entire tract. These values suggested

Table 10. Distribution of dry matter, lignin and chromium on a percentage of the actual quantity found in different organs of the gastrointestinal tract on a dry matter basis.

Organ	Dry Matter (percent)	Lignin (percent)	Chromium (percent)
Rumen	72.30	72.40	47.70
Omasum	2.65	2.97	3.35
Abomasum	3.34	3.38	8.03
Small intestine(1)	1.58	0.42	1.15
Small intestine(2)	2.51	1.29	2.15
Small intestine(3)	3.10	2.36	4.50
Cecum	4.75	5.43	10.86
Large intestine(1)	7.24	8.44	16.50
Large intestine(2)	2.56	3.33	5.90
	100.00	100.00	100.00

that compared to dry matter in the rumen lignin value amounted to 101% and chromic oxide 66%. This suggested that chromic oxide moved out of the rumen much faster than did the dry matter.

In the omasum and the abomasum lignin continued to show a close relation to the dry matter portion (omasum 112%, and abomasum 101%). Chromic oxide in these sections indicated marked differences from that of lignin and dry matter. The difference was more pronounced in the abomasum (omasum = 126%, abomasum = 241%).

The major differences observed by chromium/lignin ratio were in the rumen and omasum. The relative distribution suggested that in these sections chromic oxide moved more rapidly than did lignin and dry matter.

Lignin throughout the entire small intestine showed a somewhat different distribution than the dry matter. Lignin distribution value in the 3 sections of the small intestine amounted to 27, 51 and 130% of the corresponding D.M. values respectively. Chromic oxide proportions found in the lower gut was more than twice those of the dry matter. Lignin was also concentrated in the lower gut when compared to dry matter.

The low value for chromium in the rumen and a high value in the abomasum, lower S.I., cecum, and in both sections of large intestine could be due to the rapid movement of chromic oxide out of the rumen followed by an accumulation in the preceding sections.

Data in the present study clearly indicated that chromic oxide was not a suitable indicator to study the digestibility or the flux of nutrients in the rumen. Balch (1957) used chromic oxide capsules in steers and reported a rapid movement of this marker out of the rumen. He indicated only a small portion remained in the rumen to move along with the dry matter of the ingesta. Corbett _et al_. (1959, Johnson _et al_. (1961), Langlands (1963), reported that chromic oxide as a premix or capsule did not move along with the roughage ration. Bolin _et al_. (1960) reported that chromic oxide was passing out of the rumen very rapidly when incorporated uniformally in a pelleted ration. Kane _et al_. (1953) and Elam _et al_. (1961) have shown a considerable diurnal variation in the fecal excretion of chromic oxide. Dinnuson (1964) reported when both lignin and chromic oxide were used as indicators in a study to measure indigestibility the chromic oxide apparently moved out of the rumen more rapidly than did the lignin. Yang (1964) indicated that when both lignin and chromic oxide were used in flux studies of nutrients, a secretion was noted for all the nutrients when chromic oxide values were used. This could have been due to a more rapid movement of chromic oxide out of the rumen.

Erickson _et al_. (1970) indicated that indigestibility studies using both chromic oxide and lignin gave comparable results for the feed/feces ratios but not for the feed/rumen ratios. The present study also suggested that chromic oxide used in capsule form moved out of the rumen very rapidly but that lignin probably moved with the dry matter.

With regard to the rumen, the above few studies have indicated that chromic oxide moved out of the rumen rapidly and hence was not a suitable indicator. This present study also showed that chromic oxide appears to be causing serious errors in calculated flux patterns in other sections. This is probably due to its differential passage through such sections. Also this result would make questionable some of the values reported in the past where chromic oxide was used in sectional studies.

SUMMARY

Lignin was used as a nonabsorbable marker to study the indigestibility and the flux pattern of different nutrients (dry matter, Ligno-cellulose, Mg, K, Na, Ca, and Zn) in the different organs of the gastrointestinal tract of sheep. Sixteen sheep and four different forages (Baumen's Thesis, 1968) were used in this study.

The lignin ratio technique indicated that there was an average of 39% indigestibility of dry matter for the entire tract. The indigestibility of dry matter was found to be significantly different for the different sections of the G.I. tract ($P < 0.0005$). Some variations were noted in the indigestibility between grasses and legumes. The values at 6 hour and 12 hours post prandial did not show much variation in the indigestibility of dry matter.

The flux of the dry matter showed that there was 52% apparent absorption from the rumen. Apparent absorption also occurred from the omasum, middle S.I., lower S.I., cecum, and the large intestine. Apparent secretions of D.M. occurred in the abomasum and in the upper small intestine.

The overall indigestibility of ADF amounted to 48% for the entire tract. The flux of this nutrient demonstrated that there was about 42% disappearance of this nutrient from the rumen. However thereafter the flux did not vary much.

The overall indigestibility of the minerals (Mg, K, Na, Ca, and Zn) was determined for the different sections of the G.I. tract. For all the minerals a highly significant indigestibility was noted for the different sections ($P < 0.0005$). Analysis of variance showed that there was a significant difference between grasses and legumes for their indigestibility for Mg, and K. Similar variation was noticed in the case of Zn as well.

