

ABSORPTION AND SECRETION OF
NUTRIENTS THROUGHOUT THE
ALIMENTARY TRACT OF YOUNG CALVES
FED DIFFERENT LEVELS OF
FIBER AND PHOSPHORUS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY

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1964

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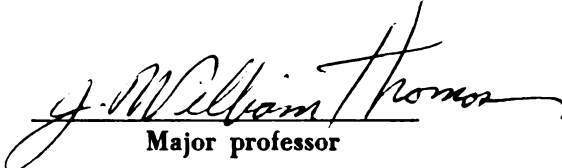
Absorption and Secretion of Nutrients Throughout the
Alimentary Tract of Young Calves Fed Different Levels
of Fiber and Phosphorus

presented by

Modesto G. Yang

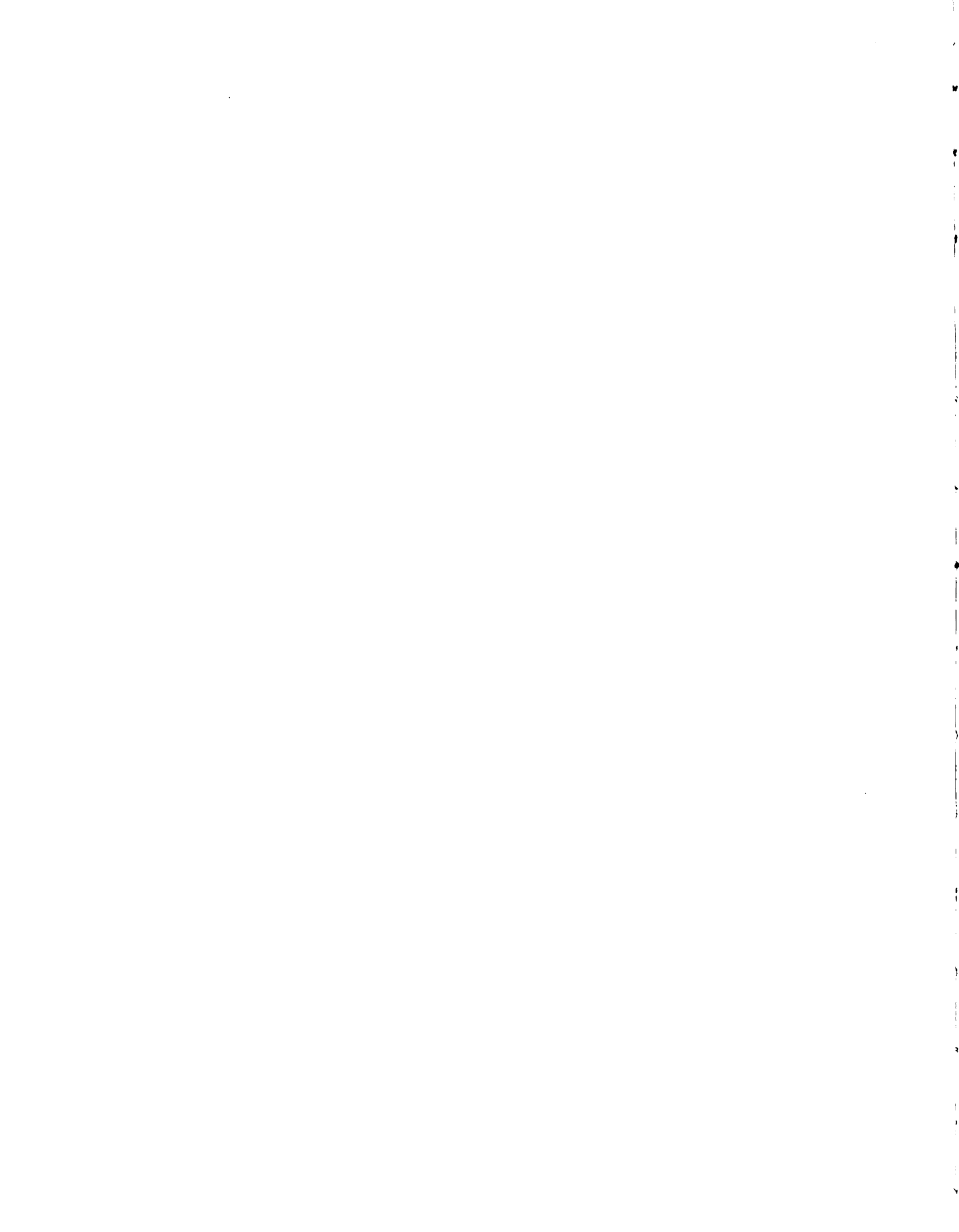
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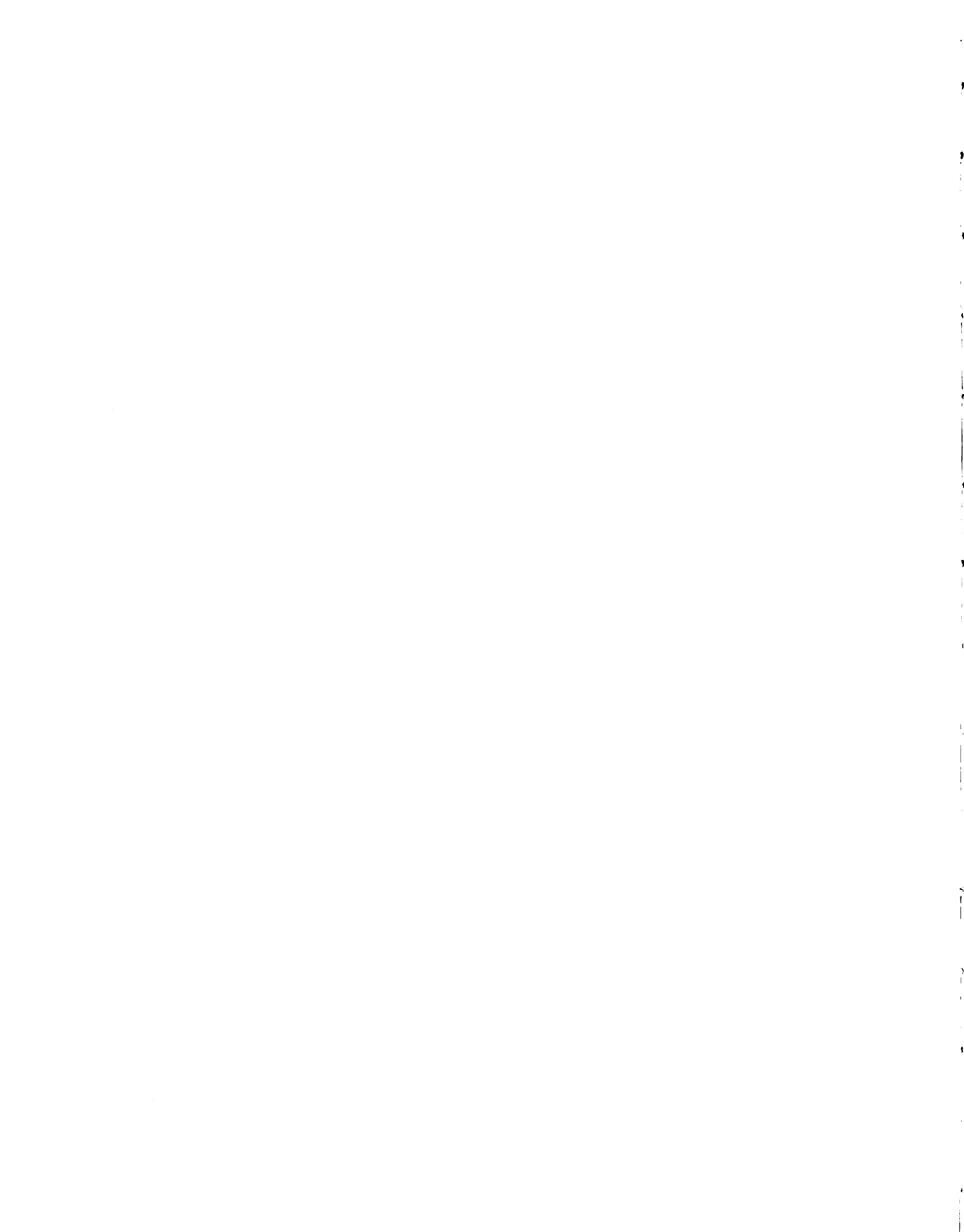
Ph.D. degree in Dairy Nutrition


Major professor

Date May 15, 1964







ABSTRACT

ABSORPTION AND SECRETION OF NUTRIENTS THROUGHOUT THE ALIMENTARY TRACT OF YOUNG CALVES FED DIFFERENT LEVELS OF FIBER AND PHOSPHORUS

by Modesto G. Yang

Two separate trials were performed to evaluate the effects of different levels of dietary phosphorus and fiber from semi-synthetic diets on the performance of male Holstein calves from birth until 12 weeks of age. There were no statistical differences in feed intakes or body weight gains among groups of calves fed 3.0, 3.1, or 3.4 g of phosphorus daily per 100 lb body weight (P levels 1, 2, and 3 in Trial I) or rations containing 0.135, 0.196, 0.222, or 0.291% phosphorus (P levels 1, 2, 3, and 4 in Trial II). Blood serum concentrations of calcium, phosphorus, and phosphatase activity and percentage fat-free rib bone ash were not appreciably affected by levels of phosphorus in the diets of calves but bone mass (g of bone ash per 100 lb body weight) was greatest for calves fed phosphorus level 3 in both trials.

The calves that were fed a low-fiber ration (10% fiber) consumed significantly less dry matter per unit body weight than those fed a high-fiber ration (33% fiber, Trial I). Similarly in Trial II, much less of a 9% fiber ration was consumed than one of 20% ($P < .0005$).

Subsequent to the 12-week performance period, the calves in Trial I were force-fed Cr_2O_3 for one week while in Trial II the calves were fitted with collection bags for total collection of feces. The calves in both trials were killed at the end of the week and their gastrointestinal contents removed, weighed, and sampled for various measurements.

The percentage distribution of dry digesta in respective sections of the alimentary tract was very similar for calves fed the low- and high-fiber rations within each trial although the calves fed the high-fiber rations had more total dry digesta in the entire tract per 100 lb body weight. The wet ruminal digesta were correlated ($r = +0.57$) to daily fecal output and rumen retention time to daily feed consumption ($r = +0.46$).

An average of 405 and 1140 millimoles of volatile fatty acids (VFA) was found in the entire tract of calves fed the low- and high-fiber rations respectively in Trial I, while in Trial II the quantities were 618 and 676. An average of 55-88% of the total VFA was in the rumen of calves in both trials. Approximately 8.5% of the total VFA was in the omasum and 1.5% in the abomasum and small intestine. The large intestine and cecum contained on the average 11-36% of the total. In Trial I neither phosphorus nor fiber levels significantly affected the molar percentage distribution of acetic, propionic and butyric acids in the ruminal digesta. The average molar

percentages were 66, 24, and 10 respectively for the three acids. In Trial II the molar percentages were 71, 23, and 6 for calves fed the low-fiber rations compared to 65, 27, and 8 for calves fed the high-fiber ration.

Considerably less lactic acid than VFA was present in the alimentary tract of the calves. Only 7.1 to 14.5 millimoles per calf were detected. From 52.6 to 78.6% of the lactic acid in the entire tract was found in the small intestine of calves in both trials.

The concentration of a nutrient in two consecutive sections of the tract was used in conjunction with the marker ratio equation for estimating degree of secretion and/or absorption of nutrients in eight sections of the alimentary tract. Significantly less dry matter and organic matter were absorbed in the rumen of calves fed the high-fiber rations than those fed the low-fiber rations while the reverse was true for fiber absorption in both trials. In general, dry matter and organic matter were secreted into the omasum, abomasum and the first half of the small intestine. In the lower half of the small intestine, large intestine, cecum, and rectum, dry matter and organic matter were absorbed.

Phosphorus, calcium, and ash were absorbed in the rumen. In the omasum and abomasum the fate of these three nutrients was variable. Secretion of these three nutrients was definite for the upper section of the small intestine. Re-absorption occurred in the remainder of the tract.

The absorption of sodium took place in the rumen and omasum while secretion occurred in the abomasum and upper section of the small intestine. Sodium absorption again occurred in the lower section of the small intestine and secretion in the large intestine and cecum. Finally absorption of sodium took place in the rectum.

Water was absorbed in the omasum and secreted into the abomasum and upper small intestine. The lower small intestine, large intestine, cecum, and rectum absorbed practically the equivalent amount of water secreted by the abomasum and upper small intestine.

Absorption of VFA occurred in the omasum and abomasum while a considerable amount was produced in the large intestine and cecum. Some degree of absorption of VFA was found in the rectum prior to the voiding of digesta as feces.

Lactic acid was absorbed in all sections of the alimentary tract except abomasum and upper sections of the small intestine where production exceeded absorption.

A method was developed to estimate the caloric value of the VFA absorbed. On the average the rumen supplied energy in the form of VFA to equal 55% of the total net energy required for maintenance and growth while the cecum supplied 7.4%. Of the total energy supplied by VFA, 50% came from acetic and the remaining 50% from propionic and butyric acids.

Comparison of Cr_2O_3 and lignin as the indigestible markers to determine degree of digestion indicated that

values obtained were in general greater when lignin was used to determine absorption of nutrients in the rumen but not for other sections of the gastrointestinal tract.

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By
Modesto G. Yang

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Dairy

1964

ACKNOWLEDGMENTS

The author expresses his sincere appreciation to:

Dr. J. W. Thomas, Professor of Dairying for his guidance and counsel throughout the course of this study and the writing of this manual.

Dr. C. A. Lassiter, Head, Department of Dairying, for providing the graduate research assistantship.

Dr. R. S. Emery, Associate Professor of Dairying, for his personal counsel and the reading of this manuscript.

Mrs. D. C. Carpenter, Technician, for the determination of the lactic acid.

Mr. E. Hill, Technician, for his help in the sacrifice and the removal of the alimentary tract of the calves.

Dr. L. J. Bratzler, Professor of Food Science, who arranged for the facilities in the Meats Laboratory.

Mrs. E. R. Walker, Stenographer, for her help in typing part of this manual.

Dr. E. J. Benne, Professor of Biochemistry for the determination of the proximate constituents of the rations.

Mrs. Lillian D. Yang, my wife, for her sacrifices and encouragement in the pursuit of a higher education.

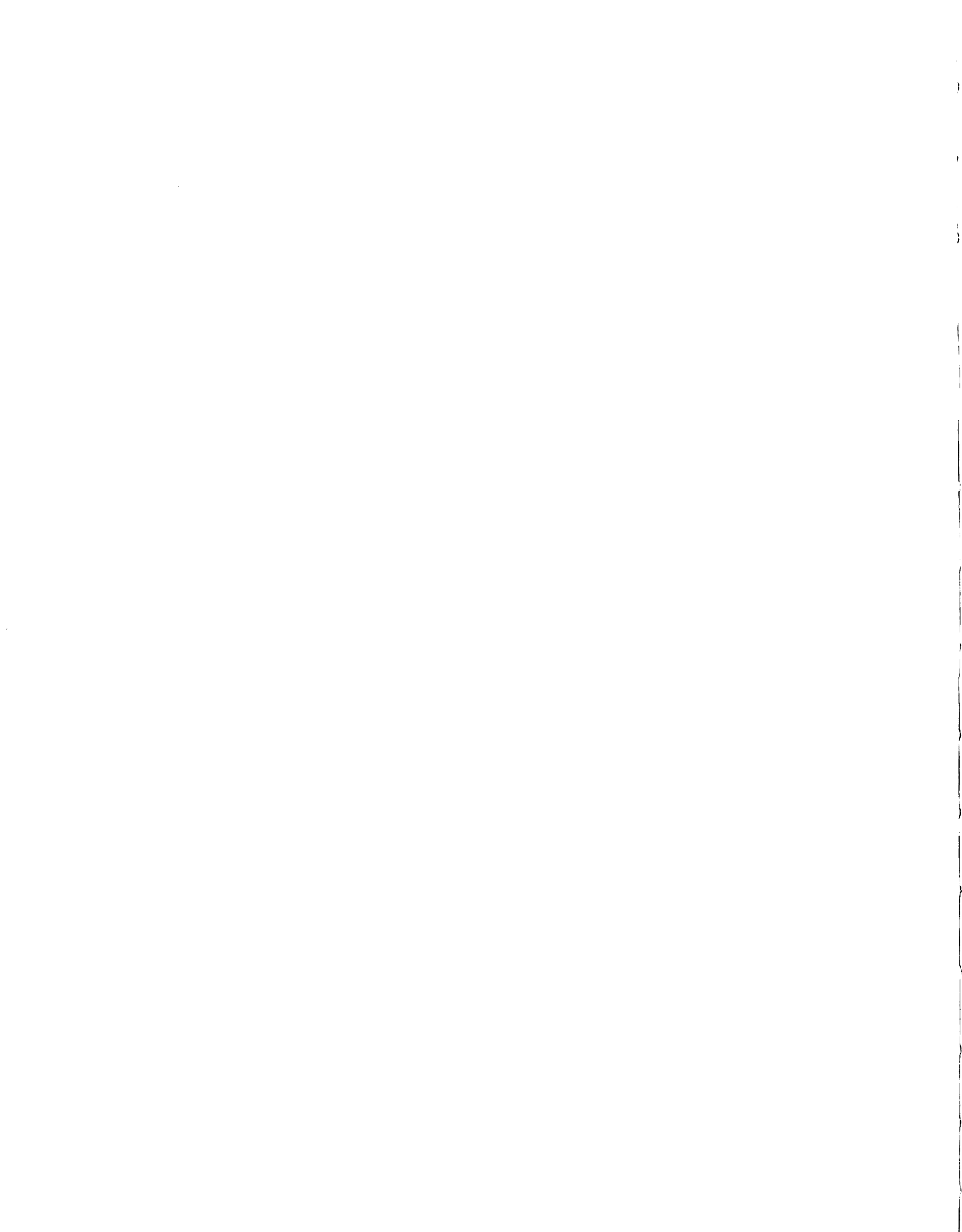


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CHAPTER I

INTRODUCTION

Even though the need of providing cattle with sufficient amounts of phosphorus is well documented in the scientific literature, much disagreement presently exists among nutritionists regarding the amount considered adequate for very young calves. The lack of agreement exists mainly because of the difficulty in interpreting criteria used in the evaluation of the phosphorus status of animals. Depraved appetite and unthriftiness are two of the common symptoms of prolonged phosphorus deficiency often observed in cattle and are sometimes used as criteria to estimate phosphorus requirement of cattle. The importance of evaluating the phosphorus requirement of young calves and the influence of dietary phosphorus on appetite is, therefore, obvious.

Recently the "High-roughage" system of feeding calves was proposed by investigators from the Ohio Station. The dietary level of the roughage or fiber may decrease the intake of the calf by reducing its alimentary capacity to hold feed. The effect of dietary levels of fiber on appetite are therefore of practical importance in the rearing of young calves specially when their rumina are not as yet fully developed. The first part of the present experiments was

designed to determine the phosphorus requirement of the calf between 30 and 84 days of age and to evaluate the importance of levels of phosphorus and fiber on calf appetite.

Because the study of absorption and secretion of nutrients in the alimentary tract is difficult, very little experimentation has been done on this problem by nutritionists and other biologists. Even lesser amount of work has been done to study specifically the degree of digestion or to follow the fate of digesta throughout the alimentary tract of animals. If sufficient basic information were available on the processes of digestion, a calf ration could possibly be formulated to better meet the physiological needs of the calf. The second part of the experiments was therefore planned to study the extent of absorption and secretion of nutrients throughout the alimentary tract of the calf.

CHAPTER II

REVIEW OF LITERATURE

Secretion and Absorption in the Gastrointestinal Tract

Although much work has been done to determine total digestion which is mainly the end result of secretion and absorption few attempts have been made to trace the fate of digesta within each section of the alimentary tract. Several methods have been developed mostly to study the absorption of volatile fatty acids by the rumen but are also applicable to the study of other nutrients in the digestive tract. The following is a list of the methods used to study quantitative changes of digestion at different sections of the gastrointestinal tract:

1. Perfusion of isolated but living organs and the determination of constituents entering and leaving the organ in the perfusate.

2. Determination of the concentration of the constituents in the organs in question at different time intervals after feeding.

3. Measurements of changes in concentration of constituents of digesta in in vitro and in vivo systems.

4. Placing solutions in emptied organs and measuring changes in concentration of constituents or changes in ratios with reference to an indigestible marker.

5. Use of radioactive constituents and determination of radioactivity decrease in the organ or activity increase in the peripheral blood.

6. Constant infusion of radioactive material into the systemic system and measurement of decreased activity after eating.

7. Killing of experimental subjects and sampling of digesta in each section of the gastrointestinal tract.

8. Cannulas placed at different sections of the gastrointestinal tract and measurement of concentration and amount of constituents in digesta leaving the cannulated organ and entering the next.

9. Use of pouches established in organs.

10. Use of arterio-venous technique.

11. Temporary isolation of organs of interest by blocking passage of digesta or use of ligatures on anesthetized animals.

These techniques have yielded information with varying degrees of success. The results obtained by those who used these techniques to study absorption and secretion in the digestive tract of animals are discussed separately according to the nutrient under investigation as follows.

Phosphorus (P)

Chandler and Cragle (26) used cerium 144 as a marker to study the net result of secretion and absorption of P in the different sections of the gastrointestinal tract of young calves. They found more P was secreted into the rumen and omasum than absorbed. There was a net absorption of P from the distal half of the small intestine to the posterior colon.

Lofgreen et al. (83) injected radioactive P into the jugular veins of calves and found that the radioactivity was higher in the contents of the rumen, omasum, abomasum and jejunum than that of the cecum, colon, and rectum, when the blood level of radioactive P was maintained high by repeated injections during a short period of time. The small intestine rapidly excreted P^{32} into the tract when calves were injected only once and killed at intervals thereafter. The concentration of the isotope increased much more slowly in the rumen, omasum and abomasum. The authors interpreted the rapid increase of radioactivity in the small intestine as an indication that this segment of the gastrointestinal tract was important in the excretion of P. In an earlier experiment, these same workers (3) fed P^{32} labeled casein to young calves. Tissue distribution of P^{32} was determined 24 hours after feeding. The results showed that the rumen, omasum, and especially the jejunum appeared to have high radioactivity and that this was due to the high phosphate exchange rates in these organs.

Smith et al. (119 and 120) used the same technique as Lofgreen et al. (83) and found that in sheep P^{32} was rapidly secreted into the rumen and omasum but very little into the small intestine. In mature cattle the main site of P^{32} secretion was in the rumen but in young calves (2 months of age) the main site of secretion was the small intestine. In calves that were fasted for 24 hours post injection the specific activity of P^{32} increased in the abomasum and small intestine. The increase in specific activity in these organs indicated that the secretion of endogenous P was continuous and that there was a slight or no dilution of the radioactivity due to food P.

Scarbrick and Ewer (112) introduced P^{32} into the rumen of sheep and in ten minutes were able to detect radioactivity in the ruminal vein. They also injected 2.8 g of P as a solution of NaH_2PO_4 and Na_2HPO_4 into the rumen contents and found an increase of inorganic P in the ruminal vein from 6.2 mg % to 24 mg % and in the carotid from 5.8 mg % to 17 mg %. Under normal conditions (no extra P fed except what was in the feed) the ruminal vein had on the average 0.24 mg P more per 100 ml plasma than the plasma in the carotid although the results were variable. Parthasarathy (100) in contrast to Scarbrick and Ewer (112) found no evidence of net absorption of P in the rumen of sheep by the arterio-venous difference technique. Parthasarathy found that phosphate was absorbed from the omasum and small intestine.

Calcium (Ca)

Smith (116) inserted cannulas into the duodenum and ileum of different calves and used polyethylene glycol as a marker. He found 86% of the Ca fed was absorbed by the time it reached the end of the small intestine. Net exchange of Ca in the large intestine was negligible.

Chandler and Cragle (26) found a net secretion of Ca in the rumen and abomasum and a net absorption in the remainder of the gastrointestinal tract of calves. Injection of Ca⁴⁵ intravenously in 21 cattle varying in age from 7 to 36 months revealed that Ca was secreted into all sections of the gut but that the major secretion of Ca took place in the small intestine (60).

Wallace et al. (143) found that the small intestine of rats played a predominant role in the excretion of Ca while the reabsorption of Ca took place in the cecum and colon. They demonstrated this by the determination of the radioactive Ca present in the different sections of the gastrointestinal tract at periods after intramuscular injection of Ca⁴⁵. Their experimental technique and results were comparable to those of Hansard et al. (60). Most in vitro experiments can be interpreted to be in contradiction to the findings of Wallace et al. (143). Schachter and Rosen (114) were able to demonstrate active transport of Ca⁴⁵, i.e., against a concentration gradient from the mucosal surface to the serosal surface of the small intestine of rabbit,

rat, and guinea pig. Calcium was determined to be more efficiently transported at the duodenal end than at the ileal end. Further work by Schachter et al. (113) and Kimberg et al. (76) both showed that Ca was transferred from the medium bathing the mucosa to the medium bathing the serosa all along the small intestine of rats. The greatest rate of transfer was at the proximal third followed by distal third and mid third in a decreasing order. They found rats fed a low Ca diet had a greater transfer rate of Ca⁴⁵.

In the study of mineral absorption and secretion, factors such as pH, ionic concentration and rate of passage are very important. Studies by Storry (124) have led him to theorize that neutralization of digesta in the lower regions of the small intestine of sheep will result in an increased proportion of Ca bound to suspended material of dietary and bacterial origin, thus reducing the amount available for absorption. This theory was supported by his findings (Storry, 123) that pH values between 7.1 and 7.5 occurred in the lower half of the small intestine of sheep fed hay and concentrates and Harrison's (62) contention that Ca is absorbed in the ionic form. Dobson and Phillipson (38) are of the opinion that the electrical potential difference between rumen contents and plasma will tend to prevent the movement of Ca from the rumen contents into the plasma if this ion moved as a freely diffusing ion because the blood is 30 millivolts positive with respect to the rumen contents.

Marcus and Lengemann (88) found that rats fed a solid diet had a slower movement of the diet out of the stomach than those fed a liquid diet. By plotting percentage absorption of the Ca fed versus time after the rats were given the diets, they concluded from the curves that absorption from a solid diet occurred at a slower rate than from a liquid diet for the first 6 hours after feeding.

There is very little information on the interaction of Ca and P with each other and with other ions. Crammer and Haqq (31) found that changes in osmolarity or sodium concentration did not alter Ca absorption rate nor the maximum absorptive capacity of the small intestine of dogs fitted with Thiry-Vella fistulas. Lueker and Lofgreen (85) conducted a trial to determine the effect of dietary Ca/P ratios on the absorption of these elements by sheep. They were able to demonstrate that the ratio 1:1, 3:1, or 6:1 had no effect on the amount of Ca or P absorbed but that the amount of absorption was related to the amount of each mineral fed. The amount of metabolic fecal P increased as P absorption increased and decreased when Ca absorption increased. Metabolic fecal Ca was found to be independent of Ca or P absorbed. In connection with this, Vermeulen (142) reported that rats fed large amounts of Ca had an increase in urinary Ca excretion and a decrease in urinary phosphate excretion. The reverse, when large amounts of P were fed. In chicks, Wasserman and Kallfelz (152) found an increase

in concentration of Ca within the lumen of the duodenum produced a greater Ca passage into and out of the plasma so that the efflux/influx ratio did not change with different concentrations. This would mean that there would not be an increase in the urinary Ca excretion which is in contrast to those results obtained by Vermeulen (142) provided the Ca excreted into the lumen was not reabsorbed in another level or section of the gastrointestinal tract.

Sodium and Potassium (Na and K)

Renkema et al. (105) alternated 2 heifers and a cow on low and high Na diets. During low Na periods, feces, fecal juice and urine were very low in Na concentration suggesting that the gut and kidney reabsorbed endogenous Na. In these low Na periods, K concentration in the feces was markedly greater than during high Na periods. This increase in K concentration during a low Na intake suggests that K compensates to maintain osmotic pressure in the fecal juice. In a study using gastrointestinal tracts of cattle obtained from slaughter houses, Van Weerden (140) found that the chyme from the upper small intestine was hypertonic and became more hypotonic toward the large intestine. He concluded that the hypertony in the small intestine was due to organic non-electrolytes while in the large intestine hypotony was due to strong selective absorption of Na against a concentration gradient.

Parthasarathy (100) previously mentioned, also found that Na and K were absorbed not only from the cecum but also from the small intestine of sheep. These two minerals were also absorbed from the rumen where Na was absorbed against a concentration gradient and K because of its high concentration. In contrast to this report, Parthasarathy and Phillipson (101) observed that Na and K were absorbed from the rumen only when their concentrations were greater than that of the blood. There was a secretion of these two minerals into the rumen when the blood concentrations were greater than the ruminal concentration. In support of Parthasarathy (100), Dobson (37) found that Na was absorbed from rumen contents against a concentration and an electrical gradient into the plasma.

Smith (116) inserted cannulas into the duodenum and ileum of different calves and used polyethylene glycol as a marker to measure the net result of digestion to the end of the abomasum and to the end of the small intestine. There was no net absorption of Na up to the end of the abomasum. Mean net absorption of Na was 40% at the end of the small intestine and almost complete at the large intestine. Eighty to ninety-five per cent of the K was absorbed at the end of the small intestine. Later Smith (118) reported that in calves the total number of equivalents of cations leaving the ileum was constant. The concentration of Na and K leaving the ileum was found to be 150 milli-equivalents per

liter when the magnesium concentration was low but when the magnesium concentration was increased, there was a linear fall in the Na and K concentrations (118).

Care and Ross (25) used sheep to study the effects of deoxycorticosterone acetate on magnesium homeostasis. Intramuscular injection of this hormone caused a greater retention of water and Na and a reduction in the positive balance of K.

Chloride (Cl^-)

Smith (116) reported that there was no net absorption of Cl^- up to the end of the abomasum based on Cl^- intake and Cl^- that came through the abomasum. Eighty to ninety-five per cent of the dietary Cl^- was absorbed at the end of the small intestine. In dogs, Annegers (2) noted that Cl^- secreted into the jejunum was more than that secreted into the ileum while the reverse was true for absorption.

Dobson and Phillipson (38) found that Cl^- was absorbed from the rumen against a concentration gradient because of the electrical potential difference between the rumen contents and the plasma. Parthasarathy and Phillipson (101) partially substantiated this when they found that Cl^- was absorbed against a concentration gradient provided the concentration in the rumen was 135 mg per ml or over. When less, Cl^- moves into the rumen from the blood.

The state of an electrical potential is dependent on the activity of the gastrointestinal tract at the time of measurement. Tidball (132) injected Bethanechol (a

parasympathetic agent that stimulates the gastrointestinal tract) in dogs and found that this drug caused secretion in the small intestine. During this process the lumen was electrically negative with respect to the serosal surface. During absorption the mucosal surface was either slightly negative with respect to the serosa or there was no difference between the two sections.

Magnesium (Mg)

Smith (117) using calves found that net Mg absorption was positively correlated with transit time of digesta through the small intestine. On the average, there was an increase of 8.5% of the Mg intake absorbed per hour of extra transit time. Care and Ross (24) found a decrease in plasma Mg concentration when sheep were started on young grass. These authors postulated that this might be due to a reduced permeability of the intestinal wall to Mg or that the concentration of Mg within the lumen was diminished. Also one might postulate that the increased rate of passage of the young grass through the gastrointestinal tract caused a decrease in absorption of Mg.

Magnesium absorption into the tissue of the guinea pig small intestine was found to be influenced by aldosterone. Ross and Care (110) found that the uptake of Mg by the guinea pig small intestine was decreased by the inclusion of aldosterone in the medium bathing the tissue. In an earlier

paper studies by Ross (109) have led to the conclusion that in rats Mg moved from the mucosal surface to the serosal surface in the small intestine, although the rate was greater in the ileum than in the lower jejunum. In a later study, Care and Ross (25) found that deoxycorticosterone acetate caused a reduction in the intestinal absorption and positive balance of Mg. Deoxycorticosterone acetate did not affect the Mg excretion in the urine.

Volatile fatty acids (VFA)

By taking rumen samples at intervals after feeding and measuring the decrease in concentration of the VFA Emery et al. (43) estimated that the VFA supplied from 3 to 13% of the cow's (total ?) energy. Conrad et al. (30) estimated rate of blood flow from the gastrosplenic vein with tagged red blood cells. From the knowledge of the amount of blood leaving the forestomachs and the concentration of acetic and propionic acids, they calculated that calves absorbed 63 and 25 g of acetic and propionic acids respectively per 24 hours from one lb of feed containing two parts alfalfa hay and one part concentrates. These two acids made up 29% of the total calories in the digested organic matter of the feed. Using data obtained from the weight of the rumen contents at various time intervals after feeding and the rate of in vitro production of VFA Stewart et al. (122) were able to show data comparable to that of Conrad et al. (30). Stewart et al. (122) fed alfalfa hay

and concentrates to steers weighing about 1500 lb and estimated that 108 g valeric, 518 g butyric, 559 g propionic, and 1743 g acetic acid were produced and that the VFA equaled 36-42% of the digested calories. The energy equivalent of the VFA was 63% of the energy for maintenance. Sutherland et al. (87) used techniques comparable to those of Stewart et al. (122) and found that VFA supplied 76% of the energy requirement for maintenance of sheep fed finely ground pelleted diets. Davis et al. (35) maintained a constant radioactivity in the blood of a 160 kg steer by infusion of radioactive acetate and measured the decrease in specific activity due to absorption of acetic acid after the steer was fed hay and concentrates. They calculated that 67 g of acetic acid were added to the blood acetate pool per hour. Presumably, a great part of the added acetate came from the gastrointestinal tract during fermentation. Badawy et al. (7) previously stated that in sheep, the omasum absorbed 18 g of VFA (as acetic acid) per day while the abomasum absorbed 4 g per day.

Gray et al. (56), Conrad et al. (29), and Johnson et al. (69) used comparable techniques to study absorption of VFA. Gray et al. (56) killed sheep at different times after feeding wheaten hay and found by the use of the lignin ratio technique that 40-69% of the VFA in the digesta of the rumen was absorbed in the omasum. Johnson et al. (69) used 4-5 months old calves and demonstrated with chromic oxide as an

indigestible marker that 51% of the VFA in the reticulum disappeared in the omasum and 83% of that in the omasum disappeared in the abomasum. They also used radioactive butyrate injected into the omasum and were able to detect radioactivity in the blood from the omasal vein. The average concentration of VFA in the omasal vein was greater than that in the carotid artery. Conrad et al. (29) demonstrated that the digesta in the abomasum had only 1 to 2% of the VFA concentration in the rumen using 5-15 months old calves that were fed two parts alfalfa hay and one part concentrate. A very strong but indirect evidence that VFA were absorbed prior to the digesta reaching the abomasum.

Barcroft et al. (11) and Flatt et al. (46) both placed solutions containing VFA into clean empty rumina and estimated the disappearance therefrom. Barcroft et al. (11) estimated that 1-5 g of VFA as acetic acid were absorbed per hour from the sheep's rumen and concluded that the rate of absorption for sodium salts of acetic, propionic and butyric acids was in the order of acetate > propionate > butyrate. The smaller the molecular weight of the acid, the faster was its disappearance from the rumen (11). Flatt et al. (46) used equimolar solutions of acetic, propionic, and butyric acids with pH adjusted to 6.2. The rumen of calves absorbed 2.66, 2.26, and 1.69 g of butyric, propionic and acetic acids respectively per hour but when absorption was expressed on a molar basis the rate was almost equal

for the three acids (46). Studies by Brown et al. (22) with perfusion of goat rumina led them to conclude that the absorption rate of VFA paralleled the respective concentrations of acids in the rumen. The proportions of VFA in the rumen digesta were the same as that in the perfusate leaving the organ (22). Tsuda (137) found a difference in the absorption rate for VFA depending on whether salts or free acids were used. The rate of absorption was fastest for acetate followed by butyrate then propionate when the acids were in the form of salts but the rates were equal when in the form of free acids (137).

In contrast to Barcroft et al. (11), results obtained by Gray (52) showed that the proportion of the weights of sodium salts of acetic, propionic and butyric acids did not change after the solution had been placed in the rumen of sheep for 6 hours. Propionic acid disappearance was increased by feeding lucerne hay immediately after the introduction of a VFA solution into an empty rumen. The solution contained 75.9% acetic, 14.6% propionic and 9.5% butyric acid by weight. In another experiment, Gray and Pilgrim (55) confirmed that the rate of absorption was propionic>butyric>acetic when sheep were fed wheaten hay and propionic>acetic>butyric when the sheep were fed lucerne hay. This conclusion was based on indirect evidence from an examination of concentration and ratios of VFA obtained from rumen digesta at intervals after feeding. The rate of VFA production besides absorption can

also influence the concentration and ratios of the VFA and should be considered in order to form a valid conclusion. Rhodes and Woods (106) presented data which may be interpreted to be in support of that obtained by Gray (52). Lambs fed different physical forms of a diet had wider acetate/propionate ratios in rumen digesta with increasing length of time after feeding (106).

When a solution of organic acids is placed in empty organs, the pH of the solution has to be well defined if comparisons were to be made among experiments. The pH of the solutions used was not mentioned by the authors in many of the articles discussed above. Danielli et al. (33) reported that at pH 7.5 only ionized fatty acids were absorbed while at pH 5.8 both ionized fatty acids and non-ionized acids were absorbed through the rumen wall of sheep. The order of absorption at alkaline pH was acetate>propionate>butyrate while at an acid pH the order was butyrate>propionate>acetate. Contrary to this report Gray (54) found that little or no absorption of VFA occurred when an alkaline solution of VFA was placed in the rumen. However, when the pH was acidic the rate of absorption of VFA was comparable to that obtained by Danielli et al. (33). A closer examination of the results obtained by Danielli et al. revealed that at alkaline pH the disappearance of VFA from the rumen was variable and the indirect measurement of the amount of VFA in the rumen could cause considerable error. Masson and

Phillipson (89) added acetic acid to rumen liquor and placed the mixture in an empty rumen and found absorption of acetic acid when the solution was either acid or alkaline, although the absorption rate was two times faster for the acidic solution. They (89) also confirmed that the absorption of acetic acid was proportional to its concentration in the rumen. The concentration of acids in the blood leaving the rumen was acetic>propionic>butyric when equimolar solutions of the acids were introduced into the empty rumen (89). Kiddle et al. (75) reported proportionately more acetic acid and less butyric were in the blood leaving the rumen than in the rumen contents. Similar findings were reported by Annison et al. (4) when they compared VFA concentrations in the portal vein blood and the rumen contents.

Studies of the absorption and concentrations of VFA in sections of the lower gastrointestinal tract have not been as thorough as those on the rumen. Ward et al. (144) reported that quantitatively the cecum or the colon had as great or greater concentrations of VFA than the rumen. Earlier, Elsdon et al. (42) had determined the concentration and total amount of VFA in different sections of the gastrointestinal tract of the ox, sheep, and horse, and found that 10-14% of the total VFA was in the lower gastrointestinal tract. McAnally and Phillipson (91) found low concentrations of VFA in blood draining the abomasum and small intestine while that draining the rumen and cecum was very high. All these findings

indicate that high concentrations of VFA are found in the cecum and large intestine of animals. These conclusions are in close agreement with those reported by Boyne et al. (20) who expressed the total VFA concentration in each gut section as a per cent of that found in the rumen of the sheep. Values for omasum, abomasum, small intestine, cecum, and colon were 67, 6, 22, 87, and 86% respectively. By the time the digesta reached the abomasum the VFA had almost completely disappeared and the concentration in the cecum and colon approached that of the rumen. The absorption of VFA from the gut was also established early by Schambye and Phillipson (115) when they found a greater concentration of VFA in the portal blood than in the carotid blood. Annison (3) in an attempt to find other organic acids in the rumen digesta came to the conclusion that acids having a carbon chain greater than six are not normally present; however, 2-methylbutyric acid was found when sheep were fed a diet rich in casein. Also isobutyric and isovaleric were present in the rumen when sheep were fed various diets. The sources of the branched-chain organic acids were probably amino acids. Phillipson (103) found an abnormally large quantity of lactic acid and a decrease of the acetic to propionic ratio in the ruminal digesta of sheep fed a flaked maize diet. The above references indicate that VFA were absorbed from the rumen and other organs of the gut but on the other hand, lactic acid was probably metabolized before having a chance to be absorbed.

According to Phillipson (102) sheep fed certain roughages and concentrates temporarily accumulated lactic acid in the rumen for 3-4 hours after eating. This was confirmed in a subsequent experiment by Phillipson and McAnally (104) who introduced sodium lactate into the rumen of sheep and found that it disappeared in 2-4 1/2 hours. To substantiate this, they found that lactate was converted to VFA in an in vitro fermentation and also that the concentration of lactic acid in the abomasum was greater than that of the rumen. Ward et al. (144) made similar findings. Lactic acid was found in substantial amount in all sections of the gut of Hereford steers except the rumen (144).

Water (H₂O)

The quantitative measurement of H₂O absorption and secretion along the gastrointestinal tract has been relatively easier, because H₂O determination in samples does not require complicated chemical procedures and yet there are very few reports that have measured H₂O balance throughout the gastrointestinal tract.

Ridges and Singleton (107) established cannulas 2 inches below the pylorus of goats and measured the rate of digesta flow. Their results showed that 12-15 liters of fluid were added per day into the forestomachs. Hogan and Phillipson (65) estimated that the H₂O secreted into the forestomachs of sheep was three liters per 12 hours which is about half the volume estimated by Ridges and Singleton

for goats. Hogan and Phillipson also found that between the duodenum and the terminal ileum there was a decrease of H₂O flow from 4300 ml to 2400 ml per 12 hours or a net absorption of four liters per day. The large intestine absorbed most of the H₂O out of the digesta from the terminal ileum (65).

Another organ that absorbs H₂O is the omasum. Gray et al. (56) found that 35-64% of the H₂O in the digesta of the rumen was absorbed in the omasum of sheep while Badawy et al. (6, 7, and 8) reported this value as 48-55%. Badawy et al. also reported that the increase in water content in the abomasum was 123-197% over that in the omasum.

Major Nutrients

The extent of digestibility of the proximate constituents of feeds along the gastrointestinal tract of ruminants has not been thoroughly investigated and the major portion of the published articles are by scientists from the British Kingdom.

Hale et al. (57, 58, and 59) in a series of experiments used fistulated cows to determine partial digestion of roughages in the rumen by the use of the lignin ratio technique. When 10, 20, or 30 lb of hay were fed, the digestibility of dry matter in the rumen was 46.7, 48.7, and 45.7% while total dry matter digestibility from a total collection trial was 46.9, 55.8, and 56.3% respectively. Thus the rumen accounted for 99.5, 87.3, and 84.4% of the total dry matter digested

in the case of 10, 20, and 30 lb of hay intake, respectively. Also a mean of 66% of the total crude fiber digested was accounted for by the rumen. Periodic emptying of the rumen and sampling of the contents indicated that the soluble portions of the diet were rapidly digested during the first 6 hours after feeding and that the greatest proportion of digestion of cellulose took place during the second 6 hours, when cows were fed mainly beet pulp and alfalfa hay (58 and 59). A ceiling for digestion of dry matter in the rumen was reached after the twelfth hour. Disappearance from the rumen accounted for the following per cent of the feed: dry matter 48%, protein 60%, nitrogen-free extract 65%, crude fiber 27%, cellulose 43%, and carbohydrates 83%. In this connection Weller et al. (154) using the lignin ratio technique concluded that digesta reaching the omasum was "well digested" which agreed with the conclusion of Hale et al. (58 and 59). In an earlier experiment, Weller and Gray (153) estimated the disappearance of starch in the reticulo-rumen and omasum of sheep by measuring the amount passing the abomasum of sheep. When 148 g of starch were fed only 5% of that fed passed the abomasum, but when 20-40 g were fed 10% passed the abomasum (153). The importance of the rumen in digestion processes was again stressed by Gray (53) who found that the rumen digested 70% of the cellulose fed while the cecum and colon digested the remainder based on the lignin ratio technique.

Balch (9) obtained results comparable to those of Hale et al. (58 and 59) by sampling near the reticulo-omasal orifice at frequent intervals and found that 26-62% of the digestion of dry matter fed was done in the rumen and 12-34% in the hind gut. McGilliard (93) found the disappearance of dry matter in the hind gut of cattle to be 25-48% of the amount fed. Campling et al. (23) in a study to evaluate the factors affecting voluntary intake used similarly obtained samples (9) and the lignin ratio technique to show that the reticulo-rumen accounted for 65% and 59% of the total digestible crude fiber in grass hay and straw respectively. In both hay and straw-fed cows there was a negative digestibility of crude protein in the rumen.

Ridges and Singleton (107) calculated that 85-100% of the crude fiber and 11% of the nitrogen fed were lost in the fore-stomachs based on the rate of flow determined by cannulas established 2 inches below the pylorus of goats. The goats were fed hay and concentrates.

Earlier, Kameoka and Morimoto (71) used the same techniques as Ridges and Singleton (107) but the cannulas were placed between the omasum and abomasum in 3 goats weighing 21 to 30 kg each. The goats were fed hay and different concentrates. The stomachs excluding the abomasum digested 93 to 105% of the crude fiber, 66 to 97% of the nitrogen-free extract, and 72 to 85% of the organic matter when expressed as a percentage of the total digestion calculated from total digestion trials.

Hogan and Phillipson (65) established re-entrant cannulas at the duodenum and ileum of different sheep and found that 70% of the dry matter and 36% of the nitrogen fed in the form of hay and concentrates disappeared in the four stomachs and the remainder in the small intestine. The large intestine apparently did not further absorb the dry matter and nitrogen coming from the small intestine.