The flux pattern of the minerals for different organs showed a somewhat similar pattern. Mg and K indicated a high rate of apparent absorption from the rumen. Indirect evidence indicate ruminal absorption of Ca and Zn. For Na, Ca, and Zn the ruminal values were considered as the base values. In general, for all the minerals a high endogenous secretion was observed in the upper S.I. Reabsorption of these minerals occurred in the middle S.I. and in the remaining sections.

Comparison of the indicators (lignin and chromic oxide) for the flux pattern of nutrients was made by using the ratio technique. The chromium/lignin ratio indicated that there was a highly significant difference in rates of passage of chromium and lignin through the different organs of the G.I. tract ($P < 0.0005$). The greatest difference in the differential rates of passage of these two indicators observed in the rumen. The comparison of the distribution of lignin and chromic oxide to that of the dry matter indicated that chromic oxide was moving out of the rumen much faster than lignin or the dry matter. Also this tendency has resulted in the accumulation of chromic oxide in the lower sections of the G.I. tract thereby showing a higher proportions in these sections than did by lignin or dry matter.

This work thus clearly demonstrates that chromic oxide given by capsule is not a suitable indicator for the study of the flux pattern of nutrients from the different sections of the G.I. tract. This is especially true for the rumen, because in this section both chromium/lignin ratio as well as the distribution of these indicators demonstrated a high differential rate of passage for this indicator.

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APPENDIX

Table 1. Concentration of chromium, lignin and ADF in the different sections of the G.I. tract and in diet for the 16 sheep.

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
1	Diet	23.60	3.389	34.83
	Rumen	15.50	5.810	33.20
	Omasum	30.75	8.389	37.23
	Abomasum	46.13	7.269	36.65
	S.I.(1)	6.00	1.077	2.86
	S.I.(2)	14.75	3.464	14.92
	S.I.(3)	21.25	4.950	24.90
	Cecum	42.75	7.773	33.70
	L.I.(1)	41.63	7.428	34.02
	L.I.(2)	50.25	8.958	38.89
2	Diet	13.80	2.679	30.87
	Rumen	6.00	6.061	34.92
	Omasum	95.00	7.775	33.73
	Abomasum	29.00	61.85	33.77
	S.I.(1)	5.00	1.412	5.54
	S.I.(2)	8.63	3.535	16.70
	S.I.(3)	13.75	4.750	23.92
	Cecum	25.75	7.125	34.52
	L.I.(1)	27.00	7.909	34.39
	L.I.(2)	32.50	8.624	37.84
3	Diet	13.50	3.389	34.83
	Rumen	9.75	7.455	36.72
	Omasum	22.75	8.322	35.06
	Abomasum	23.75	7.588	38.06

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
	S.I.(1)	6.25	1.144	5.10
	S.I.(2)	9.38	2.799	13.82
	S.I.(3)	12.50	5.765	25.39
	Cecum	26.25	7.769	32.90
	L.I.(1)	25.50	7.587	34.28
	L.I.(2)	25.50	9.327	35.47
4	Diet	13.90	2.679	30.89
	Rumen	10.38	5.680	33.54
	Omasum	21.50	6.880	32.78
	Abomasum	37.50	5.197	25.34
	S.I.(1)	10.13	1.795	7.92
	S.I.(2)	13.25	3.846	17.68
	S.I.(3)	18.25	5.714	26.00
	Cecum	26.75	1.795	7.92
	L.I.(1)	26.50	7.816	44.28
	L.I.(2)	27.00	8.547	35.45
5	Diet	11.00	7.692	36.72
	Rumen	6.13	13.656	47.02
	Cmasum	13.00	15.010	42.94
	Abomasum	26.50	13.673	44.55
	S.I.(1)	7.13	4.959	14.54
	S.I.(2)	8.13	5.259	15.41
	S.I.(3)	13.38	11.881	35.90
	Cecum	16.00	14.533	34.71
	L.I.(1)	15.63	15.884	36.60
	L.I.(2)	16.38	17.409	41.61

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
6	Diet	10.20	6.522	32.28
	Rumen	7.70	15.778	4.47
	Omasum	10.00	14.817	38.41
	Abomasum	20.75	13.679	37.06
	S.I.(1)	2.75	0.772	1.27
	S.I.(2)	8.00	4.408	12.41
	S.I.(3)	16.67	10.777	30.87
	Cecum	24.50	13.641	35.43
	L.I.(1)	22.00	14.475	35.56
	L.I.(2)	17.88	15.172	41.08
7	Diet	21.40	3.389	34.83
	Rumen	12.00	6.379	34.83
	Omasum	21.38	7.472	28.78
	Abomasum	33.00	7.366	33.78
	S.I.(1)	12.00	1.770	7.51
	S.I.(2)	19.50	4.464	18.70
	S.I.(3)	24.38	4.760	34.69
	Cecum	52.50	8.571	35.92
	L.I.(1)	49.00	8.237	34.69
	L.I.(2)	47.25	8.710	38.54
8	Diet	71.80	7.692	36.72
	Rumen	33.00	19.314	52.75
	Omasum	145.00	16.095	43.44
	Abomasum	138.75	18.301	47.93
	S.I.(1)	45.00	4.469	12.29
	S.I.(2)	53.00	4.600	15.59
	S.I.(3)	87.30	5.047	44.66