Harris and Phillipson (61) fed chopped hay to sheep fitted with cannulas immediately posterior to the abomasum. In this trial 50% of the consumed organic matter disappeared in the forestomachs and more nitrogen and ash left the abomasum than were given in the food. These results are in contrast to those obtained earlier at the same station by Hogan and Phillipson (65) but are in close agreement with those obtained by McGilliard (93) who found that 23-55% of the dry matter fed disappeared in the forestomachs and that more ether extractable material, ash and nitrogen left the abomasum than were fed.

Three sheep fed three different diets were killed 16 hours after their last feeding by Rogerson (108). Soluble ash expressed as a per cent of the dry matter in respective sections of the gut indicated that in 2 out of 3 cases the concentration was higher in the omasum and abomasum than in the feed which suggests that these two organs secrete more than they absorb.

Badawy et al. (6, 7, and 8) published a series of three articles on experiments involving sheep killed four

hours after a feeding of concentrates and hay. Total nitrogen expressed as a ratio to lignin was the same in the rumen and omasum; a sharp rise of the ratio was noted for the proximal half of the small intestine followed by a sharp decrease in the lower small intestine and cecum. There was no further change in the colon. Ash content was higher in the abomasum than the omasum suggesting absorption of minerals in the omasum and/or secretion of large amount of minerals in the abomasum.

Boyne et al. (20) found that the rumen of sheep contained 75% of the total dry matter in the whole tract immediately after a meal but contained only 60% 12 hours after feeding. These values are close to those reported for sheep killed after a 16-hour fast by Rogerson (108) and Badawy et al. (7) previously cited. Rogerson (108) found that the rumen and reticulum contained 58, 60, and 73% of the dry matter in the whole gastrointestinal tract when the sheep were fed all grass hay, grass hay plus casava meal and all corn grain diets respectively.

Summary

Quantitation of absorption and secretion in sections of the gastrointestinal tract of animals is more difficult than quantitation of total digestion. New methods are constantly being devised to estimate digestion in the various sections of the gastrointestinal tract of ruminant which may indicate that nutritionists are not satisfied with the methods used in the past.

Both influx and efflux of calcium, phosphorus, sodium, and potassium appear to occur throughout the gastrointestinal tract of animals. Apparently absorption must be greater than secretion in some sections of the tract if the animals were to grow normally. More phosphorus and calcium are secreted into the rumen than absorbed while the reverse is true for potassium, sodium, and chloride. Sodium and chloride have been found to be absorbed from the rumen against a concentration gradient of the blood.

In general, very little is known concerning the function of the omasum in regulating mineral balance. Radioactivity has been detected in the omasal digesta when either radioactive phosphorus or calcium was injected intravenously.

Cannulas established a few inches posterior to the abomasum showed that there was no net absorption of sodium or chloride compared to that ingested but there was a net absorption of phosphorus and calcium as estimated by marker ratio technique.

The rate of transfer in and out of the proximal sections is faster than the distal sections of the small intestine for chloride, magnesium, and calcium. In young cattle the main site of endogenous source of calcium and phosphorus seems to be the small intestine as interpreted from results obtained by tracer and marker ratio techniques.

Phosphorus, calcium, sodium, and potassium are absorbed more than secreted by the large intestine.

Several factors have been implicated to influence the rate of absorption and secretion of minerals in various sections of the gastrointestinal tract and should be considered in future experimentations. These factors are pH, ionic strength, possible interactions among minerals and rate of passage of the digesta and electrical gradient in the blood and digesta.

The production and absorption of volatile fatty acids in the rumen have been known for a long time. From 40 to 70% of the volatile fatty acids in the ruminal digesta are absorbed in the omasum. Further absorption occurs in the abomasum so that digesta in this organ and in the small intestine contain only a small quantity of volatile fatty acids. The concentration of volatile fatty acids in the large intestine is at least as high as that in the rumen. Ten to fourteen per cent of the total volatile fatty acids has been found in the lower tract.

In goats and sheep 6-15 liters of water have been reported to be added into the forestomachs. A great portion of the secreted water is reabsorbed in the small intestine. Further absorption of water occurs in the large intestine. Another organ that has been found to absorb water is the omasum. The omasum absorbs 35-64% of water from the ruminal digesta.

In general, the rumen can account for 70-100% of the dry matter digested or from 23 to 62% of the dry matter fed.

For crude fiber, the rumen can account for 59-65% of that digested. Posterior to the forestomachs, values for dry matter digestion ranged from 12 to 48% of that fed.

Characteristics of the Alimentary Tract

The study of the development of the visceral organs is not only an interesting field by itself but is also very important in the economics of animal production. In the dairy industry considerable amount of our present work is directed toward the study of the ruminant stomach--its volume, weight of tissue and other physical and microscopic characteristics. An important item in this respect is the dressing percentage which is usually less with dairy than with beef animals. The study of the development of the alimentary tract and dressing percentage of dairy animals assumes economic importance since an increasing number of dairy animals are being raised or sold for beef. The effects of diets on the physical characteristics of the forestomachs have been extensively studied (47, 49, 111, 150, 151, and 155).

Warner et al. (150 and 151) in two different experiments killed calves at various ages under several feeding regimes. Results obtained indicated that the rumen volume measured under a certain set of conditions was greatest for calves fed hay but the air dry rumen tissue did not differ significantly between calves fed a calf starter or hay. The tissue weight and the volume of the rumen were least for calves maintained on milk alone. Wing and Ammerman (155)

arrived at the same conclusion when calves were fed for long periods of time on milk and mineral supplements. They found that calves fed milk and minerals did not have normal papilla in their rumen when slaughtered at 9-11 months of age.

These observations have both been confirmed and disproved in other ways by the same group of workers as well as others. Flatt et al. (47) introduced purified materials into the rumen by way of an established fistula and concluded that the most important stimulus for the papilla development of the rumen was the end products of fermentation rather than the presence of coarse material. Sander et al. (111) placed acetic, propionic and butyric acids, sodium chloride, or glucose in the rumen of young calves and found that only propionic and butyric acids caused marked papillary development in the rumen. Tamate et al. (127) introduced butyric acid by means of stomach tube to milk-fed calves and observed increased papillary development over those fed milk only which is in agreement to the data reported by Sander et al. (111). Gilliland et al. (49) showed that a calf starter containing 10% by weight of a VFA mixtures did not influence rumen development when the criteria used were weight of stomach compartments and percentage of ruminal mucosa. Five out of eight calves fed the starter containing VFA had ruminal parakeratosis as compared to one out of eight calves receiving the same starter but without added VFA (49).

Wardrop's publications (146 and 147) on the normal histological changes of the forestomach tissues of lambs at

different ages demonstrated that the histological structures of the rumen papilla of milk fed lambs were normal but less developed than those lambs fed lucerne chafe.

Lambs killed by Wardrop and Combe (148) at intervals of 2 weeks from birth until they were 16 weeks old and pastured on rye grass plus subterranean clover had 4.8, 6.5, and 6.3% of their live weight as empty gastrointestinal tract at 0, 3, 8, and 16 weeks of age respectively. Wardrop and Combe (149) found that the weight and volume of the contents of the forestomachs of the lambs just mentioned increased with age of the lambs. The weight of the rumen contents as a percentage of the live weight increased for the first 8 weeks and then remained constant at 6.8% while abomasal contents remained relatively constant with age. The ratios obtained by dividing the volume of the rumen contents by the volume of the abomasal contents increased from less than 1.0 at 0 weeks of age up to 8.8 at 8 weeks of age. A closer examination of their data revealed that the ratio from 8 weeks on was not a constant.

Godfrey (50 and 51) did exactly the same type of experiments using calves instead of lambs and reported results that were in close agreement with those of Wardrop and Combe (147 and 148). Furthermore, a much earlier paper by Kesler et al. (74) reported that correlations were highly significant between body weight and weight of rumen tissue or weight of rumen contents and between body weight gain and

weight of rumen contents.

Palsson and Vergés (99) using lambs from different planes of nutrition at a predetermined body weight found a greater dressing percentage for those lambs on the low plane of nutrition and least for those on the high plane of nutrition. Also, Wardrop (145) concluded that the growth rates of the forestomachs of lambs were influenced both by planes of nutrition and types of diet. Blaxter et al. (16) found that the omasum of a calf fed milk and hay was 10.8 times greater in volume compared to another fed only milk.

Phosphorus Requirement of Calves

A considerable amount of effort has been spent to determine the phosphorus requirement of farm animals but the calf from birth to 6 months old has received little attention.

Lofgreen et al. (81) found with the use of two very young calves that the endogenous fecal P was 4.3 and 4.2 mg per kg of body weight. A calf weighing 100 lb would, therefore, need only approximately 0.2 g P per day for maintenance which is a very low requirement value. The National Research Council, 1958 (98) considers six g of P daily for a 100 lb calf as the total requirement for normal growth plus maintenance and a margin of safety.

Tillman et al. (136) fed P at the levels of 1.5, 2.0, and 2.5 g per 100 lb body weight daily regardless of the amount of feed consumed by Hereford steers averaging 350 lb live weight. When response criteria were weight gains, feed

consumption, efficiency of feed utilization, percentage digestibility of P or percentage net retention of P, then 2.0 g P per 100 lb body weight did not meet the P requirement of these animals but 2 g were enough when the response criteria were autoradiographs of bone or plasma inorganic P level.

Wise et al. (157) used calves weighing between 200 and 275 lb and ages between 12 and 18 weeks and found that the minimum requirement was 0.22% of the air-dried ration. The criteria used were performance of the calves plus blood and bone data. Mitchell (94) calculated that 150 lb Holstein heifers required 0.52% P (dry matter basis) in their diet for maintenance, growth, activity, and mineral utilization. These values are much higher than those obtained by other investigators reported in this review. Archibald and Bennett (5) reported that 6-month old heifers gained equally well on rations containing 0.18 or 0.31% P. In contrast Jones et al. (70) using 8-month old heifers found that increasing the amount of P in the rations from 0.26 to 0.36% increased the growth rate of the heifers. According to Huffman et al. (67) heifers fed a 0.20% P diet had lower body weight gain and feed consumption when compared to another group of heifers fed a 0.4% P diet from 3 months until 8 months of age. The respective average amounts of P consumed from the two diets were 7.9 and 15.3 g per animal daily. Theiler et al. (129) reported that 3-6 months were required to produce

symptoms of deficiency when 12-18 months old cattle were fed 2.23 g of P daily. When comparable animals were fed 5 g P daily the weight gain was improved over those fed only 2.23 g daily. Increasing to 13 g daily further increased weight gain. Van Landingham et al. (138) reported that normal blood P level and body weight gains were maintained when the P consumption of heifers increased from 8.7 to 13.1 g per animal per day from one to 24 months of age. Calculated on a unit of body weight the P consumption was 3.1 to 1.1 g per 100 lb of live body weight over the same period of time.

As can be seen in the discussions above estimates of P requirement for young calves have been few and contradictory. The lack of agreement among estimates for P requirement is not surprising because of the complexity involved in the measurements. Some of the major factors which may cause disagreement in estimates for P requirement are as follows:

Response Criteria

Some of the response criteria used by various investigators to study P requirement have been:

- A. Animal performance: (1) feed intake; (2) efficiency of feed utilization; (3) body weight gain; and (4) height at withers.
- B. Bone characteristics: (1) ash, P and Ca content of bones; (2) bone growth as measured by

autoradiographs and epiphyseal cartilage width;
(c) breaking strength of bone; and (4) density
of bone.

C. Blood studies: (1) serum inorganic P concentra-
tion; and (2) serum alkaline phosphatase activity.

D. Balance studies: (1) apparent total digestibility
and (2) percentage net P retention.

The sensitivity of detecting changes in the various
criteria used to evaluate the P status of the animals often
depends on the length of the experimental period. Serum in-
organic P and bone growth as measured by autoradiographs are
two criteria that exhibited changes earlier than ash and P
content of bone according to Wise et al. (158).

Tillman et al. (136) concluded that the amount of P
required for maximum weight gain and feed intake was greater
than for bone growth or maintenance of plasma inorganic P
level. In this case, and many other similar reports the
criteria used to determine requirement have been important.
Wise et al. (157) found that the measurements of height at
withers, weight of entire ninth rib, and per cent of P in
rib (costal ends of ribs) were insensitive to changes of P-
level in the diets of calves. Combs (27) found that femor
bone ash (entire femor?) was the most precise criterion for
evaluating dietary P status in pigs while P content of bone
ash and ash or P content in soft cartilaginous tissue from
tail and ear were relatively insensitive to P levels in the
diets.

Availability of Phosphorus (P)

One of the most important reasons for the lack of agreement among the estimates made by various workers for the P requirement for cattle can probably be directly attributed to the different biological availabilities of the sources of P used.

Lofgreen (80) found that the true digestibility of dicalcium phosphate, bone meal, soft phosphate, and calcium phytate was 50, 46, 14, and 33% respectively. Wise et al. (158) reported that dicalcium phosphate was slightly more utilizable than defluorinated rock phosphate or Curacao Island phosphate while soft phosphate or colloidal clay phosphate was very poorly utilized by calves.

Tillman and Brethour (135) compared the availability of phytin phosphate and monocalcium phosphate. They found that sheep utilized the P from both sources to the same degree. In another report Tillman and Brethour (134) found that the availability of P from phosphoric acid was of the same order of magnitude as that of dicalcium phosphate.

Calcium: Phosphorus Ratio

Although the influence of dietary Ca/P ratios on the estimates of P requirement is not as important as the other two factors already mentioned the ratio nevertheless should be considered in experiments involving P utilization and/or requirement.

Wise et al. (156) used calcium carbonate, defluorinated rock phosphate and dibasic sodium phosphate to adjust the Ca/P ratios from 0.4:1 to 14.3:1 and found that the performance of Hereford calves was influenced by dietary Ca/P ratio. The average total weight gain and feed efficiency were markedly decreased with Ca/P ratios lower than 1:1. Ratios between 1:1 and 7:1 gave similar and satisfactory results. Ratios above 7:1 were adverse but not as bad as when the ratios were lower than 1:1. Gallup and Briggs (48) found that Ca/P ratios from 0.7:1 to 5.6:1 were not important in affecting P balances but that the total amount of P expressed as grams supplied daily per 100 lb live weight was the main factor in determining the P balance in sheep.

Appetite of Calves

The author will not review the subject of appetite in its entirety. The different theories concerning appetite were covered in detail recently by Veltman (141) and reviews by Anand (1), Balch and Campling (10) and Mäkela (86). The subject has many facets and theories but in this case only the P content of the diet as related to appetite will be discussed.

According to Eckles et al. (40), Huffman (66), Huffman et al. (67), van Landingham et al. (138), Theiler et al. (128) and Becker et al. (14) cattle fed rations deficient in P may develop anorexia and depraved appetite, i.e., the eating of wood, bone, hair, etc. Maynard and Loosli (90) in their text-book show a calf chewing wood because of P deficiency. Kleiber et al. (77) reported that P deficiency resulted in a

severe emaciation of the animals. The loss in weight was attributed mainly to a loss in appetite and thus less food consumption. Eckles et al. (41) and Malan et al. (87) reported similar findings. Crampton et al. (32) found that the voluntary intake of forages by animals was related to the forage content of P.

Wise et al. (157) in two experiments found that as P levels in the diets increased the consumption of the diets also increased. In the first experiment calves consumed 0.9 and 1.2 lb per day more during a six week period when the rations contained 0.18 and 0.30% P respectively than when the rations contained only 0.09 or 0.12%. In a second trial, the average feed intake of calves fed 0.22, 0.30, and 0.38% of P was very similar but 0.6 lb per day more than those fed a 0.14% P ration during a six week period. Tillman et al. (136) found that steers fed 1.5, 2.0, and 2.5 g of P daily per 100 lb body weight consumed different amounts of feed in a cyclic pattern. When the P intake was calculated as a percentage of the rations the 3 levels were 0.14, 0.17, and 0.20% and the feed consumption cycles were respectively 10-12, 8-9, and 6-7 days in duration. The cycles were described (133) as a series of arcs joined end to end with the series ascending as the cattle increased in body weight when feed intake was graphed on the ordinate and P intake per unit body weight on the abscissa weight. Within each cycle or arc of the series the feed consumption increased at first and then

plateaued. Each cycle lasted a certain length of time depending on the amount of P fed. The greater the level of P in the food the shorter the length of each cycle indicating that feed consumption was directly related to the amount of P fed. Another earlier experiment completed by Long et al. (84) showed that feed intake increased linearly with increased amounts of supplemental P in the ration over the range 0.07, 0.11, and 0.15% of total P. No further increase in feed consumption was observed when the total P in the ration was 0.19%.

Data on the effect of dietary P on the appetite of laboratory animals are completely lacking; a recent experiment by Jenkins and Phillips (68) showed that food consumption decreased within 2-3 and 4-8 days in dogs following the feeding of diets containing 0.17 and 0.23% P respectively.

Summary

The amount of feed consumed by farm animals has been found to be related to the phosphorus content of the diet when the phosphorus content was 0.19% or less. However, when diets containing 0.20% or more phosphorus were consumed, the feed intake did not vary appreciably. Prolonged phosphorus deficiency has been repeatedly reported to cause depraved appetite in animals.

Specific information on the phosphorus requirements for calves between birth and six months of age was not available. In general diets containing 0.2 to 0.3% phosphorus

were inadequate while those containing 0.3% or more were adequate for normal body weight gain of young dairy animals.

CHAPTER III

EXPERIMENTAL PROCEDURES

General Plan

In two separate trials, rations containing large and small amounts of fiber were fed to male Holstein calves from 3 days of age to about 13 weeks of age. In Trial I, 6 and 5 calves were fed the rations containing the small and large amounts of fiber respectively. Tables 1 and 2 show respectively, the ingredients and chemical composition of the two rations. In addition to this ration treatment the calves in each ration were divided into three groups and an attempt was made to feed 1.8, 2.3, or 3.0 g of phosphorus per 100 lb of live body weight per day respectively, starting on the 5th and continuing to the 13th week of the experiment. The quantity of P needed was supplied in the form of CaHPO_4 and given by means of capsules and a bolting gun whenever the amount was not met by the ration. In an attempt to equalize the Ca/P ratio at the 3 levels of P feeding, sufficient CaCO_3 was added to the capsules so that the ratio was near 2.77: 1.0. The amounts of P and Ca supplied via capsules were increased according to weekly body weights and decreased by the amounts of P and Ca supplied in the rations consumed by the calves the previous week.

TABLE 1.--The composition of the basic rations fed ad libitum to calves for 12 weeks, Trials I and II

Ingredients	Trial			
	I		II	
	Fiber Contents of Rations			
	Low (% of rations on an as fed basis)	High	Low	High
Degermed corn meal	53.0	--	--	--
Soybean flake	--	50.0	5.0	10.0
Ground alfalfa hay	14.0	15.0	--	--
Soybean meal (50%)	12.0	9.0	--	--
Blood meal	5.6	8.0	20.0	16.0
Solka floc	--	--	--	12.0
Ground corn cobs	--	--	10.0	10.0
Corn starch	8.4	5.0	59.0	40.0
Molasses	5.0	5.0	5.0	5.0
Tallow	--	6.0	--	5.0
Urea (42%)	1.0	1.0	--	1.0
Salt (T.M.)	1.0	1.0	1.0	1.0
Vit.-Antibiotic mix	a	a	a	a
Mineral	b	b	c	c

^aEnough to supply 8000 I.U. vit. A., 500 I.U. vit. D₃, and 25 mg chlortetracycline per lb ration.

^bExtra phosphorus was supplemented so that the supplement and the feed^c phosphorus totaled 1.8, 2.3, and 3.0 g per 100 lb of live body weight daily. The phosphorus supplement was CaHPO₄. Extra CaCO₃ was included so that Ca/P ratio was approximately 2.77:1.

^cCaHPO₄ and CaCO₃ were added to each basic ration in order to have 4 levels³ of phosphorus and a Ca/P ratio near 2.77:1.

TABLE 2.--The chemical constituents of the rations fed ad libitum to calves for 12 weeks, Trials I and II

	Trial I				Trial II			
	Low	High	Low	High	Low	High	Low	High
Fiber Contents of Rations								
d	d	1	2	3	4	Phosphorus Levels in Rationse		
		(% expressed on a dry matter basis)						
Crude fiber	6.5	26.6	5.4	16.0	5.4	16.0	5.4	16.0
Crude protein	22.6	22.5	18.6	17.6	18.6	17.6	18.6	17.6
Ether extract	0.9	7.5	0.9	6.2	0.9	6.2	0.9	6.2
N-free extract	65.8	37.8	66.3	53.4	66.3	53.4	66.3	53.4
Acid detergent fiber ^a	10.20	32.50	8.60	17.60	7.61	19.82	8.86	20.09
Acid detergent lignin ^b	2.36	4.05	0.97	0.99	1.12	1.15	1.06	0.97
Estimated TDN ^c	72.20	70.30	73.4	66.9	73.4	66.9	73.4	66.9
Ash	4.30	5.60	4.21	4.61	4.61	4.16	4.51	4.21
Ca	0.345	0.544	0.502	0.392	0.565	0.509	0.660	0.653
P	0.290	0.243	0.137	0.133	0.195	0.197	0.202	0.241
K ^c	0.945	0.889	0.700	0.620	0.700	0.620	0.700	0.620
Na ^c	0.546	0.546	0.492	0.474	0.492	0.474	0.492	0.474

^aDetermined according to the method of Van Soest (139).

^bDetermined according to the method of Van Soest (139) and used for the calculation of absorption and secretion of other nutrients by the ratio technique.

^cEstimated from Tables I and IV in Morrison's Feeds and Feeding (96).

^dPhosphorus supplied in the form of CaHPO₄ so that the total phosphorus consumed daily totaled 1.8, 2.3, and 3.0 g per 100 lb live weight.

ePhosphorus levels 1, 2, 3, and 4 were supplied as a percentage of the rations fed to the calves.

Since in Trial I no significant differences were found in the criteria used to measure adequacy of P and in most instances the calves consumed enough or exceeded the amount of predetermined P desired from their rations, a second trial was initiated. In Trial II, 24 calves were randomly assigned to one of eight dietary treatments consisting of low-fiber ration and high-fiber ration each with 4 levels of P. The P levels in the rations were made up by the addition of CaHPO_4 at the time the rations were made. CaCO_3 was also added to make the Ca/P ratio the same as in Trial I. The ingredients and chemical composition of the rations used in Trial II are shown in Tables 1 and 2 respectively.

In both trials the rations were fed ad libitum. Records of feed consumption were kept. In addition, all calves were fed milk obtained from the University Holstein herd at the rate of 8% of the initial birthweight until they were 30 days of age. The allotted daily milk was given in two equal portions at 7:00 A.M. and 4:00 P.M. Water was available at all times.

The calves were weighed as they became available at 3 days of age and at weekly intervals thereafter. All calves were placed in individual stalls and bedded with wood shavings.

The calves were bled once, two days after the withdrawal of milk and twice during the 12th and the 13th week of the experiment. The blood obtained was allowed to clot

and the serum frozen for future analyses. An aliquote of the serum obtained in Trail II was analyzed for alkaline phosphatase activity immediately upon the removal of the clot by centrifugation.

For one week following the twelve weeks of growth study, the calves in Trial I were allowed only enough rations so that there would be no feed refusal or weighback. This was done in order to obtain a constant intake before slaughtering. Each calf received 2 g of Cr_2O_3 everyday during this week in two equal portions at 8:00 A.M. and 5:00 P.M. In Trial II the calves were continued on ad libitum intake; they were fitted at this time with plastic bags similar to those described by Noller et al. (97) for total collection of feces. The daily feces were collected from most calves for 3-4 days but only 1-2 days from a few calves. The calves in Trial II were also induced to defecate by passing rubber tubing into their rectum. The fresh feces obtained were immediately mixed with an equal volume of 50% H_2SO_4 and preserved for determinations of volatile fatty acids and lactic acid. The H_2SO_4 solution was used to extract the organic acids from the feces and stop the microbial activity in the feces. The mixture of H_2SO_4 and feces was placed in a refrigerator for at least 48 hours and then the solids in the mixture removed by centrifugation. The supernatant was saved for future analyses of organic acids.

Following the fecal collection period for Trial II and one week of reduced but steady intake in Trial I all calves

were fasted for about 16 hours, reweighed and then slaughtered. The weights obtained prior to and immediately after the fast were used to determine the effect of low- and high-fiber rations on the shrinkage of the calves. During the fast, water was available at all times. The calves were killed at the end of the 16-hour fast by first stunning with a blow on the head and bled immediately by severing the jugular vein. A mid-ventral incision was made to allow tying of the esophagus just before it entered the rumen. Another ligature was made at the rectum near the anal orifice just prior to the removal of the whole digestive tract from the abdominal cavity. The digestive tract was separated into reticulo-rumen, omasum, abomasum, upper and lower small intestine, large intestine and cecum. In order to prevent movement of digesta within the small intestine, ligatures were placed at short intervals on the small intestine before separating it from the omentum and dividing into 2 equal portions. The digesta in each organ were removed quantitatively then weighed, mixed and a sample taken immediately for pH determination using a Beckman Model G pH meter and glass electrode assembly. Another sample was placed in a jar and brought to the laboratory of which a portion was used for dry matter determination and the dry digesta saved for analyses of Ca, P, K, Na, and ash. Another portion of the fresh digesta was weighed and placed in a known volume of a 50% H_2SO_4 solution for organic acids analysis. The rest of

the sample was placed in a deep freeze until all calves were killed. The frozen samples were thawed and Van Soest detergent fiber and lignin determined. The digesta from the omasum of the calves in Trial I were not saved for any chemical analysis and the percentage of dry matter was estimated by visual comparison with digesta obtained from other organs.

The water holding capacity of the rumen was determined by measuring the weight of water held in the organ under 40 mm of water pressure with the organ half way submerged in H₂O. This was done in order to determine if the high-fiber ration had any effect on rumen volume. Also, in Trial II the weight of each organ was determined after the digesta were removed, while in Trial I the mucosa in the rumen was completely separated from the muscle layers. The dry weight of the mucosa was determined.

The weight of the carcass (head and legs removed) with the hide on was used for the calculation of dressing percentage. The entire left 9th and 10th ribs were removed and the distal 10% used for analysis. These distal ends were dried, extracted with ethanol followed by petroleum ether and the dry-fat-free bone used for ash analysis.

Technique Used in the Measurements of Absorption and Secretion of Nutrients

The indicator method of determining digestibility was adopted to measure absorption and/or secretion of nutrients

along the gastrointestinal tract of calves. The following equation, $\% \text{ digestibility} = (100 - \frac{\% \text{ indicator in feed}}{\% \text{ indicator in feces}} \times \frac{\% \text{ nutrient in feces}}{\% \text{ nutrient in feed}} \times 100)$, as given on page 303 of the textbook by Maynard and Loosli (90) was used.

The indicators used in Trial I were lignin and chromic oxide (Cr_2O_3) and in Trial II lignin. In order to measure the degree of absorption and secretion in the different sections of the gastrointestinal tract as the digesta moved posteriorly, two consecutive sections of the tract were used in relation to the above equation. The digesta in a given organ was considered to be the feed for the next posterior organ. The digesta in the second organ would be equivalent to the feces for the calculation using the ratio technique equation. The digesta in the second organ would also be the feed for the next posterior or third organ. Using two consecutive organs in relation to the above equation the degree of digestion in the following alimentary sections was calculated:

1. rumen--using feed as fed and rumen digesta as feces;
2. omasum--using rumen digesta as the feed and omasal digesta as the feces;
3. abomasum--using omasal digesta as the feed and abomasal digesta as the feces, and so on for;
4. upper small intestine;
5. lower small intestine;

6. large intestine;
7. cecum, and
8. rectum--using the digesta in the large intestine as the feed and the feces voided as the feces.

In Trial II because fecal samples were available from total collection of feces, two methods were used to calculate total digestibility, i.e., total collection method and lignin ratio technique. In Trial I the digesta in the large intestine were used as feces and compared to the feed consumed in order to calculate total digestibility. This approximation was justifiable because between the time the digesta were in the large intestine and the time the digesta were voided as feces the degree of digestion was minor as will be shown later in the results. Also since in Trial I, the digesta in the omasum were not sampled, the digestion in the abomasum was calculated by using rumen digesta as the feed and the abomasal digesta as the feces. This calculation is not absolutely proper because the digesta from the rumen pass through the omasum before entering the abomasum. Nevertheless a comparison between the rumen and the abomasum relative to a marker will be indicative of the total digestion of the ruminal digesta in the omasum plus the abomasum.

Chemical Methods

Calcium and ash.--Calcium in blood serum, rations, digesta, and feces was determined by the method of Mori (95).

This method is a complexometric titration using 1, 2-diaminocyclohexane - N, N, N¹, N¹ - tetraacetic acid (CDTA, Chenta Complexone IV, Geiger Pharmaceuticals, Basel). The end point is a change in color of the Calcein indicator from a green fluorescence to a dull blue color when viewed with light from an incandescent lamp. The blood serum protein was precipitated with a 10% trichloroacetic acid solution and the precipitate removed by filtering with Whatman No. 2 filter papers. The protein-free serum filtrate was then used for Ca analysis.

The organic matter in the rations, digesta, and feces was removed by ashing the dry digesta at a temperature of 500-550° C for 6 hours and this weight used for calculating ash content. The ash was then dissolved in concentrated HNO₃ and distilled water to wash down adhering ash on the sides of the crucibles. The crucibles were then heated on a hot plate until the solution boiled for a few minutes. The ash in HNO₃ solution was quantitatively filtered through a low ash Whatman No. 42 filter paper and made to a known volume. This final clear solution was used for Ca analysis.

Phosphorus--Blood serum, digesta, rations, and feces were analyzed for P by the method of Fiske and SubbaRow (45) as outlined by Hawk et al. (63) using the same solutions that were described for the analysis of Ca.

Blood Serum Alkaline Phosphatase.--Blood serum alkaline phosphatase was determined by the method of Bodanski (18) as

outlined by Hawk et al. (63).

Sodium and Potassium.--Sodium analyses were performed on the rations, digesta, and fecal solutions and K analyses on the ration and fecal solutions obtained in Trial II only. These two minerals were determined by the flame photometric method using a Beckman Model DU spectrophotometer with flame attachment. The procedures followed were those recommended by Beckman Instrument Manual No. 334-A (15). Attempts were made to estimate the K and Na concentrations in the digesta solutions used for VFA analyses by the Beckman cationic and sodium electrodes (Beckman No. 39047 and 39278), and a voltmeter (Keithley 600A Electrometer). The results were not repeatable probably due to interference from protein and other substances present in the solutions and the results are not included in this manuscript.

Volatile Fatty Acids.--Acetic, propionic, and butyric acids in the digesta and fecal extracts were determined by gas chromatography using an Aerograph Model 600. The carrier gas was nitrogen supplied by a compressed tank at the rate of 35 ml per minute. The fuel was hydrogen supplied by an Aerograph hydrogen generator Model 650 at the rate of 25 ml per minute. A five-foot commercial column packed with 15% versamid 900 5% iso-phthalic acid on 60/80 Chromosorb W with a diameter of 1/8 inch was used. The signal from the hydrogen detector gold plated head was picked up and recorded continuously by a Model SRL Sargent recorder.

Lactic Acid.--Lactic acid determinations were done on the digesta and fecal extracts using the method of Barker and Summerson (12).

Fiber and Lignin.--Fiber and lignin were determined in the rations, fresh digesta and feces by the method of Van Soest (139). Since the digesta and fecal samples had different water content, several concentrations of the detergent solution were used to make the final sample--detergent mixtures equal in detergent concentrations.

Chromic Oxide.--The digesta (Trial I) was analyzed for Cr_2O_3 by the method of Bolin *et al.* (19).

Bone Ash.--The distal 10% of the left 9th and 10th ribs was dried, extracted in a continuous-reflux apparatus with 95% ethanol and petroleum ether each for 12 hours and the dry-fat-free bone ashed in a muffle oven at 600° C for 12 hours.

Statistical Methods

The data collected for all measurements except feed intake data and those in Tables 21, 22, 23, 30, and 31 were analyzed statistically by analysis of variance (121) and treatment means were subjected to the multiple range test of Duncan (39). Feed intake data were analyzed according to the Kruskal-Wallis analysis (36). No statistical analysis was made on the values in the five tables mentioned above

since the concentration was hardly measurable for several nutrients in some sections of the gastrointestinal tract. The concentration was essentially zero, but to calculate whether secretion or absorption occurred an approximate minimum value was used. The diagram below shows the experimental design used in Trials I and II.

Fiber Contents of Rations	<u>Phosphorus Levels of Rations</u>		
	1	2	3
Low	2	2	2
High	2	2*	2

*In Trial I, only one calf was in this cell, all other cells had 2 calves each. The missing datum was calculated according to Snedecor (121) before the data were analyzed by analysis of variance.

In Trial II instead of two calves per cell and three levels of P there were, respectively, three and four.

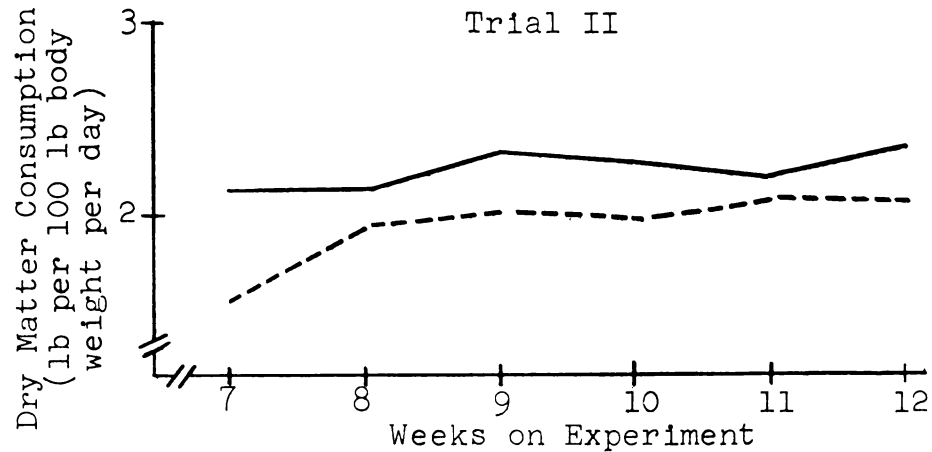
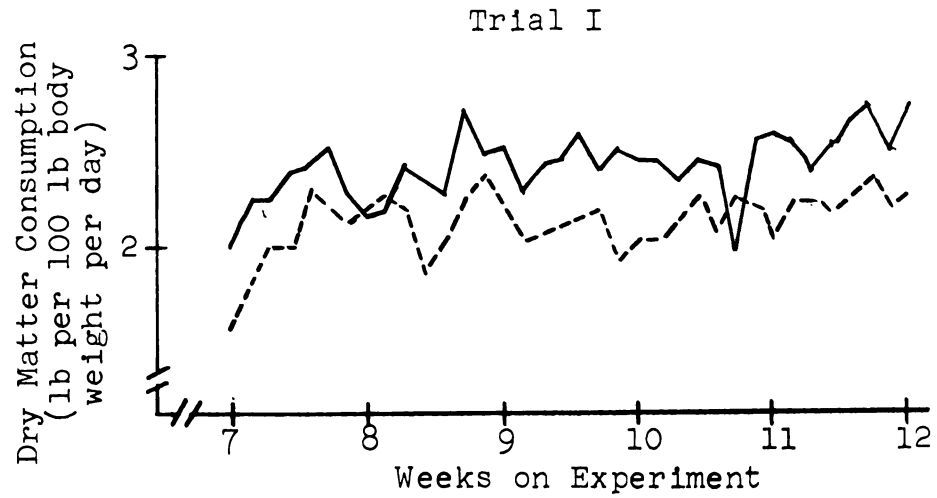
CHAPTER IV

RESULTS

I. Feed Consumption

During the first four weeks of the experiment when the calves were still fed milk the amount of dry feed consumed was negligible (Appendix, Table 1). In Trial I the average daily dry matter consumption increased from 0.76 lb per 100 lb body weight during the last week of milk feeding to 1.50 lb during the first post-weaning week. Similarly expressed for Trial II, the dry matter consumed was 0.91 and 1.36 lb. In Trial I the average dry matter consumed daily by calves during the first six weeks of the experiment was 0.68 and 0.87 lb per 100 lb body weight respectively for the low- and high-fiber rations. In Trial II during this same period the average daily dry matter consumption was 0.60 and 0.75 lb per 100 lb body weight respectively for the two groups of calves. In both trials the differences in feed consumption were not statistically significant ($P > .05$) during the first six weeks of the experiment.

From the 7th through the 12th week of the experiment the calves in both trials consumed more of the high-fiber rations than the low-fiber rations ($P < 0.0005$) (Figure 1).



Legend:

High-fiber ration = _____

Low-fiber ration = - - - - -

Figure 1. Average Dry Matter Consumption of Calves Fed the Low- and High-Fiber Rations from the 7th to the 12th Week of Experiments (dry matter consumption significantly different at $P < 0.0005$ in both trials).

Apparently, the greater bulk in the high-fiber rations did not cause the calves to eat less. The calves fed the high-fiber rations may have consumed more feed than those fed the low-fiber rations to meet their energy requirements since the high-fiber rations were less digested than the low-fiber rations (Section X).

II. Growth, Shrinkage and Dressing Per Cent

The rations utilized in these trials apparently supplied the necessary nutrients for moderate weight gains even though these rations were made of semi-synthetic ingredients and the calves were weaned from milk when they were only 30 days of age. Weight gains in Trial II were much less than in Trial I, although the difference between calves fed the low and the high-fiber diets was not appreciable in either trial (Table 3).

Nearly 45 and 60% of the weight gains were made during the last four weeks of the experiment for Trials I and II respectively. The average daily gain during the 12-week period was 0.7 lb while during the last 4-week period gain averaged 1.2 lb for Trial II. In Trial I the respective weight gains during the two periods were 1.2 and 1.5 lb.

The 16-hour shrinkage for the high-fiber group was more than the low-fiber group in Trial I (6.7 versus 4.0% $P < .05$) but no appreciable difference was observed in Trial II (Table 3).

TABLE 3.--Average weight gain, shrinkage and dressing percentages of calves fed low- and high-fiber rations, Trials I and II

Measurements	Trial I		Trial II	
	Fiber Contents			
	Low	High	Low	High
Weight gain (lb, 0 to 12 week)	97.7	98.2	59.3	58.5
Weight gain (lb, 8 to 12 week)	42.7	43.2	34.7	36.2
Shrinkage (%, 16-hour fast)	4.0*	6.7	4.6	3.8
Dressing (%)	61.1**	53.6	63.8	62.2

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

The dressing percentage was affected by the weight of the gut and fill at the time of slaughter. The data on tissue weight and gut contents which are presented in Sections IV and VII were probably responsible for the greater dressing percentage of the calves fed the low-fiber rations compared with those fed high-fiber rations. The difference in Trial I was statistically significant ($P < .01$) and that in Trial II was not.

III. Effect of Phosphorus

A. Phosphorus consumption

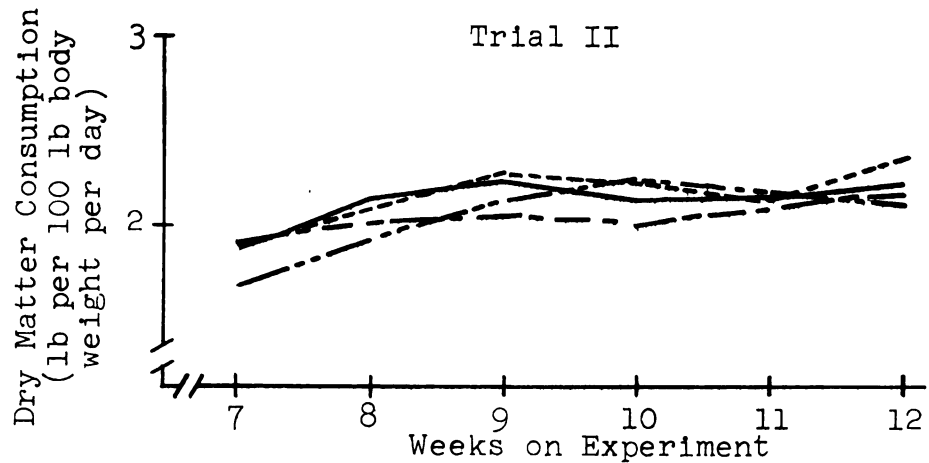
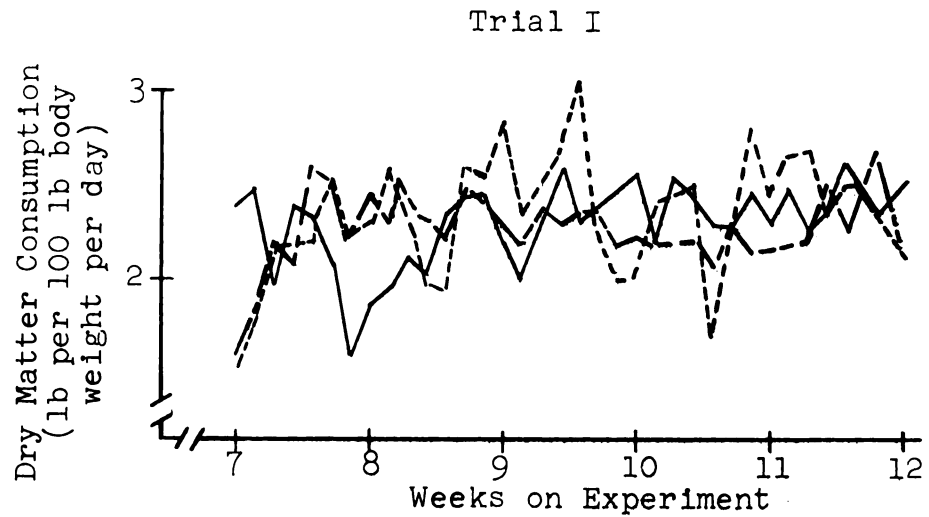
In Trial I the calves in most instances consumed more P from their rations than the predetermined amounts of 1.8,

2.3, and 3.0 g daily per 100 lb body weight (Appendix, Table 2). During the entire experiment the averages of total P consumed daily were 3.01, 3.11, and 3.41 g per 100 lb body weight for the three respective predetermined P levels and were not statistically different ($P > .05$). This mixed ration contained more P than that based on published values of ingredients used.

In Trial II, the only source of P for the calves was the rations and the daily amounts of P consumed, therefore, followed the daily amounts of rations consumed. These data are presented in the following paragraphs.

B. Feed consumption

There were no statistical differences in feed intake among the groups of calves fed the different levels of P, when expressed either as a per cent of P in the ration (Trial II) or as grams of P per 100 lb body weight (Trial I). In Trial I the calves fed rations containing P levels 1, 2, and 3 consumed respectively 0.76, 0.75, and 0.81 lb of dry matter per 100 lb body weight daily from the 1st through the 6th week of the experiment. In Trial II similarly expressed for P levels 1, 2, 3, and 4 the dry matter consumption was 0.71, 0.70, 0.71, and 0.56 lb. The average dry matter intake for each P level from the 7th through the 12th week of the experiment is presented in Figure 2 for both trials. Feed consumption varied from day to day in both trials and no cyclic pattern was observed in feed consumption as reported by Tillman et al. (133



Legend:

P level 1 = _____
 P level 2 = - - - - -
 P level 3 = - - - - -
 P level 4 = - - - - -

Figure 2. Average Dry Matter Consumption of Calves Fed Different Levels of Phosphorus from the 7th to the 12th Week of the Experiments.

and 136). The average daily dry matter intakes for calves fed rations containing P levels 1, 2, and 3 in Trial I were respectively 2.30, 2.38, and 2.28 lb per 100 lb body weight. For calves fed rations containing phosphorus levels 1, 2, 3, and 4 in Trial II the dry matter intakes were respectively 2.53, 2.56, 2.42, and 2.40 lb daily per 100 lb body weight during the 7th through the 12th week of the experiment. Although no significant statistical differences in feed consumption were observed among the different P levels, calves fed P level 2 consumed the greatest amount of ration for both trials when consumption was based on a unit body weight.

The levels of Ca used in this present study were not expected to influence the effects of P on feed consumption or other measurements since the Ca/P ratios (Appendix, Table 2) were within the limits that other workers have found ineffective in this respect (48 and 156).

C. Body weight gain

No statistically significant differences were observed among the mean weight gains of the calves fed the different levels of P ($P > .05$) (Table 4). The average daily weight gains were 1.17, 1.12, and 1.20 lb respectively for the calves fed P levels 1, 2, and 3 in Trial I and expressed similarly were 0.68, 0.79, 0.66, and 0.67 for calves in Trial II during the 12 weeks of growth. Calves in Trial II that were fed P level 2 (0.195 to 0.197% P of the dry matter) had the most weight gains but in Trial I no particular group actually excelled.

TABLE 4.--Average weight gains of calves receiving different levels of phosphorus, Trials I and II

Week on Experiment	Trial I			Trial II			
	Phosphorus levels						
	1	2	3	1	2	3	4
0 to 12 week (1b)	98.5	94.3	101.0	57.0	66.7	55.8	56.2
8 to 12 week (1b)	42.0	47.0	39.5	30.8	40.8	32.0	38.0

D. Blood data

Most of the serum inorganic P and Ca concentrations and phosphatase activities obtained during the 4th, 12th, and 13th weeks of the experiment were near the normal ranges expected from young calves (Table 5). These values are comparable to those reported by several investigators (80, 156, 157, and 158). No explanation can be given as to why some of the values were somewhat higher than normal.

In general the changes in P concentration and phosphatase activity with time were normal. The P concentration in the serum measured on the 12th and 13th weeks was less than that measured on the 4th week of the experiment and this decrease in P concentration with age was accompanied by an increase in the serum phosphatase activity. The phosphatase activity was also inversely related to the P concentration at each sampling time in both trials.