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
	Cecum	111.25	16.938	43.92
	L.I.(1)	97.50	17.176	44.66
	L.I.(2)	96.88	17.824	46.82
9	Diet	12.00	2.679	30.87
	Rumen	7.38	6.545	35.92
	Omasum	11.13	7.485	32.26
	Abomasum	31.50	6.977	32.71
	S.I.(1)	5.79	1.647	7.59
	S.I.(2)	10.25	3.822	16.39
	S.I.(3)	17.50	5.924	26.94
	Cecum	36.50	7.775	40.00
	L.I.(1)	37.00	8.533	39.12
	L.I.(2)	34.00	8.052	37.13
10	Diet	8.40	6.522	32.28
	Rumen	5.75	12.573	41.96
	Omasum	12.75	13.267	34.14
	Abomasum	27.75	12.409	35.75
	S.I.(1)	8.00	3.631	11.27
	S.I.(2)	10.00	5.234	15.31
	S.I.(3)	14.50	10.649	31.09
	Cecum	16.50	15.257	45.03
	L.I.(1)	17.00	15.022	31.09
	L.I.(2)	14.90	14.415	39.05
11	Diet	19.30	7.692	36.72
	Rumen	6.50	15.024	48.75
	Omasum	13.63	15.764	46.00

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
	Abomasum	25.50	15.485	46.90
	S.I.(1)	10.25	5.048	16.17
	S.I.(2)	11.25	6.899	20.56
	S.I.(3)	22.25	11.085	32.82
	Cecum	42.38	15.829	38.89
	L.I.(1)	44.25	15.866	42.55
	L.I.(2)	41.63	17.154	48.89
12	Diet	15.00	6.522	32.28
	Rumen	7.75	14.537	45.16
	Omasum	10.75	14.658	40.32
	Abomasum	23.00	12.031	40.47
	S.I.(1)	6.65	3.378	32.07
	S.I.(2)	9.375	7.433	20.55
	S.I.(3)	18.75	9.761	26.45
	Cecum	32.75	14.830	38.84
	L.I.(1)	33.75	15.740	38.90
	L.I.(2)	32.25	16.682	43.52
13	Diet	25.30	3.389	34.83
	Rumen	17.75	6.918	37.06
	Omasum	30.00	8.333	34.27
	Abomasum	42.00	6.170	30.76
	S.I.(1)	11.75	1.527	7.43
	S.I.(2)	22.25	3.615	16.30
	S.I.(3)	36.00	4.615	24.10
	Cecum	58.25	8.675	36.87
	L.I.(1)	55.00	9.535	36.12
	L.I.(2)	59.00	10.760	39.31

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
14	Diet	12.50	2.679	30.87
	Rumen	9.75	6.117	34.42
	Omasum	12.25	6.996	32.26
	Abomasum	20.00	7.097	34.23
	S.I.(1)	7.25	19.24	9.08
	S.I.(2)	11.13	4.012	19.84
	S.I.(3)	18.55	4.605	24.04
	Cecum	26.50	7.999	34.53
	L.I.(1)	26.50	8.566	34.89
	L.I.(2)	26.00	9.371	37.04
15	Diet	10.50	6.522	36.72
	Rumen	7.35	13.565	44.51
	Omasum	15.25	13.084	35.18
	Abomasum	55.00	13.83	41.59
	S.I.(1)	10.50	3.96	12.26
	S.I.(2)	10.13	5.09	14.85
	S.I.(3)	15.50	8.31	38.17
	Cecum	24.00	14.87	38.29
	L.I.(1)	24.00	15.15	38.17
	L.I.(2)	23.50	15.69	42.14
16	Diet	15.60	7.69	32.28
	Rumen	7.25	13.85	47.25
	Omasum	19.00	15.25	44.22
	Abomasum	26.25	13.14	40.76
	S.I.(1)	10.65	5.46	17.15
	S.I.(2)	12.13	6.72	21.93
	S.I.(3)	18.00	9.90	35.45

continued

Table 1--continued

Sheep Number	Section	Chromium (in ppm)	Lignin (percent of D.M.)	ADF (percent of D.M.)
	Cecum	26.00	14.55	42.28
	L.I.(1)	29.88	15.56	48.82
	L.I.(2)	33.00	15.81	45.84

Table 2. Analysis of variance on the lignin and chromium oxide ratio throughout the G.I. tract.

Source	S.S.	D.F.	M.S.	F
Treatments	503.48	7	71.93	
Hours	16.58	1	16.58	0.26
Rations	308.28	3	102.76	1.60
Hours x Rations	178.62	3	59.54	0.93
Sheep w Treatment	514.31	8	64.29	12.44
Location w Sheep	661.51	128	5.17	61.37
Samples w Locations	12.13	144	0.08	
Total	4659.21	287		