TABLE 5.--Average blood and bone data of calves fed different levels of phosphorus, Trials I and II

Time of Measurement	Item and Units	Trial I				Trial II			
		1	2	3	1	2	3	4	
4th week 12-13th wk.	Phosphatase Activity, Bodanski units/100 ml blood serum	12.3	5.2	3.8	6.5	5.9	7.1	5.3	
		20.6	8.3	15.8	7.3	6.7	9.4	5.3	
4th week 12-13th wk.	P, mg/100 ml blood serum	7.2	15.6	10.0	8.3	7.9	8.0	8.3	
		5.8	8.2	5.4	7.2	8.0	7.2	7.8	
4th week 12-13th wk.	Ca, mg/100 ml blood serum	10.9	13.0	11.3	14.7	14.1	17.2	14.0	
		10.6	14.7	11.7	14.3	16.4	14.9	14.3	
Slaughter	Fat-free bone ash, per cent	49.4	50.1	49.7	49.3	50.9	50.8	50.6	
Slaughter	Bone ash, g/100 lb body weight	0.420	0.423	0.512	0.369*	0.441	0.479	0.462	

*Phosphorus level 1 significantly different from levels 3 and 4.

E. Bone data

Although phosphorus levels in the rations did not significantly ($P > .05$) influence the percentage bone ash, the greatest values were those for level 2 in both trials and all the values were normal for young calves (Table 5).

Since the bones obtained were a percentage of the length of the 9th and 10th ribs the weight of the bone ash could be compared directly and the values when expressed as a unit of body weight would reflect the rate of bone growth, assuming that all calves started with equal bone weight. When the bone ash weight was, therefore, expressed in terms of g of bone ash per 100 lb of body weight, increasing the P levels increased the g of bone ash per unit body weight in both trials. In Trial I the differences among levels of P were not statistically significant; however, in Trial II P level one had significantly less bone ash per unit body weight than level 3 or 4 (Table 5, $P < .05$). Not only was the influence of P levels reflected in the weight of bone ash per unit of body weight, the influence also appeared in the length, width, and thickness of the bone. By visual judgment the bones from the calves fed the lower levels of P were in general smaller in dimension than those from calves fed the higher levels.

On the basis of percentage bone ash the different levels of P fed were equally satisfactory while on the basis of g of bone per unit body weight P level 3 in both trials gave the greatest rate of bone growth.

IV. Distribution of Gastrointestinal Contents

A. Wet digesta

Wet digesta in the reticulo-rumen averaged 17.3 lb per calf with a range of 10.8 to 25.8 lb in Trial I. In Trial II the average was 11.0 lb per calf with a range of 5.9 to 20.9 (Appendix, Table 3). Similar wide ranges were also observed for other sections of the alimentary tract of calves in both trials. The average wet digesta in the omasum, abomasum, upper small intestine, lower small intestine, large intestine, and cecum were, respectively, 1.1, 1.9, 1.5, 1.8, 1.3, and 1.2 lb per calf in Trial I while in Trial II the averages listed in the same order were 1.2, 0.6, 1.1, 1.6, 1.5, and 0.6 lb. The reticulo-rumen, abomasum and cecum contained more material per calf in Trial I than in Trial II while the upper and lower sections of the small intestine contained about the same amount in both trials.

B. Dry digesta, g per 100 lb body weight

Calves in both trials fed the high-fiber rations had more dry matter in their alimentary tract than those fed the low-fiber rations when the calves were killed after a 16-hour fast (Table 6). For instance in Trial I the total dry matter found in the entire tract was 668 for calves fed the low-fiber ration compared to 1084 g per 100 lb body weight for calves fed the high-fiber ration. In Trial II the respective amounts of dry matter were 687 and 702 g.

TABLE 6.--Average percentage distribution and total dry matter in each section of the alimentary tract of calves fed the low- and high-fiber rations, Trials I and II

Sections of Alimentary Tract	Trial I				Trial II			
	Fiber Contents of Rations							
	Low		High		Low		High	
g/100 lb Body Weight	% of Total	g/100 lb Body Weight	% of Total	g/100 lb Body Weight	% of Total	g/100 lb Body Weight	% of Total	
Reticulo-rumen	478	72	790	73	408	55	362	51
Omasum	24	4	40	4	97	16	115	16
Abomasum	55	8	88	8	29	5	23	3
Upper small intestine	21*	3	37	3	24	4	32	5
Lower small intestine	23*	3	41	4	28	5	37	5
Large intestine	44	7	49	5	73	11	102	15
Cecum	24*	4	40	4	29	5	30	5
Total	668	100	1084	100	687	100	702	100

*Difference between low- and high-fiber rations in respective sections of alimentary tract significant at $P < .05$.

In Trial I the dry contents in each section of the alimentary tract of the calves fed the low-fiber ration were less than that found in the respective section of the calves fed the high-fiber ration but only in the small intestine and cecum were the differences statistically significant ($P < .05$). No statistically significant differences were observed in the mean dry digesta weight in the respective sections of the alimentary tract between the two groups of calves in Trial II (Table 6).

C. Distribution throughout the gastrointestinal tract

The percentage distribution of dry digesta in respective sections of the alimentary tract was very similar between the calves fed either the low or the high-fiber ration within each trial (Table 6). In Trial I about 72% of the total dry digesta was found in the reticulo-rumen and in Trial II about 53%. Except for the differences in the ingredients used to make the rations for the two trials (Table 1) no other obvious factors can explain for the differences observed between the two trials in percentage distribution of dry matter in the rumen and other sections of the tract.

The omasum of calves contained approximately 4 and 16% of the total dry digesta in Trials I and II, respectively. The percentage distribution in the next organ (abomasum) increased to about 8% in Trial I and decreased to near 4% in Trial II. The percentage distribution ranged from 3-5% in both trials for each of the two sections of the small

intestine. Dry digesta in the large intestine and cecum amounted to 8-10% in Trial I and 16-19% in Trial II.

V. Relationships Involving Gastrointestinal Contents, Trial II

A. Rumen retention time

The ratio of weight of dry ruminal digesta to weight of dry feed consumed per day has been defined by Thomas et al. (130) as rumen retention time. The regression equation $\hat{Y} = 1.091 - .0007X$ with a standard deviation from regression of 0.246 obtained by regressing rumen retention time (Y) on g of dry matter consumed (X) can be used to predict rumen retention time (\hat{Y}), when only feed consumption data are known. Rumen retention time, in turn, can be used to predict rumen fill. Since the calves were slaughtered only at one time (16 hours after fasting) the regression equation is limited to predict rumen retention time for this one time only; further more, the correlation ($r = +0.46$) between rumen retention time and feed consumption was not sufficiently high even though significant ($P < .05$) to be of value.

B. Rumen digesta versus daily fecal output

When the total wet ruminal digesta (in g) of the calves fed the high-fiber diet was correlated with their daily wet fecal output (in g) the r value was +0.57 ($P < .05$). The regression equation was $\hat{R} = 1.853 + 1.156F$ (where \hat{R} = g of wet ruminal digesta and F = g of daily wet feces) with a

standard deviation from regression of 780 g. This equation can be used as an estimator of rumen fill of calves at 16 hours after fasting the calf.

When similar statistical analyses were made on the data available from the calves fed the low-fiber ration the correlation ($r = +0.43$) was not significant ($P > .05$). The discrepancy between the low-and high-fiber fed calves could have been caused by a difference in the rate of passage of digesta or absorption of dry matter from the rumen and fecal output rate in the two groups of calves.

C. Ruminal, omasal and abomasal digesta

The rumen contained on the average 12.3 and 4.6 times more wet and dry digesta than the omasum, respectively. The values given are only averages since only insignificant differences were observed statistically ($P > .05$) for either levels of phosphorus or fiber.

Similarly, the rumen contained 6 to 256 times (average 33 times) more wet digesta and 15 to 1252 times (average 128 times) more dry digesta than the abomasum. The above wide ranges of values demonstrated that the weight of the digesta (wet or dry) in the rumen, omasum, or abomasum were not a constant for calves treated similarly.

VI. Rumen Capacity

The average rumen water holding capacity was 30.5 and 35.0 in Trial I and in Trial II 26.1 and 27.3 lb per 100 lb

body weight for the low- and high-fiber rations, respectively. The calves fed the high-fiber rations in both trials had slightly greater rumen capacity than those fed the low-fiber rations, but the difference was not statistically significant ($P > .05$). The high-fiber rations, therefore, did not significantly stretch the rumen wall.

VII. Gastrointestinal Tissues

In Trial II only the weights of the entire tract, proximal half of the small intestine and cecum expressed as g of tissue per 100 lb body weight, were significantly less ($P < .05$) in the calves fed the low-fiber diet when compared to those fed the high-fiber diet (Table 7). The average weights of the reticulo-rumen, omasum, and abomasum were, respectively, about 1055, 263, and 244 g per 100 lb body weight for all calves.

In Trial I the average reticulo-rumen tissue weight was 1222 and 1056 g per 100 lb body weight for calves fed the low- and high-fiber rations, respectively. The heavier tissue weight was that of calves fed the low-fiber diet just as was true in Trial II. The increase in the rumen tissue weight of the calves fed the low-fiber ration was probably due to the increase in the musculature of the rumen since the weights of dry rumen mucosa obtained from calves in Trial I were 71.7 and 69.5 g per 100 lb body weight for the calves fed the low- and high-fiber rations respectively. The levels of P did not significantly ($P > .05$) affect the dry rumen

TABLE 7.--Average wet tissue weight of the sections of the alimentary tract of calves fed low- and high-fiber rations, Trial II

Sections of Alimentary Tract	Fiber Contents of Rations	
	Low (g wet tissue/100 lb body wt)	High (g wet tissue/100 lb body wt)
Recticulo-Rumen	1068	1042
Omasum	250	277
Abomasum	229	259
Upper small intestine	452**	561
Lower small intestine	571	626
Large intestine	425	419
Cecum	66*	83
Total	3062*	3268

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

mucosa weight, although calves fed P level 2 had a value of 80.4 compared to 68.6 and 62.7 g per 100 lb body weight for calves on levels 1 and 3, respectively.

VIII. pH of Digesta

The pH of digesta in sections of the alimentary tract of calves in both trials was not appreciably affected by either levels of P or fiber fed except in the rumen of calves in Trial I (Tables 8 and 9). There was a tendency for the pH to be lower in the ruminal digesta of calves fed the larger amounts of P or fiber. The pH in other sections did not show any particular pattern due to amounts of P or fiber fed.

TABLE 8.--Average pH of the contents in sections of the alimentary tract of calves fed different levels of phosphorus, Trials I and II

Sections of Alimentary Tract	Trial I			Trial II			
	Phosphorus Levels of Rations						
	1	2	3	1	2	3	4
Reticulo-Rumen	6.58	6.07	6.20	7.28	7.20	6.98	6.92
Omasum	5.85	6.32	6.00	6.02	6.32	6.13	6.14
Abomasum	2.90	3.12	2.60	3.17	4.37	3.65	3.67
Upper small intestine	6.47	6.42	6.42	6.33	6.36	6.43	6.28
Lower small intestine	7.22	7.30	7.15	7.17	7.12	7.10	7.18
Large intestine	6.60	6.45	6.47	6.16	6.30	6.34	6.33
Cecum	6.62	6.27	6.52	6.45	6.53	6.44	6.53

TABLE 9.--Average pH of the contents in sections of the alimentary tract of calves fed low- and high-fiber rations, Trials I and II

Sections of Alimentary Tract	Trial I		Trial II	
	Fiber Contents of Rations			
	Low	High	Low	High
Reticulo-Rumen	6.82**	5.75	7.12	7.05
Omasum	6.33	5.78	5.95	6.36
Abomasum	2.85	2.90	3.50	3.93
Upper small intestine	6.41	6.47	6.28	6.42
Lower small intestine	7.18	7.25	7.11	7.17
Large intestine	6.41	6.60	6.36	6.20
Cecum	6.40	6.55	6.46	6.46

** Difference between low- and high-fiber rations significant at $P < .01$.

IX. Total and Distribution of Organic Acids in the Gastrointestinal Tract

A. Volatile fatty acids

An average of 405.0 and 1140.0 millimoles of volatile fatty acids (VFA) (acetic, propionic, and butyric acids) was present in the entire tract of calves fed the low- and high-fiber rations respectively in Trial I, and 618.0 and 676.0 respectively, in Trial II (Table 10). The amount of VFA present in the entire gastrointestinal tract of individual calves ranged from 345.0 to 1632.2 millimoles in Trial I and 324.7 to 1337.2 in Trial II (Appendix, Table 5).

TABLE 10.--Average total volatile fatty acids and lactic acid in the contents of the entire alimentary tract of calves fed low- and high-fiber rations, Trials I^a and II

Acid	Trial I		Trial II	
	Fiber Contents of Rations			
	Low	High (millimoles)	Low	High
Volatile fatty acids	405	1140	618	676
Lactic acid	13	16	7	7

^aNo estimates were made for VFA or lactic acid in the omasum of calves in Trial I; values given for Trial I do not include organic acids in omasum.

An average of 81.3 and 87.7% of the total VFA found in the entire gastrointestinal tract was found in the reticulo-rumen of calves fed respectively the low- and high-fiber

rations in Trial I and 61.1 and 54.6% in Trial II (Table 11). The difference in the distribution of VFA in the rumen of calves between trials was probably due to the difference in distribution of gastrointestinal contents rather than to a difference in VFA concentrations (Appendix, Table 3). Also the percentage distribution should be decreased somewhat in Trial I since the VFA in the omasum was not included in the calculations of total VFA. If the percentage distribution in the omasum of Trial I was assumed to be 8.5 (average distribution in omasum of Trial II) then the reticulo-rumen would contain only 77% of the VFA of the entire gastrointestinal tract.

TABLE 11.--Average distribution of volatile fatty acids in sections of the alimentary tract of calves fed low- and high-fiber rations, Trials I and II

Sections of Alimentary Tract	Trial I		Trial II	
	Fiber Contents of Rations			
	Low (% of total)	High (% of total)	Low (% of total)	High (% of total)
Reticulo-Rumen	81.3	87.7	61.1	54.6
Omasum	a	a	8.7	8.3
Abomasum	0.6	0.5	0.8	0.4
Upper small intestine	0.1	0.1	0.3	0.2
Lower small intestine	0.6	0.6	1.2	0.8
Large intestine	9.7	5.8	18.5	25.7
Cecum	7.8	5.3	9.5	10.0

^aVFA in omasum, Trial I were not determined.

Only 1-2% of the total VFA was found in the abomasum plus the small intestine of calves in both trials. A rise in the amount of VFA occurred in the tract distal to the small intestine. The large intestine and cecum together contained on the average 11.1 to 17.5% of the total VFA in the gastrointestinal contents in Trial I, and 28.0 to 35.7% in Trial II.

B. Volatile fatty acids molar percentage distribution

In Trial I (Table 12) the molar percentages of acetic, propionic and butyric acids were 66, 24, and 10 respectively in the reticulo-ruminal digesta. The average molar percentage of acetic acid was significantly smaller in the reticulo-ruminal digesta than in the large intestine plus cecum ($P < .05$). The average molar percentages of propionic and butyric acids were respectively 17 and 8 in the large intestine plus cecum, and were not significantly different from those in the reticulo-ruminal digesta.

In Trial II (Table 13) the molar percentages for acetic propionic, and butyric acids in the rumen of calves fed the low-fiber ration were significantly different from that obtained from calves fed the high-fiber ration. The molar percentages for the low- and high-fiber rations were respectively acetic, 70.8, 65.2 ($P < .05$) propionic, 22.9, 26.6 ($P < .05$) and butyric 6.4, 8.4 ($P < .01$).

The rumen was the only organ wherein molar percentage distribution of the VFA was affected by the levels of fiber

TABLE 12.--Average molar percentage distribution of volatile fatty acids in the rumen and large intestine and cecum of calves, Trial I

Sections of Alimentary Tract	Fiber Contents of Rations		
	Acetic	Propionic	Butyric
Reticulo-rumen	66*	24	10
Large intestine and cecum	75	17	8

*Difference between sections of alimentary tract significant at $P < .05$.

TABLE 13.--Average molar percentage distribution of volatile fatty acids in sections of the alimentary tract of calves fed low- and high-fiber rations, Trial II

Sections of Alimentary Tract	Fiber Contents of Rations					
	Low			High		
	Acetic	Prop-ionic	Butyric	Acetic	Prop-ionic	Butyric
Reticulo-Rumen	70.8*	22.9*	6.4**	65.2	26.6	8.4
Omasum	68.8	22.6	8.6	69.5	22.2	8.3
Large intestine	69.6	20.7	9.7	68.7	22.0	9.4
Cecum	69.9	21.4	8.7	69.2	22.2	8.7

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

fed to the calves. In the remaining organs (omasum, large intestine, and cecum) the molar percentage of the VFA was essentially the same, being acetic 69-70, propionic 21-22, and butyric 8-10.

C. Lactic acid

Lactic acid found in the entire gastrointestinal tract averaged 7.1 and 14.5 millimoles per calf for Trials I and II respectively (Table 10). The amount of lactic acid found in the tract was much less than for the volatile fatty acids. The distribution of lactic acid in the seven sections of the gastrointestinal tract (Table 14) was very different from the distribution of VFA. In both trials the lactic acid was found to be mainly in the small intestine. From 77.1 to 78.6% of the lactic acid in the entire gastrointestinal tract was found in the small intestine of calves in Trial II and 54.4% in Trial I. About 23% of the total was distributed among rumen, omasum, abomasum, large intestine, and cecum in Trial II. The rumen contained a greater proportion of the total lactic acid in the tract (36-37%) of Trial I than in Trial II (10-11%).

The distribution of lactic acid was very similar in respective sections of the gut for the calves fed the low- and high-fiber rations (Table 14). No significant effect ($P > .05$) can be attributed to either fiber levels or P levels on lactic acid distribution in the gut.

TABLE 14.--Average distribution of lactic acid in sections of the alimentary tract of calves fed low- and high-fiber rations, Trials I and II

Sections of Alimentary Tract	Trial I		Trial II	
	Fiber Contents in Rations			
	Low	High	Low	High
	(% of total in entire tract)			
Reticulo-Rumen	35.9	36.9	11.0	9.9
Omasum	-----*	-----*	2.1	1.9
Abomasum	3.0	2.0	4.0	3.5
Upper small intestine	22.5	28.2	37.1	36.6
Lower small intestine	31.7	26.4	40.0	42.0
Large intestine	4.8	4.0	4.3	4.9
Cecum	2.5	1.9	1.6	1.4

*Was not determined.

X. Absorption and Secretion of Nutrients

The values obtained by using the marker ratio technique as applied in these present experiments can be either positive or negative. A positive value indicates that absorption exceeds secretion while a negative value indicates the reverse. A negative value can be an infinitely large negative number and yet the absolute total changes in terms of grams of a nutrient can be insignificant depending on the amount present in the more anterior organ of a pair of consecutive organs and on the rate of passage of digesta in the two organs.

A. Digestion of dry matter, organic matter, and fiber

In general, the average absorption of dry matter, organic matter, and fiber obtained in Trial II agreed with the results obtained in Trial I (Tables 15 and 16). Dry matter, organic matter, and fiber were digested in the rumen. The amount of fiber but not the levels of P in the rations (effects of P not shown in tables) affected the degree of digestion of the three nutrients. The dry matter and organic matter of the high-fiber rations in both trials were significantly less digested in the rumen than those of the low-fiber rations, while the reverse was true for digestion of the fiber portions of the low- and high-fiber rations.

The values obtained for individual calves for absorption from the rumen ranged from 51 to 86 for dry matter, 54 to 87 for organic matter, and 12 to 57 for fiber in Trial I and in Trial II the values listed in the same order were: 71 to 92, 71 to 92, and 29 to 68 (Appendix, Tables 10 and 11).

Little or no absorption of any of the three nutrients occurred in the omasum, abomasum, and upper section of the small intestine. In fact, secretion of these three nutrients into these sections must be greater than the absorption rate for the average values were negative, especially in the upper section of the small intestine. The secretion of fiber in any organ was, of course, impossible. The discrepancy for this nutrient was minor because of the small negative value of the fiber digestion when compared to other nutrients.

TABLE 15.--Average percentage apparent absorption of dry matter, organic matter and fiber by sections of the alimentary tract, calculated by lignin ratio technique, Trial I^a

Sections of Alimentary Tract	Nutrients					
	Dry Matter		Organic Matter		Van Soest Fiber	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	82	57 **	84	61 **	19	42 *
Abomasum	3	12	5	7	9	6
Upper small intestine	-698	-574	-753	-1097	-14	-33
Lower small intestine	64	73	66	73	5	24
Large intestine	57	37	58	33	16	11
Cecum	60	36	58	33	17	10
Total ^b	82	65 **	84	68 **	34	50 *

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^bCalculated by comparing feed and large intestinal digesta.

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

TABLE 16.--Average percentage apparent absorption of dry matter, organic matter, and fiber by sections of the alimentary tract, calculated by lignin ratio technique, Trial II^a

Sections of Alimentary Tract	Nutrients					
	Dry Matter		Organic Matter		Van Soest Fiber	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	85	81 *	87	81 **	40	59 **
Omasum	-14	- 9	-26	-14	- 8	-15
Abomasum	- 3	-51	7	34	- 17	-40
Upper small intestine	-555	-804	-478	-602	24	-10 *
Lower small intestine	59	70	61	75	- 7	4
Large intestine	48	60	47	55	8	18
Cecum	42	54 *	41	49	6	10 **
Rectum	5	2	10	2	- 1	- 7
Total ^b	86	79 **	85	79 **	34	39

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^bCalculated by comparing feed and feces.

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

Also, the method used to determine fiber was an empirical one. The Van Soest method (139) used in these experiments probably includes some insoluble mineral fractions as part of the fiber.

As the digesta passed from the upper into the lower small intestine, dry matter, organic matter, and fiber were absorbed. Further down the tract more absorption occurred, thus by the time the digesta reached the rectum about 2-8% of the fiber and organic matter of the large intestinal digesta were absorbed prior to defecation (Table 16).

B. Absorption and secretion of phosphorus, calcium and ash

The results obtained in both trials were very comparable to each other for the average absorption and secretion of P, Ca, and ash (Tables 17 and 18). In general, the trends of the absorption and secretion of these nutrients (especially in the rumen) were similar to those of dry matter, organic matter, and fiber. More secretion than absorption of P and Ca occurred in the abomasum for 6 out of 24 and 10 out of 24, and in the omasum for 5 out of 24 and 14 out of 24 calves in Trial II (Appendix, Table 11). Based on these values one could say that the abomasum and omasum absorbed predominantly more P and Ca than was secreted.

In the upper section of the small intestine there was a definite secretion of P and Ca followed by an absorption of P in the remainder of the tract. In Trial II Ca was

TABLE 17.--Average percentage apparent absorption of phosphorus, calcium, and ash by sections of the alimentary tract, calculated by lignin ratio technique, Trial I^a

Sections of Alimentary Tract	Nutrients					
	P		Ca		Ash	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	66	54	81	54 *	68	52
Abomasum	25	69	46	42	2	34
Upper small intestine	-1851	-623	-901	-421	-629	-1622
Lower small intestine	67	66	41	49	53	68
Large intestine	76	66	37	14	76	57
Cecum	70	72	42	17	72	57
Total ^b	74	72	78	55 *	68	57

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^bCalculated by comparing feed and large intestinal digesta.

*Difference between low- and high-fiber rations significant at $P < .05$.

TABLE 18.--Average percentage apparent absorption of phosphorus, calcium, and ash by sections of the alimentary tract, calculated by lignin ratio technique, Trial II^a

Sections of Alimentary Tract	Nutrients					
	P		Ca		Ash	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	37	35	86	78	59	62
Omasum	- 5	23	- 7	-14	34	36
Abomasum	44	-62 *	7	-154	-149	-326
Upper small intestine	-1714	-1454	-2152	-291	-576	-485
Lower small intestine	76	83	19	53	60	68
Large intestine	70	78	-78	-20	65	80 *
Cecum	59	77	-80	-35	54	72
Rectum	- 12	1	8	4	12	20
Total ^b	67	72	76	69	75	76

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^bCalculated by comparing feed and feces.

*Difference between low- and high-fiber rations significant at $P < .05$.

absorbed in the lower section of the small intestine followed by a secretion in the large intestine and cecum while in Trial I absorption of this mineral started in the lower section of the small intestine and continued in the large intestine and cecum. There was a slight absorption of Ca in the rectum before the digesta were voided as feces.

Trends in absorption and secretion of ash were similar to the trends of P and Ca in Trial I and P in Trial II (Tables 17 and 18).

C. Absorption and secretion of sodium

Sodium was absorbed from the rumen and omasum and secreted into the abomasum and upper section of the small intestine and then reabsorbed in the lower section of the small intestine (Table 19). Up to this point of the tract, the average values reflected reasonably well the general trends of Na transfer. From the large intestine to the cecum and rectum the average values in Table 19 probably did not give a true picture of the fate of Na. The negative average values were the results of a few animals (16-24% of the animals) that had very large secretion values (Appendix, Table 11). Also, the fact that the total absorption of this ion was from 68.6 to approximately 100% complete (Appendix, Table 11) which would suggest that the large average secretion values into the large intestine and cecum were probably not representative of what occurs in these organs.

TABLE 19.--Average percentage apparent absorption of sodium by sections of the alimentary tract, calculated by lignin ratio technique, Trial II^a

Sections of Alimentary Tract	Fiber Contents of Rations	
	Low	High
Reticulo-rumen	22	33
Omasum	64	33
Abomasum	- 1	-465
Upper small intestine	-5283	-36009
Lower small intestine	68	81
Large intestine	-6772	-2468
Cecum	-15702	-3345
Rectum	58	30
Total ^b	95	85 **

^aSodium absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^bCalculated by comparing feed and feces.

**Difference between low- and high-fiber rations significant at $P < .01$.

D. Absorption and secretion of water

Since H₂O intake by the calves was not measured the absorption of H₂O from the rumen cannot be determined, but as presented in Table 20, 66-67% of the H₂O in the ruminal digesta was absorbed from the omasum. Appendix Table 11 shows that the individual values for all the calves ranged from 31.2 to 79.5%.

As the relatively dry omasal digesta (Appendix, Table 4) entered the abomasum, H₂O was added into the abomasum; further addition of H₂O occurred in the upper section of the small intestine.

The remainder of the gastrointestinal tract (lower section of the small intestine, large intestine, cecum, and rectum) reabsorbed the H₂O that was secreted by the abomasum and the upper section of the small intestine.

E. Production and absorption of volatile fatty acids

The fact that the VFA (acetic, propionic, and butyric acids) are produced and absorbed in the rumen has been known for a long time (11, 30, 103, 120, and 126). The VFA in the ruminal digesta, which were not absorbed in the rumen, were absorbed further down the gut in the omasum and abomasum (Tables 21 and 22). When ruminal acetic, propionic, and butyric acids entered the omasum 41, 37, and 16% of these acids were respectively absorbed in the omasum of calves fed the low-fiber rations. For the calves that were fed the

TABLE 20.--Average percentage apparent absorption of water by sections of the alimentary tract, calculated by lignin ratio technique, Trials I and II^a

Sections of Alimentary Tract	Trial I		Trial II	
	Fiber Contents of Rations			
	Low	High	Low	High
Omasum	---	---	67	66
Abomasum	---	---	-211	-586
Upper small intestine	-1774	-1296	-923	-1481
Lower small intestine	55	63	58	62
Large intestine	84	68	80	87
Cecum	81	60	74	81
Rectum	---	---	26	24

^aWater absorption in all sections of gut in both trials not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

TABLE 21. Average percentage apparent absorption of volatile fatty acids by sections of the alimentary tract, calculated by lignin ratio technique, Trial I^a

Sections of Alimentary Tract	Volatile Fatty Acids					
	Acetic		Propionic		Butyric	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Abomasum	89	94	98	97	99	99
Upper small intestine	-763	-294	-448	-69	-638	-333
Lower small intestine	-2338	-1705	64	69 ^c	64	69 ^c
Large intestine	-149	-14955	-20462	-19046	-18278	-8264
Cecum	-428	-23500	-61734	-26743	-29797	-10336
Large intestine ^b	47	24	39	29	16	37

^aValues in table are simple averages, no statistical analyses applied.

^bCalculated by using cecal digesta as the feed and the digesta in the large intestine as the feces.

^cOne out of 24 calves had a large negative value. This was not included in the average shown here.

TABLE 22.--Average percentage apparent absorption of volatile fatty acids by sections of the alimentary tract, calculated by lignin ratio technique, Trial II^a

Sections of Alimentary Tract	Volatile Fatty Acids					
	Acetic		Propionic		Butyric	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Omasum	41	48	37	53	16	48
Abomasum	54	34	90	73	87	56
Upper small intestine	21	-537	-11181	-3434	-479	-861
Lower small intestine	-1215	-949	91	5	59 ^c	75
Large intestine	-3502	-2954	-7255	-3273	-3694	-3387
Cecum	-3716	-4877	-9412	-7039	-4476	-4558
Rectum	17	16	9	11	15	16
Large intestine ^b	10	27	14	27	- 8	19

^aValues in table are simple averages, no statistical analyses applied.

^bCalculated by using cecal digesta as the feed and the digesta in the large intestine as the feces.

^cOne out of 24 calves had a large negative value. This value was not included in the average shown here.

high-fiber rations the absorption of the acids listed in the same order were 48, 53, and 48%.

Further absorption of VFA occurred in the abomasum (Tables 21 and 22) so that by the time the digesta left this organ the concentrations of VFA were very low (Appendix, Tables 6, 7, and 8). This low concentration of VFA in the abomasal digesta influenced the values of production obtained for the upper section of the small intestine. Any slight increase in the concentration of VFA in the upper small intestine when compared to the low concentration in the abomasum gave a very large production percentage value. The importance of the small intestine in either production or absorption of VFA was, therefore, over emphasized by the values given in Tables 21 and 22. On the other hand, the production of VFA in the large intestine and cecum was reasonable and very important. The importance of the large intestine and cecum in contributing VFA as energy sources will be discussed in Section XIV.

F. Production and absorption of lactic acid

The omasum partially absorbed the lactic acid from the ruminal digesta. The amount absorbed was probably insignificant since there was a low concentration of lactic acid in the ruminal digesta and a large variation among concentrations found in individual calves (Table 23 and Appendix, Table 9).

The abomasum and upper section of the small intestine secreted or produced the major portion of the lactic acid in

TABLE 23. Average percentage apparent absorption of lactic acid by sections of the alimentary tract, calculated by lignin ratio technique Trials I and II^{ab}

Sections of Alimentary Tract	Trial I		Trial II	
	Fiber Contents of Rations			
	Low	High	Low	High
Omasum	---	---	8	60
Abomasum	---	---	-788	-1480
Upper small intestine	-6319	-15956	-21614	-10153
Lower small intestine	43	79	67	77
Large intestine	97	89	96	97
Cecum	96	82	96	95
Rectum	---	---	-2	-13
Large intestine ^c	19	-78	-7	3

^aTrial I, values in table are simple averages, no statistical analyses applied.

^bLactic acid absorption in all sections of gut in Trial II not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

^cCalculated by using cecal digesta as the feed and the digesta in the large intestine as the feces.

the entire gut. What the abomasum and upper small intestine produced, the remainder of the tract (lower section of small intestine, large intestine and cecum) absorbed.

XI. Importance of Rumen Relative to Total Digestion of Nutrients

The rumen accounted ($\%$ nutrient digested in the rumen \div $\%$ total digestibility of nutrient \times 100) for 88 to 103% of the total dry matter and organic matter and 58 to 148% of the total fiber digested when lignin was the indicator used in the ratio technique (Table 24). The rumen also accounted for more than 50 to 148% of the total absorbed P, Ca, and ash. The corresponding values for these nutrients decreased when Cr_2O_3 was used in the ratio technique (values enclosed in parentheses, Table 24).

More P, ash, and fiber were secreted into the rumen than absorbed from the rumen when calculated by the Cr_2O_3 ratio technique but by using the lignin ratio technique more of these nutrients were absorbed than secreted. The absorption of Na from the rumen amounted to only 23-38% of the total absorbed which was much less than the percentage absorption of P, Ca, or ash (Trial II, Table 24).

XII. Total Collection Versus Lignin Ratio Technique

The validity of using either total collection method or lignin ratio technique in the study of digestibility of feed by animals has been thoroughly investigated by other

TABLE 24.--Percentage of the total digestion
accomplished in the rumen, Trials
I and II

Nutrients	Trial I ^a		Trial II	
	Fiber Contents of Rations			
	Low	High	Low	High
Dry Matter	99.5 (42.2)	87.9 (27.2)	98.7	102.2
Organic Matter	99.7 (44.2)	89.3 (32.3)	101.2	102.5
Fiber	57.9 (b)	83.4 (b)	115.4	148.1
Phosphorus	89.1 (b)	75.2 (b)	56.2	48.3
Calcium	104.0 (36.2)	97.2 (21.6)	113.6	113.6
Ash	100.5 (b)	91.5 (b)	79.7	80.7
Sodium	---	---	23.0	38.4

^aValues in parentheses obtained by using chromic oxide as the indigestible marker; those not enclosed in parenthesis were obtained with lignin.

^bThe digestion in the rumen was negative when chromic oxide was used as the indigestible marker (Tables 28 and 29).

workers (72 and 73). Both methods are accurate for the determination of total digestibility and well accepted by most workers as shown by the frequent usage of these methods. Since lignin ratio technique is an acceptable procedure for the estimation of total digestibility it was reasoned that this technique would be just as acceptable for measuring changes between successive sections of the gastrointestinal tract.

The average total digestibility of nutrients calculated by the total collection method and by the lignin ratio technique were in general very similar and within the range of normally accepted values (Tables 25 and 26). The lignin ratio technique values were greater for every nutrient than those calculated with the total collection method. Reasons for the percentage digestibility of P calculated by the lignin ratio technique being smaller compared to digestibility calculated by total collection method are not apparent. Even assuming that the values calculated by the two methods are somewhat different for total digestibility this does not invalidate the use of the technique to determine absorption and secretion between adjacent organs. An important method of proof to indicate that the various nutrients did not change forms or characteristics so as to affect the values obtained for their concentration necessary for the calculation

TABLE 25.--Average percentage total absorption (apparent digestibility) of nutrients calculated by total collection method, Trial II

		Nutrients							
	Dry Matter	Organic Matter	Ash	Ca	P	K	Na	Fiber	Lignin
According to Fiber Content of Ration									
Low-Fiber	71.4	72.0	54.4	53.8	79.2	65.8	88.9	-47.4	-142.2
High-Fiber	61.0**	61.2**	56.0	38.8	79.6	61.8	71.5**	-18.0	-104.6
According to Level of P in Ration									
1	66.1	66.5	57.1	26.5	77.2	64.4	87.6	-30.1	-129.3
2	64.5	65.2	52.8	39.8	75.4	66.0	78.0	-58.9	-143.2
3	67.7	68.6	47.2	58.5	80.9	61.2	79.5	- 6.9	- 90.4
4	66.6	66.2	63.7	60.4	84.3	63.5	75.6	-34.9	-130.5

**Difference between low- and high-fiber rations significant at $P < .01$.

TABLE 26.--Average percentage total absorption (apparent digestibility) of nutrients calculated by lignin ratio technique, Trial II

		Nutrients							
		Dry Matter	Organic Matter	Ash	Ca	P	K	Na	Fiber
According to Fiber Content of Ration									
Low-Fiber		86.1	85.4	74.5	75.6	66.5	83.8	95.4	34.2
High-Fiber		79.3**	79.4**	76.4	69.0	71.5	81.3	84.6**	38.9
According to Level of P in Ration									
1		84.6	84.2	78.4	66.1	60.4	85.4	95.3	40.4
2		79.6	78.3	70.1	63.9	68.8	84.3	87.1	25.0
3		82.4	82.8	69.7	78.8	67.4	78.8	88.8	40.5
4		84.3	84.2	83.5	80.4	79.5	81.7	88.8	40.2

**Difference between low- and high-fiber rations significant at $P < .01$.

of digestibility in the various sections of the gut is to assume that the amount of lignin voided in the feces equaled the amount consumed. The average total digestibility of the various nutrients calculated by the lignin ratio technique with the assumption that lignin intake equaled lignin output were almost identical to those calculated by total collection method (Tables 25 and 27).

XIII. Lignin Ratio Versus Chromic Oxide Ratio Technique

The main difference between results obtained by Cr_2O_3 and lignin ratio technique was an appreciable decrease in the digestibility of nutrients in the rumen when Cr_2O_3 was used as the indigestible tracer (Tables 28 and 29 compared with Tables 17 and 18). Fiber, P, and ash had more net secretion than absorption in the rumen when Cr_2O_3 was used as the tracer. The rumen was the only organ where secretion-absorption values obtained by the lignin and chromic oxide ratio technique were not in agreement and this was true for dry and organic matter, fiber, P, Ca, and ash but not for any of the VFA and lactic acid (Tables 30 and 31). Values obtained for other sections of the alimentary tract calculated by either Cr_2O_3 or lignin ratio technique were comparable for every nutrient determined (Tables 28, 29, 30, and 31 compared with Tables 15, 17, 20, 21, and 23).

TABLE 27.--Average percentage total absorption (apparent digestibility) of nutrients calculated by lignin ratio technique with the assumption that lignin intake equaled lignin output, Trial II

		Nutrients							
		Dry Matter	Organic Matter	Ash	Ca	P	K	Na	Fiber
According to Fiber Content of Ration									
Low-Fiber	71.8	72.2	50.8	53.5	34.8	63.5	88.8	-47.8	
High-Fiber	61.8**	61.1**	55.8	39.8	42.5	62.4	71.4**	-18.6	
According to Level of P in Ration									
1	66.8	66.4	56.9	25.1	22.7	65.7	87.5	-29.6	
2	64.5	65.3	45.8	39.5	31.2	65.9	77.9	-59.5	
3	67.8	68.3	47.2	61.8	42.9	61.2	79.5	- 7.5	
4	68.2	66.6	63.5	60.3	57.8	59.0	75.5	-36.1	

**Difference between low- and high-fiber rations significant at $P < .01$.

TABLE 28.--Average percentage absorption of dry matter, organic matter, and fiber by sections of the alimentary tract, calculated by the chromic oxide ratio technique, Trial I^a

Sections of Alimentary Tract	Nutrients					
	Dry Matter		Organic Matter		Fiber	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	34	20	37	21	-210	-97
Abomasum	51	10 *	53	10 *	54	- 1 **
Upper small intestine	-240	-476	-250	-452	55	-30
Lower small intestine	56	69	62	79	8	23
Large intestine	42	34	38	32	-12	3
Cecum	42	21	50	30	-17	-10
Total	81	73	84	65	33	44

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

*Difference between low- and high-fiber rations significant at $P < .05$.

**Difference between low- and high-fiber rations significant at $P < .01$.

TABLE 29.--Average percentage absorption of phosphorus, calcium, and ash by sections of the alimentary tract, calculated by chromic oxide ratio technique, Trial I^a

Sections of Alimentary Tract	Nutrients					
	P		Ca		Ash	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Reticulo-rumen	-44	-12	28	12	-24	-14
Abomasum	70	43	70	31	35	52
Upper small intestine	-700	-593	-231	-406	-199	-1343
Lower small intestine	68	76	38	67	49	76
Large intestine	66	71	35	6	64	57
Cecum	62	67	25	- 9	60	48
Total	76	66	78	55	70	54

^aNutrients absorption in all sections of gut not significantly ($P > .05$) affected by levels of P fed. The results broken down according to level of P are not included in this table.

TABLE 30.--Average absorption of volatile fatty acids by sections of the alimentary tract calculated by chromic oxide ratio technique, Trial I^a

Sections of Alimentary Tract	Volatile Fatty Acids					
	Acetic		Propionic		Butyric	
	Fiber Contents of Rations					
	Low	High	Low	High	Low	High
Upper small intestine	- 117	- 39	- .134	48	- 210	- 139
Lower small intestine	-2680	- 1465	60	75 ^c	60	60 ^c
Large intestine	- 251	-25838	-27966	-25810	-25303	-11718
Cecum	- 507	-25255	-55273	-40005	-30503	-16528
Large intestine ^b	49	32	42	35	20	40

^aValues in table are simple averages, no statistical analyses applied.

^bCalculated by using cecal digesta as the feed and the digesta in the large intestine as the feces.

^cOne out of 24 calves had a large negative value. This value was not included in the average shown here.

TABLE 31.--Average percentage absorption of lactic acid and water by sections of the alimentary tract, calculated by chromic oxide ratio technique, Trial I^a

Sections of Alimentary Tract	Nutrients			
	Lactic Acid		Water	
	Fiber Contents of Rations			
	Low	High	Low	High
Upper small intestine	-6319	-15956	-574	-1010
Lower small intestine	43	79	51	74
Large intestine	97	89	78	64
Cecum	96	82	72	48
Large intestine ^b	19	- 78	27	31

^aValues in table are simple averages, no statistical analyses applied.

^bCalculated by using cecal digesta as the feed and the digesta in the large intestine as the feces.

XIV. Caloric Value of the Absorbed Volatile Fatty Acids

An attempt was made to estimate the caloric value of the absorbed VFA from the data obtained in Trial II. The method used has never been employed by other investigators to estimate energy supplied by VFA or other nutrients absorbed from various organs of the alimentary tract and is presented as a model.

The method involves certain assumptions; some of the assumptions could have been varified to some degree if proper experimental measures had been taken. The assumptions involved will be pointed out as the method is explained. The following discussion is, therefore, intended only to illustrate a method which may be useful in estimating the amount of VFA absorbed from sections of the gut.

Information necessary for the construction of Figure 3 is given in Table 32. The concentration of the three volatile fatty acids and the amount of dry matter in each organ were the averages found for the 24 calves used in Trial II (Table 32). The concentration of each acid was plotted as the ordinate on the semi-logarithm paper against time in hours as the abscissa. Each line was drawn from two points, either rumen at eight hours and omasum at 16 hours or cecum at 16 hours and feces at 24 hours. The points at the 16 and 24 hours correspond respectively to the concentrations of the VFA found in the omasum and cecum when the calves were killed (16 hours after the last meal) and for the concentration of VFA in the feces. The rumen value was placed at 8 hours based on the assumption that the material measured in the omasum at 16 hours had spent an average of 8 hours in the rumen. The time used to place the point for the concentration of the VFA in the rumen is very important because the initial or zero time concentration is dependent on the extrapolated value.

The zero time concentration obtained was used in the following function:

$$f = \frac{-C_0}{K} e^{-Kt} - 1$$

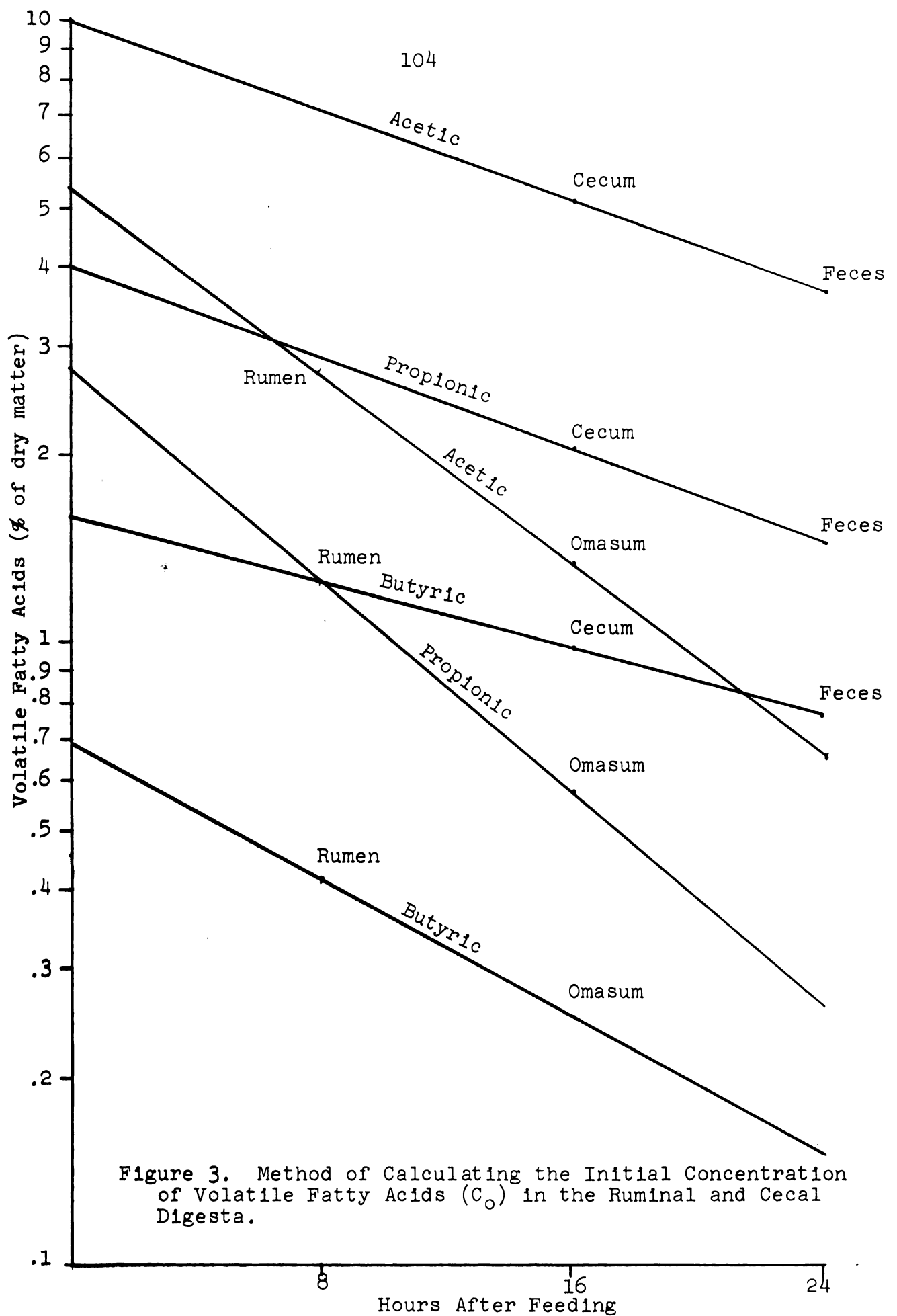


Figure 3. Method of Calculating the Initial Concentration of Volatile Fatty Acids (C_0) in the Ruminal and Cecal Digesta.

TABLE 32.--Information necessary for the construction of Figure 3 and the data derived from this figure and the data used to compute energy of absorbed VFA

	% VFA (dry matter basis)				Integrated % Total Changes in 24 Hours			VFA Absorbed in 24 Hours (g)	
	Acetic	Propionic	Butyric	Acetic	Propionic	Butyric	Acetic	Propionic	Butyric
Rumen	2.661	1.225	0.413	69.51	35.34	8.97	414.3	210.6	53.5
Omasum	1.335	0.576	0.251	---	---	---	---	---	---
Cecum	5.112	2.040	0.981	127.33	51.97	20.66	58.6	23.9	9.5
Feces	3.683	1.445	0.766	---	---	---	---	---	---

1. Average dry matter in rumen and cecum is 596 and 46 g respectively.

2. Average body weight of 24 calves = 159 lb.
Energy required for maintenance = 1966 kcal; based on 1230 kcal/100 lb (Brody, 21).

3. Average daily gain/calf = 1.26 lb.
Energy required for growth = 3045 kcal; based on 2417 kcal/lb (Blaxter and Rook, 17).

4. Total energy required for maintenance and growth = 5041 kcal.

5. Caloric values of acetic, propionic, and butyric acids absorbed from:
the rumen = 1408.6, 1044.6, and 318.3 and from
the cecum = 199.2, 118.5, and 56.5 kcal respectively, based on 3.40, 4.96, and 5.95
kcal per gram of acetic, propionic, and butyric acids respectively
(Brody, 21).

where f = total integrated decrease in VFA concentration from 0 to 24 hours after feeding;

C_0 = concentration of VFA at the zero time;

e = natural logarithm;

t = 24 hours or approximate average transit time of feed through the gastrointestinal tract;

$K = .0577$ a constant derived by the following relationship

$$K = \frac{.693}{T_{1/2}} .$$

$T_{1/2}$ was assumed to be 12 hours, or the one-half time between 0 and 24 hours, the length of time interval used to collect fecal output. This equation was derived by integrating the exponential equation $C_t = C_0 e^{-Kt}$ from zero to 24 hours where C_t = concentration of VFA at any time between zero and 24 hours. The exponential equation was found to best describe the curve made in another experiment to study the rate of disappearance of dry matter in the rumen from 14 different forages using the nylon bag technique (Yang and Thomas, 1960).

C_0 was obtained from Figure 3, f was then calculated and the amount of VFA absorbed was assumed to be the product of f times the amount of dry matter in the rumen or in the cecum. The amount of dry matter in these organs was assumed to be a constant with time after feeding and the values used were the averages found for the 24 calves in Trial II. Using the average data given on the lower half of Table 32 the VFA absorbed from the rumen supplied 55% of the total net energy required for maintenance and growth while the cecum supplied 7.4% or a total of 62.4% from the two organs. Fifty per cent of the energy

came from acetic acid and the remaining 50% from propionic and butyric acids. The rumen and cecum supplied 88 and 12% respectively of the energy derived from absorbed VFA.

If the VFA concentrations found in the rumen at 16 hours (Table 32) were assumed to be the initial concentrations, C_0 , (no decrease in concentrations due to time) then the minimum energy equivalent of the absorbed acetic, propionic and butyric acids would respectively be 13.9, 9.3, and 0.4 per cent of the energy necessary for maintenance and growth. The total would be 24% compared to 55% using the calculations and assumptions in the preceding paragraphs.

The above data, using the average of the 24 calves can be compared to that of Sutherland et al. (126) and Stewart et al. (122). They found 63-76% of the maintenance requirement coming from VFA absorbed from the rumen. The two estimates in the present experiment were 141 and 61% of the maintenance requirement. When the same procedure was applied to the data from the individual calves the net energy supplied by the rumen ranged from 21.7 to 321.8 and by the cecum from 1.3 to 63.6% of the energy for maintenance and growth (Appendix, Table 12). Because of the numerous measurements necessary for the calculation, and the fact that the experiments were not planned to estimate caloric values of absorbed VFA, the large variation observed for individual calves was not surprising.

CHAPTER V

DISCUSSION

From a physical view point, a larger quantity of the low-fiber ration should have been consumed by the calves than the high-fiber ration since the capacity of the rumen was the same for both groups. The low-fiber rations were about two times as dense as the high-fiber rations, but the latter did not appreciably stretch the rumen wall. Furthermore, the calves in both trials were able to digest the low-fiber rations more than the high-fiber rations as measured by apparent total digestibility. The calves fed the low-fiber rations, therefore, did not have to consume as much dry matter to derive equal energy as the calf fed the high-fiber rations.

In Trial I the attempt to feed P according to body weight failed. The predetermined levels of 1.8, 2.3, and 3.0 g P/100 lb body weight daily were increased to 3.01, 3.11, and 3.41 g respectively. The primary purpose of the experiment was not accomplished because of the higher than expected P concentration in the basic rations, but the data suggested that the amount of P recommended by NRC (98) of six g P for a 100 lb calf is above requirement. Differences were not significant in feed consumption, body weight gain, and

blood and bone characteristics of the calves fed the three levels of P in Trial I. In Trial II where P was fed as a percentage of the ration, the amount of P needed by the calf immediately after weaning (30-87 days) was much lower than the amount recommended by NRC (98). The difference in response to P levels near 0.135, 0.196, 0.222, and 0.291% of dry matter was small except in bone growth. Considering both trials the P requirement of calves weighing 100 to 200 lb at an age of 30 to 87 days was near 0.20% of the dry ration. Increasing the experimentally determined requirement by a "safety factor" of 25% seems reasonable. This would mean that 0.25% P of the dry ration would be sufficient for calves weighing 100 to 200 lb at 30 to 84 days of age.

The percentage distribution of dry digesta in respective sections of the alimentary tract of calves fed the low-fiber ration was similar to that of calves fed the high-fiber ration within each experiment. However, there was a difference between the calves in Trials I and II in the distribution of dry matter in respective sections of the alimentary tract. The differences in the percentage distribution of dry matter in sections of the alimentary tract of the calves in the two trials could have been caused by the differences in the ingredients used in making the rations. Even with the wide ranges observed the percentage distribution of dry matter in the rumen of calves in the present experiments (Trial I 51-55, Trial II 72-73%) was comparable to results

(58-75%) obtained by several other investigators (7, 20, and 108). Boyne et al. (20) found 75 and 60% of the total dry matter in the whole alimentary tract was in the rumen of sheep killed immediately or 12 hours after feeding. Rogerson (108) reported that the rumen contained 57.6, 59.9, and 73.0% of the dry matter of the entire alimentary tract of sheep fed all grass hay, grass hay plus cassava meal, and all corn grain diets respectively. Similar results were also obtained by Badawy et al. (7). Furthermore, the weight of dry digesta found in the sections and entire alimentary tract of the calf was very close to that of sheep reported by Badawy et al. (7), Boyne et al. (20), and Rogerson (108) but was lower than that found for mature cattle killed with feed not withheld by Elsdon et al. (42).

Wardrop and Coombe (149) reported a constant ratio of ruminal digesta volume to abomasal digesta volume and that the weight of the abomasal contents was relatively constant with age. These claims were not confirmed in the present studies where weight of digesta was used rather than volume to obtain this ratio. A closer review of the paper (149) revealed that their data did not substantiate their claims. In addition to the wide ranges in the ratios obtained by dividing ruminal digesta by abomasal digesta on wet or dry basis, the ratio was also variable when omasal digesta was used instead of abomasal.

Correlation ($r = +0.46$) between rumen retention time and feed consumption was in accord with the results obtained

by Thomas et al. (130), although the usefulness of the relation to predict rumen retention time is limited because of the small r value.

In Trial I lower pH was observed in the ruminal digesta of calves fed the high-fiber rations compared to those fed the low-fiber rations. The significance of this difference is not known. The great difference in pH observed could have been caused by a difference in the amounts of VFA found in the ruminal digesta (405 versus 1140 millimoles VFA for calves fed low- and high-fiber rations respectively). The difference in pH was not caused by the difference in ash content in the rations since they were comparable (Table 1).

The importance of VFA in ruminant nutrition has been recognized for a long time by numerous investigators (11, 33, 42, 43, 52, 54, 91, 102, 104, 122, and 126). Changes in VFA concentrations and molar percentage distribution in the rumen were usually the measurements made in order to study the effect of dietary treatments (44, 78, 79, 103, 126, and 159). Since the estimation of the absolute amounts of VFA in sections of the alimentary tract requires the sacrifice of the experimental subjects only a few such reports were available (42 and 122). In the present experiments, the total VFA present in the entire alimentary tract ranged from 345.0 to 1632.2 with an average of 772.5 millimoles in Trial I and from 324.7 to 1337.2 with an average of 647.0 millimoles in Trial II. The wide ranges in the total VFA found

in the entire alimentary tract were due both to the variations in total digesta and VFA concentration in the tract at the time of slaughtering. The coefficients of variation for the VFA concentration were for acetic 43.7, 35.9, propionic 23.4, 49.1, and butyric 68.3, 44.4 respectively for Trials I and II and for the total ruminal wet digesta 27.7 and 35.9%. In Trial I, larger amounts of VFA (1140 versus 405 millimoles) were found in the rumen because of the larger amounts of ruminal digesta in calves fed the high-fiber rations as compared to those fed the low-fiber rations (790 versus 478 g of dry digesta per 100 lb body weight). Furthermore, the concentration of VFA was somewhat higher for calves fed the high-fiber rations than those fed the low-fiber rations (Appendix, Tables 6, 7, and 8). The higher concentration of ruminal VFA in the calves fed the high-fiber rations could have been related to the rate of VFA production. The concentration observed at time of slaughter may have been nearer the peak of production of VFA in calves fed the high-fiber rations than those fed the low-fiber rations.

Elsden et al. (42) reported that more than 85% of the total VFA of the entire alimentary tract was in the reticulo-rumen of sheep, cattle, and deer killed without a prior period of fast. After fasting the calf for 16 hours the reticulo-rumen contained on the average 84.5 and 57.9% of the VFA found in the entire tract of the calf in Trials I and II respectively. The difference in the percentage

distribution of VFA in the reticulo-rumen between the two trials was principally caused by the difference in the percentage distribution of digesta in the two trials. The amount of VFA present in the omasum was about 8.5% of the total in the entire tract while the abomasum and small intestine contained only 1-2% of the total. A secondary rise occurred in the amount of VFA in the large intestine and cecum. The small amount of VFA in the abomasum and small intestine of calves in the present experiment agreed with the results found by Conrad et al. (29), Ward et al. (144), and Kumeno and Nishimatsu (91). The concentration of VFA in the large intestine and cecum of calves in the present trials was as high or higher than the concentration in the rumen and agreed with results obtained by other investigators (29, 78, and 144).

The major portion (54-79% of the total) of the lactic acid in the gastrointestinal tract was found in the small intestine unlike the VFA which were found only in traces in this section of the tract. The distribution of lactic acid was very similar for most respective organs except the rumen, between the calves in Trials I and II. The difference in distribution of lactic acid in the rumen of calves in Trials I and II could have been caused by a difference in substrates available for microbial degradation, although the method used to determine lactic acid (Barker and Summerson, 12) is not specific for lactic acid. The color development was

found to be influenced by several compounds including dihydroxyacetone, glyceric aldehyde, malic acid, rhamnose and propylene glycol (12). The fact that several compounds interfered in the determination of lactic acid should not invalidate the results obtained in the present experiments unless, of course, when the interfering substances were in some organs and not in others.

The estimation of the extent of absorption and secretion of nutrients in sections of the alimentary tract by the use of the marker ratio technique involves certain assumptions. These are: (1) The marker moves from one organ to another in the same proportion as the nutrient under investigation. (2) The marker is indigestible. (3) The flow of digesta is always aborally. (4) The digesta do not interfere with the chemical determination of the marker and nutrient of interest.

Digestibility values of dry matter and fiber determined by the lignin ratio technique are in agreement with values obtained by other investigators for the rumen (57, 58, 59, 9, and 23). However, the results obtained for P and Ca absorption in the rumen by the lignin ratio technique are not in agreement with those obtained by other workers (26, 38, and 100). This discrepancy could have been due to the consumption of wood shavings by the calves which increased the lignin concentration in the rumen. An increased concentration of the lignin in the rumen probably caused the large

absorption values obtained for P, Ca, and ash when feed was compared to the ruminal content or feces. Since the values calculated by the lignin and Cr_2O_3 ratio equation were comparable for all sections of the alimentary tract except the rumen and the entire tract (feces) proved that the consumption of wood shavings by the calves did not invalidate comparisons of successive sections of the alimentary tract with the lignin ratio equation. For example, the average absorption values for organic matter in the upper and lower sections of the small intestine, large intestine, and cecum were -925, -301; 70, 71; 46, 35 and 46, 40% respectively for lignin and Cr_2O_3 as the indicators. Another reason for the discrepancy between the values calculated by the two markers for the rumen could have been due to a consistent error which increased the lignin concentration in the ruminal digesta. There was the possibility that lignin passage from the rumen was not in proportion to the passage of other components of the digesta.

Digestibility values of nutrients in other sections of the alimentary tract estimated by the marker ratio equation as presented in this study can not be compared logically with values obtained by some methods, especially by cannulation since the latter method yields information or results of digestion of nutrients in the entire section of the tract anterior to the cannula.

When the Cr_2O_3 ratio (Trial I) equation was used to compare feed and the abomasal digesta, the average dry

matter absorbed in the forestomachs was 60% of the amount fed. Similarly, 38% of the ash in the feed disappeared in the forestomach. The percentage disappearance of dry matter in the forestomach of the present experiments agreed with those (25-70%) reported by Hogan and Phillipson (65) and McGilliard (93). Other methods that use radioactive nutrients in vivo or in vitro measure only rates of transfer either into or out of the alimentary tract. If both the influx and efflux rates of a nutrient in a section of the alimentary tract were known, then the overall rate of absorption or secretion can be calculated. Unfortunately, the author has not been able to find any report that includes measurements of absorption and secretion rates simultaneously in sections of the alimentary tract.

Chandler and Cragle (26), Hansard et al. (60), and Smith et al. (120) reported that the main site of Ca secretion was in the small intestine. More secretion than absorption of Ca was definite in the upper section of the small intestine of calves in Trials I and II of the present experiment.

The lower total Ca digestibility observed (Tables 17 and 18) for calves fed the high-fiber rations than for calves fed the low-fiber rations could have been caused by a binding effect of the fiber or related portion in the ration. When the source of fiber was soybean flake, the reduction in Ca digestibility was greater and more consistent

among calves (Trial I) than the reduction in digestibility due to Solka Floc as the source of fiber (Trial II).

Parthasarathy (100), Parthasarathy and Phillipson (101), and Dobson (37) have found that Na was absorbed from the rumen, small intestine, and cecum. Smith (116) found that no net absorption of Na occurred as compared to Na ingested when digesta was collected from the abomasum; 40% when collected at the end of the small intestine, and almost complete at the large intestine. In the present experiments absorption of Na took place in the rumen, omasum, lower section of the small intestine, and rectum while secretion took place in the abomasum, upper section of the small intestine, large intestine, and cecum.

Most studies on VFA absorption have involved the rumen (4, 30, 35, 43, 46, 55, 89, 115, 122, and 137) and results obtained were expressed in some terms of rate of absorption or energy available from the absorbed VFA. Gray et al. (56) and Johnson et al. (69) recently measured the absorption of VFA from the omasum. Gray et al. (56) reported that the omasum of sheep absorbed 40-69% of the VFA in the digesta from the rumen while Johnson et al. (69) reported 51%. These values are in close agreement to those obtained in the present experiment (acetic 41-48, propionic 37-53, butyric 16-48%). An examination of the VFA concentrations alone suggests that VFA were also absorbed in the abomasum (29, 78, and 144). Johnson et al. (69) found that 83% of the

VFA from the omasum disappeared in the abomasum. From the current experiments values for Trials I and II ranged from 44 to 99%.

The fate of VFA in the small intestine of calves in both trials was variable and probably not quantitatively important because of the low concentration of VFA in the abomasum and small intestine. However, the production of VFA in the large intestine and cecum was important since a portion was found to be absorbed in the rectum. The production of VFA in the large intestine and cecum was also substantial because of the high concentration of VFA in these two sections and because of the amount of VFA found in the feces. An average of 461.5 millimoles of VFA was excreted each day. The average molar percentage distribution of VFA in the feces was 68.5, 21.9, 9.6 for acetic, propionic, and butyric acids respectively.

All sections of the alimentary tract except the abomasum and upper section of the small intestine have been found to absorb H_2O . The abomasum and especially the upper section of the small intestine secreted large amounts of H_2O . The secretion of H_2O in these two sections of the tract is partly in accord with that reported by Ridges and Singleton (107) and Hogan and Phillipson (65).

CHAPTER VI

SUMMARY

Eleven and 24 male Holstein calves were used respectively in Trials I and II to study the dietary effects of phosphorus and fiber on the performance of calves from birth until 12 weeks of age. Body weight gains, feed consumption, blood serum levels of phosphorus, calcium and phosphatase activity, and percentage of fat-free rib bone ash were not appreciably influenced by feeding the calf 3.0, 3.1, or 3.4 g of phosphorus per 100 lb body weight (Trial I), or rations containing 0.135, 0.195, 0.222, or 0.291% phosphorus (Trial II). At slaughter (13 weeks old) bone mass (g of rib bone ash/unit body weight) was greater for calves fed 3.4 g P/100 lb body weight or rations containing 0.222% P than for calves fed other levels of phosphorus.

The calves consumed significantly less dry matter per unit body weight when fed the low-fiber rations (10% fiber) than the high-fiber rations (33% fiber) (Trial I). Similarly, in Trial II much less of the ration containing 9% fiber was consumed than of a ration containing 20% (P < .0005).

Following the 12-week performance period, the calves in Trial I were fed Cr₂O₃ for one week by means of capsule

and bolting gun and in Trial II the calves were fitted with collection bags for total collection of feces. All calves were fasted for 16 hours and killed at the end of the 13th week and their gastrointestinal tract was separated into reticulo-rumen, omasum, abomasum, upper and lower small intestine, large intestine, and cecum and the tissues and contents in each organ were weighed and sampled separately.

The percentage distribution of dry digesta in respective sections of the alimentary tract was similar for calves fed the low- and high-fiber rations within each trial. In Trial I, the percentage distribution was on the average for the rumen 71.5-72.8, omasum 3.6-3.7, abomasum 8.1-8.2, upper small intestine 3.2-3.4, lower small intestine 3.4-3.8, large intestine 4.5-6.6, and cecum 3.5-3.7. The percentage distribution listed in the same order for Trial II was 51.4-54.9, 15.8, 3.3-4.6, 4.1-4.8, 4.7-5.3, 11.0-14.8, and 4.6-5.0.

The absolute amount of dry digesta found in the alimentary tract was greater in calves fed the high-fiber rations than in calves fed the low-fiber rations in both trials. In Trial I 667.9 and 1084.1 g of dry digesta per 100 lb body weight were found in the entire alimentary tract of calves fed low- and high-fiber rations respectively, while in Trial II the weights of the dry digesta were 687.4 and 701.6 g. The weight of the wet digesta in the rumen was correlated ($r = +0.57$) with wet weight of the daily feces. Also, rumen

retention time (dry ruminal digesta ÷ daily dry matter consumption) was correlated with daily dry matter consumption ($r = +0.46$). There was no constant ratios between wet or dry ruminal, omasal, and abomasal digesta.

The wet weight of the upper small intestinal, cecal, and total alimentary tract tissues of calves fed the low-fiber rations was heavier than that of the calves fed the high-fiber rations ($P < .05$). In other sections of the alimentary tract the tissue weight was about the same for the groups of calves.

Feeding the high-fiber rations increased the water holding capacity of the rumen by an average of 4.5 and 1.2 lb of water per 100 lb body weight in Trials I and II respectively. The increase amounted to 14 and 4 per cent of the total changes for Trials I and II respectively, but the biological effects, if any, from the increase in rumen capacity are not apparent.

The amount of volatile fatty acids (VFA) present in the entire alimentary tract of calves in Trial I ranged from 345.0 to 1632.2 millimoles with an average of 405.0 and 1140.0 millimoles for the low- and high-fiber fed calves respectively, while in Trial II the range was 324.7 to 1337.2 and the averages were 618.0 and 676.0.

The rumen contained 54.6-87.7 per cent of the total VFA in the gastrointestinal tract of the calves in both trials while the omasum contained about 8.5. Practically

no VFA was found in the abomasum and small intestine. The large intestine and cecum together contained on the average 11.1 to 17.5 per cent of the total VFA in Trial I and 28.0 to 35.7 per cent in Trial II.

In Trial I the average molar percentages of acetic, propionic, and butyric acids in the ruminal digesta were respectively 66, 24, and 10. The average molar percentages for the calves fed the low- and high-fiber ration in Trial II were, respectively, acetic 70.8, 65.2 ($P < .05$), propionic 22.9, 26.6 ($P < .05$), and butyric 6.4, 8.4 ($P < .01$). The VFA molar percentage of other sections of the alimentary tract was not affected by fiber or phosphorus levels. Considerable amounts of VFA were found in the large intestine and cecum and the average molar percentages of acetic, propionic, and butyric acids were respectively 75, 17, and 8 in Trial I. In Trial II the molar percentages in the omasum, large intestine, and cecum had the following ranges: acetic 69-70, propionic 21-22, and butyric acid 8-10.

Only 7.1 and 14.5 millimoles of lactic acid were found in the entire tract per calf in Trials I and II respectively. About 53 and 78 per cent of the total lactic acid in the entire gastrointestinal tract were in the small intestine of calves in Trials I and II respectively. Most of the remainder was found in the rumen.

The degree of absorption and secretion of nutrients was determined in eight sections of the alimentary tract by using

the marker ratio equation (lignin and Cr_2O_3 , Trial I and lignin, Trial II) and the concentrations of nutrient in two consecutive sections of the alimentary tract. Significantly more dry matter and organic matter and less fiber were absorbed in the rumen of calves fed the low-fiber rations than those fed the high-fiber rations ($P < .01$). Dry matter and organic matter were secreted into the omasum, abomasum, and upper section of the small intestine and then reabsorbed in the lower section of the small intestine, large intestine, cecum, and rectum.

The trends in the absorption and secretion of phosphorus, calcium, and ash in sections of the alimentary tract were comparable to those of dry matter and organic matter.

Sodium was absorbed in the rumen and omasum and secreted in the abomasum and upper section of the small intestine and then reabsorbed by the remainder of the tract.

About 66 per cent of the water from the ruminal digesta was absorbed in the omasum. Addition of water to the relatively dry omasal digesta occurred in the abomasum and upper section of the small intestine. The water secreted by the abomasum and upper section of the small intestine was almost completely reabsorbed by the time the digesta reached the rectum.

The omasum of calves absorbed on the average 44.6, 44.7, and 31.7 per cent of the ruminal acetic, propionic, and butyric acids, respectively. Further absorption of VFA

occurred in the abomasum. The degree of absorption and secretion of VFA in the small intestine was probably quantitatively unimportant because of the low concentrations in this section of the tract and in the abomasum. The large intestine and cecum produced significant amounts of VFA, part of which was absorbed in the rectum.

Lactic acid was produced in the abomasum and small intestine and absorbed in all other sections of the alimentary tract studied.

A method was developed to estimate the caloric value of the VFA absorbed from the alimentary tract. This method essentially involved the calculation of the integrated percentage changes of the concentration of VFA between rumen and omasum, and cecum and feces. Based on the average data obtained from calves in Trial II the rumen supplied VFA equal to 55 per cent of the total net energy required for maintenance and growth while the cecum supplied 7.4 per cent. Of the total VFA energy 50 per cent came from acetic acid and the remaining 50 per cent came from propionic and butyric acids.

The degree of absorption of nutrients by the rumen using Cr_2O_3 was less when compared to lignin as the indicator. Comparable results were obtained by using lignin and Cr_2O_3 for other sections of the tract.

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APPENDIX

TABLE 1.--Average daily dry matter consumption from the 1st to the 13th week of the experiment^a

Calf No.	Weeks on Experiment												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	Trial I (lb/100 lb body weight)												
2	0.10	0.00	0.10	0.00	0.90	1.40	2.28	2.26	2.10	2.23	2.46	2.23	2.03
5	0.30	0.30	0.80	0.70	1.50	1.10	1.59	1.84	2.20	2.33	2.14	1.94	2.01
4	0.00	0.00	0.50	0.30	1.10	0.60	1.71	2.24	2.46	2.14	2.36	2.46	2.19
11	0.10	0.00	0.50	0.40	1.30	1.20	1.79	1.63	2.10	1.83	2.01	2.08	1.91
6	0.30	0.10	0.30	0.20	1.10	1.70	2.36	2.78	2.54	2.13	2.48	2.44	2.17
10	0.30	0.30	0.50	1.40	2.50	2.70	2.37	2.36	2.36	2.27	1.84	2.24	2.07
7	0.20	0.40	1.00	1.60	1.40	1.30	2.16	1.81	2.13	2.33	2.23	2.40	2.17
8	0.10	0.10	0.10	0.90	2.10	1.90	2.93	2.76	2.84	2.67	2.80	2.61	2.36
3	0.20	0.00	0.90	1.10	1.60	1.60	2.73	2.17	2.68	2.54	2.80	2.98	2.90
1	0.60	0.00	0.20	0.30	1.00	0.90	1.79	2.21	2.33	2.18	2.57	2.27	2.05
9	0.10	0.10	0.50	0.80	1.40	2.20	2.07	2.04	1.93	2.08	2.42	2.56	2.38
	Trial II (lb/100 lb body weight)												
3	0.00	0.16	0.37	0.98	0.95	1.45	1.72	2.72	2.15	1.97	2.22	2.22	2.16
10	0.00	0.09	0.05	0.24	0.75	1.27	1.68	1.79	2.09	1.94	2.25	2.11	2.06
23	0.13	0.33	0.04	0.73	1.59	1.25	1.56	1.57	1.93	1.81	1.82	1.62	1.83
1	0.10	0.15	0.20	0.49	0.85	1.72	1.66	2.08	2.26	2.42	1.88	2.46	2.87
12	0.01	0.00	0.00	0.06	0.13	0.47	0.71	1.09	1.82	1.76	1.53	1.69	1.41
18	0.15	0.34	0.61	1.29	2.06	2.34	2.34	2.14	2.06	2.56	2.57	2.72	2.65
5	0.08	0.24	0.63	0.89	0.60	1.71	1.80	2.28	2.06	1.79	2.11	2.20	2.10
16	0.14	0.14	0.35	0.90	0.89	1.74	1.56	1.94	1.87	1.26	2.17	1.54	1.97
24	0.21	0.07	0.63	1.18	1.26	1.55	1.98	2.30	2.15	1.77	2.24	2.04	1.86
25						1.23	1.02	1.68	1.80	1.71	2.15	1.96	2.16
26	0.12	0.20	0.21	0.00	0.17	0.22	0.99	1.67	1.83	2.10	1.88	2.39	2.05
17	0.00	0.24	0.57	1.17	1.37	1.73	1.68	1.92	2.16	2.44	2.29	1.79	2.01
4	0.07	0.12	0.14	0.27	1.05	1.66	1.50	1.90	1.84	2.67	1.89	2.45	1.96

TABLE 1. ---Continued

Calf No.	Weeks on Experiment												
	1	2	3	4	5	6	7	8	9	10	11	12	13
9	0.03	0.31	0.62	0.86	1.31	2.38	2.73	2.69	3.06	2.29	2.29	2.19	2.46
20	0.00	0.25	1.34	1.62	2.13	1.17	2.04	2.09	2.39	2.11	2.41	2.70	2.06
2	0.00	0.36	0.48	1.08	1.27	1.87	2.24	2.75	2.60	2.74	2.72	3.07	2.93
11	0.20	0.09	0.15	0.34	1.20	1.35	1.96	1.86	2.41	1.71	1.90	1.64	1.58
21	0.00	0.22	0.76	0.93	1.78	2.40	2.43	2.53	2.42	2.06	2.23	2.50	1.77
6	0.07	0.21	0.27	0.87	1.00	1.46	2.01	2.04	2.14	2.36	1.91	2.59	2.37
14	0.00	0.15	0.26	1.08	1.69	2.34	2.40	1.57	1.81	2.49	2.00	2.31	2.10
19	0.04	0.12	0.29	0.45	0.78	1.48	1.79	1.90	2.17	2.39	2.07	2.28	2.29
8	0.06	0.06	0.56	0.81	1.09	1.53	1.97	1.93	2.60	2.24	2.15	1.78	2.24
13	0.09	0.04	0.23	0.61	1.31	1.43	2.31	1.95	2.38	2.20	1.82	2.15	1.74
27							2.14	2.29	1.89	2.44	2.76	2.26	2.84

^aSee footnotes of Table 5 for treatments of calves.

TABLE 2.--Average daily total phosphorus consumption and P/Ca ratio in the diets from the 1st to the 13th week of the experiment^a

Weeks on Experiment	Calf Number												
	2	5	4	11	6	10	7	8	3	1	9		
	(P g/100 lb body weight)												
1	3.29	3.49	3.14	3.21	3.52	3.55	3.38	3.32	3.31	3.71	3.21		
2	3.18	3.57	3.06	3.00	3.28	3.56	3.28	3.38	3.10	2.86	3.01		
3	3.26	3.83	3.47	3.55	3.41	3.57	3.75	3.32	4.00	2.91	3.20		
4	3.08	3.37	3.04	3.18	3.86	4.48	4.19	3.95	3.93	2.83	3.59		
5	2.92	2.63	3.18	3.21	4.01	4.76	2.30	3.00	2.91	4.13	3.36		
6	2.02	1.09	1.89	2.17	4.04	3.74	2.16	2.09	2.20	2.74	4.06		
7	3.08	3.19	3.59	3.11	4.24	3.34	2.14	3.44	3.89	3.19	3.08		
8	4.78	2.14	2.99	2.28	3.63	3.17	2.25	3.23	2.82	4.37	2.65		
9	2.88	3.11	3.44	3.01	3.54	3.15	2.16	3.35	2.95	3.08	2.85		
10	2.74	2.89	2.82	2.54	2.82	3.07	2.90	3.36	2.83	2.99	3.41		
11	3.04	2.82	3.15	2.81	3.39	2.54	2.37	3.55	3.37	3.26	3.17		
12	3.03	2.66	3.11	2.72	3.18	3.54	2.49	3.13	3.05	3.33	3.28		
13	2.79	2.73	2.80	2.60	2.84	3.29	2.31	2.84	3.00	3.05	3.06		
	(Ca/P ratio)												
1	1.25	1.24	1.25	1.25	1.24	1.24	1.31	1.28	1.31	1.43	1.28		
2	1.25	1.24	1.25	1.25	1.25	1.24	1.39	1.28	1.25	1.25	1.28		
3	1.25	1.23	1.24	1.24	1.24	1.24	1.53	1.28	1.51	1.31	1.43		
4	1.25	1.23	1.24	1.24	1.00	1.23	1.66	1.52	1.57	1.36	1.49		
5	2.16	2.33	2.35	2.31	2.37	2.13	2.65	2.55	2.61	2.62	2.70		
6	2.66	3.94	3.10	2.74	2.30	2.56	2.81	2.77	2.78	2.83	2.62		
7	2.16	2.06	2.17	2.31	2.24	2.84	2.57	2.55	2.54	3.26	2.73		
8	1.16	2.93	2.34	2.88	2.51	2.73	2.71	2.76	2.90	2.30	2.83		
9	2.62	2.25	2.39	2.38	2.61	2.67	2.78	2.71	2.72	2.63	2.77		
10	2.78	2.77	2.96	2.90	3.17	2.71	2.63	2.73	2.76	2.75	2.69		
11	2.49	2.68	2.53	2.48	2.56	3.02	3.04	2.71	2.65	2.71	2.73		
12	2.69	2.83	2.69	2.64	2.67	2.49	2.54	2.80	2.80	2.76	2.72		
13	2.70	2.83	2.70	2.64	2.67	2.50	2.53	2.80	2.80	2.75	2.71		

^aSee footnotes of Table 5 for treatments of calves.

TABLE 3.--Wet digesta found in sections of alimentary tract of calves killed at 16 hours after fasting and average daily fecal output

Calf No.	Reticulo-Rumen	Section of Alimentary Tract						Avg. Daily Feces
		Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	
Trial I (g/calf)								
2	7536	295	318	454	817	0	227	1174
5	6946	331	817	499	477	363	363	3108
4	6719	109	431	182	354	658	272	1317
11	7037	486	636	590	817	863	704	1571
6	7582	331	1135	681	545	726	386	3166
10	5221	468	590	386	499	545	204	2510
7	11713	876	1180	1317	1180	636	409	1910
8	8444	1326	1407	863	590	1044	863	1535
3	4903	368	976	1044	1317	1035	499	1291
1	11395	272	908	1044	1317	272	1407	1165
9	8944	740	1294	522	1135	204	545	2401
Trial II (g/calf)								
3	2677	394	454	409	431	499	182	1174
10	8376	1036	409	681	522	1249	295	3108
23	3450	475	363	422	563	522	168	1317
1	4131	121	309	386	318	409	204	1571
12	7400	1111	499	341	704	999	318	3166
18	4908	685	72	318	913	726	141	2510
5	3814	382	341	454	486	409	318	1910
16	3496	298	91	359	608	341	422	1535
24	4599	297	18	409	477	331	272	1291
25	9489	260	386	390	613	422	232	1165
26	5103	713	218	418	259	504	413	2401

TABLE 3.--Continued

Calf No.	Reticulo-Rumen	Section of Alimentary Tract						Avg. Daily Feces
		Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	
17	4903.	409.	227.	368.	776.	545.	91.	2375.
4	4517.	244.	444.	318.	749.	590.	341.	2355.
9	5357.	1031.	209.	622.	1126.	894.	318.	3587.
20	4835.	819.	227.	726.	1135.	636.	114.	2069.
2	5539.	499.	182.	613.	908.	636.	613.	3916.
11	2906.	166.	272.	114.	341.	1053.	182.	1551.
21	3855.	729.	136.	658.	1217.	953.	182.	1916.
6	4926.	1201.	295.	499.	749.	590.	168.	2558.
14	5330.	520.	522.	409.	863.	1008.	431.	2739.
19	3310.	428.	114.	1131.	568.	590.	409.	2631.
8	8263.	1049.	681.	704.	1294.	908.	363.	3045.
13	4958.	537.	91.	645.	1090.	1276.	409.	1776.
27	3818.	127.	109.	463.	490.	359.	191.	2453.

^aSee footnotes of Table 5 for treatments of calves.

TABLE 4.--Dry matter percentage of digesta in sections of the alimentary tract of calves killed at 16 hours after fasting and average percentage dry matter of feces^a

Calf No.	Sections of Alimentary Tract							Feces
	Rumen	Omasum ^b	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	
Trial I								
2	13.40	20.00	14.41	9.84	7.59	0.00	10.65	21.72
5	14.05	20.00	23.85	8.93	7.22	16.02	11.04	18.83
4	10.20	20.00	18.08	10.28	6.90	16.44	13.59	23.99
11	13.34	20.00	13.08	8.61	7.46	16.67	14.63	22.41
6	13.80	20.00	13.60	8.65	8.51	17.42	13.68	18.58
10	11.02	20.00	15.70	8.91	8.25	17.15	13.09	23.11
7	17.27	20.00	13.30	6.98	7.00	13.95	13.31	22.72
8	16.28	20.00	14.17	8.04	5.90	15.55	11.37	23.91
3	12.86	20.00	13.89	7.14	6.30	16.43	12.99	21.92
1	18.58	20.00	17.41	7.77	6.86	10.37	8.00	24.72
9	16.93	20.00	15.49	7.50	8.76	12.62	11.63	
Trial II								
3	8.38	29.74	13.91	8.44	6.72	18.05	16.02	21.72
10	14.93	24.92	16.23	9.76	17.32	28.72	27.15	18.83
23	10.83	31.11	20.31	8.54	7.90	20.09	16.90	23.99
1	8.07	33.81	15.73	9.61	8.73	17.76	17.01	22.41
12	16.20	23.98	14.44	9.56	7.79	16.73	14.27	18.58
18	7.55	37.61	11.53	8.37	6.67	19.56	15.85	23.11
5	9.37	29.09	15.03	9.54	10.30	19.93	19.43	22.72
16	8.14	36.84	8.00	6.32	6.94	17.80	23.17	23.91
24	14.43	35.67	7.00	7.56	3.58	9.68	7.12	21.92
25	16.03	31.82	17.38	7.81	6.91	22.31	17.37	24.72

TABLE 4.--Continued

Calf No.	Rumen	Omasum ^b	Abomasum	Sections of Alimentary Tract			Large Intestine	Cecum	Feces
				Upper Small Intestine	Lower Small Intestine	Intestine			
26	9.28	32.52	13.18	12.53	8.73	19.11	16.56	24.03	
17	8.49	31.05	15.75	9.58	7.08	14.92	13.67	20.34	
4	12.88	25.68	18.28	9.95	7.51	18.71	16.49	22.29	
9	9.22	25.33	6.72	8.39	6.82	20.93	15.58	23.98	
20	13.63	33.47	6.95	5.61	4.81	22.23	19.35	25.81	
2	7.98	25.02	6.75	8.67	8.09	18.14	11.83	24.13	
11	11.07	34.70	17.73	7.00	5.80	21.74	19.09	23.72	
21	10.12	37.38	6.13	7.12	5.39	18.43	12.23	25.73	
6	15.85	30.85	15.97	10.22	8.88	16.60	14.34	24.98	
14	9.43	23.68	10.84	8.14	6.97	18.08	14.82	21.50	
19	13.03	30.90	9.37	12.32	7.91	17.78	17.02	22.58	
8	13.64	27.24	18.48	8.77	6.60	18.33	15.03	23.73	
13	13.60	37.16	11.37	7.21	5.91	21.75	16.71	26.13	
27	11.21	30.19	12.67	9.32	5.57	19.02	13.43	21.85	

^aSee footnotes of Table 5 for treatments of calves.

^bTrial I, per cent dry matter of omasal digesta was assumed to be 20 on the basis of visual comparison with digesta from other organs.

TABLE 5.--Total millimoles of volatile fatty acids in the whole alimentary tract and the experimental treatments of calves

Trial I			Trial II		
Calf No.	VFA	Treatment ^a	Calf No.	VFA	Treatment ^b
2	455.8	P ₁ F ₁	3	324.7	P ₁ F ₁
5	373.8	P ₁ F ₁	10	981.5	P ₁ F ₁
4	417.1	P ₂ F ₁	23	534.7	P ₁ F ₁
11	547.4	P ₂ F ₁	1	426.1	P ₂ F ₁
6	681.9	P ₃ F ₁	12	790.0	P ₂ F ₁
10	345.0	P ₃ F ₁	18	644.6	P ₂ F ₁
7	1383.8	P ₁ F ₂	5	673.7	P ₃ F ₁
8	909.4	P ₁ F ₂	16	492.5	P ₃ F ₁
3	561.7	P ₂ F ₂	24	570.4	P ₃ F ₁
1	1632.2	P ₃ F ₂	25	1136.9	P ₄ F ₁
9	971.2	P ₃ F ₂	26	510.4	P ₄ F ₁
			17	335.3	P ₄ F ₁
			4	711.1	P ₁ F ₂
			9	419.6	P ₁ F ₂
			20	482.7	P ₁ F ₂
			2	506.8	P ₂ F ₂
			11	474.1	P ₂ F ₂
			21	477.8	P ₂ F ₂
			6	1133.0	P ₃ F ₂
			14	556.1	P ₃ F ₂
			19	620.4	P ₃ F ₂
			8	1337.2	P ₄ F ₂
			13	959.4	P ₄ F ₂
			27	432.2	P ₄ F ₂

^aP₁F₁, 1.8 g of P/100 lb body wt, 10% fiber ration
P₁F₂, 1.8 g of P/100 lb body wt, 33% fiber ration
P₂F₁, 2.3 g of P/100 lb body wt, 10% fiber ration
P₂F₂, 2.3 g of P/100 lb body wt, 33% fiber ration
P₃F₁, 3.0 g of p/100 lb body wt, 10% fiber ration
P₃F₂, 3.0 g of P/100 lb body wt, 33% fiber ration

^bP₁F₁, 0.137% P, 8.60% fiber ration
P₁F₂, 0.133% P, 17.60% fiber ration
P₂F₁, 0.195% P, 7.61% fiber ration
P₂F₂, 0.197% P, 19.82% fiber ration
P₃F₁, 0.202% P, 8.86% fiber ration
P₃F₂, 0.241% P, 20.09% fiber ration
P₄F₁, 0.297% P, 9.05% fiber ration
P₄F₂, 0.285% P, 19.75% fiber ration

TABLE 6.--Acetic acid concentrations in digesta obtained from alimentary sections and feces of calves

Sections of Alimentary Tract										
Calf No.	Rumen	Omasum	Abomasum	Upper Small Intestine		Lower Small Intestine		Large Intestine	Cecum	Feces
				Intestine	Intestine	Intestine	Intestine			
Trial I (Micromoles/g wet material)										
2	41.0	c	2.0	1.5	7.5	b	65.6			
5	31.1	c	0.9	0.7	3.6	91.1	87.1			
4	29.9	c	2.6	0.5	4.6	84.6	64.6			
11	27.8	c	3.2	b	3.3	60.5	85.0			
6	44.9	c	10.2	2.2	8.4	75.8	69.1			
10	33.3	c	3.2	b	2.4	72.7	72.3			
7	74.5	c	6.8	b	3.8	55.1	56.5			
8	62.5	c	2.3	b	b	67.0	58.0			
3	56.4	c	2.0	2.2	0.1	59.8	75.2			
1	96.9	c	8.0	0.6	22.6	43.6	61.7			
9	73.6	c	4.0	b	0.9	43.3	40.0			
Trial II (Micromoles/g wet material)										
3	40.0	93.2	17.0	2.5	10.8	73.0	157.6			154.7
10	54.4	73.2	14.1	5.5	8.1	137.8	102.2			132.0
23	56.8	79.9	16.3	b	23.4	164.7	189.4			186.5
1	40.4	78.2	22.4	4.9	9.5	153.3	181.6			137.7
12	51.4	59.2	9.6	b	10.5	127.6	132.1			78.9
18	53.7	61.8	17.6	b	14.2	170.6	164.7			174.4
5	64.7	80.9	18.7	6.2	38.0	191.7	237.5			121.3
16	54.9	63.3	10.2	b	7.7	128.9	154.2			131.0
24	77.5	56.1	5.5	b	b	73.4	74.2			186.4
25	69.0	48.0	7.3	b	b	118.5	140.6			125.4

TABLE 6. ---Continued

Calf No.	Sections of Alimentary Tract							
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Feces
26	38.8	44.4	4.1	b	4.7	119.1	137.5	156.5
17	26.9	82.6	6.6	b	9.5	113.2	72.7	126.3
4	60.7	47.7	14.9	b	12.7	143.5	194.8	97.0
9	20.8	29.6	b	b	5.5	122.0	127.7	179.9
20	35.9	51.1	7.4	b	6.3	149.0	131.6	160.2
2	28.0	50.0	9.5	b	5.4	131.3	105.2	137.5
11	44.1	36.4	11.1	5.4	b	139.6	125.0	151.4
21	39.1	51.7	b	b	b	123.8	128.3	189.7
6	103.1	117.0	15.7	7.4	9.2	125.0	135.3	140.8
14	32.5	43.8	5.5	b	6.4	126.6	127.8	151.4
19	63.3	116.4	10.0	b	6.2	157.7	190.0	119.9
8	73.5	94.6	15.8	b	b	116.5	123.8	102.0
13	59.2	35.6	14.2	b	7.1	164.5	149.6	131.6
27	54.2	48.9	8.0	b	4.8	106.6	97.6	165.6

^aSee footnotes of Table 5 for treatments of calves.

^bTrace concentration.

^cNo determination made.

TABLE 7.--Propionic acid concentrations in digesta obtained from alimentary sections and feces of calves^a

Sections of Alimentary Tract										
Calf No.	Rumen	Omasum	Abomasum	Upper Small Intestine		Lower Small Intestine		Large Intestine	Cecum	Feces
				Intestine	Intestine	Intestine	Intestine			
Trial I (Micromoles/g wet material)										
2	14.0	c	b	b	b	b	b	b	18.2	
5	8.4	c	b	b	b	b	b	17.2	16.8	
4	16.1	c	0.6	b	b	b	b	27.7	20.0	
11	19.4	c	0.2	b	b	b	b	13.9	18.6	
6	20.8	c	1.5	b	b	b	b	16.4	15.9	
10	18.4	c	b	b	b	b	b	11.4	10.8	
7	21.7	c	1.1	b	b	b	b	8.3	12.8	
8	21.5	c	b	b	b	b	b	8.7	8.8	
3	14.4	c	b	b	b	b	b	13.1	14.0	
1	16.0	c	0.4	b	b	b	b	10.9	11.6	
9	16.0	c	0.4	b	b	3.9	b	6.5	6.4	
Trial II (Micromoles/g wet material)										
3	15.5	43.0	b	1.0	b	b	b	22.3	48.9	61.2
10	10.4	20.5	b	4.4	2.4	b	b	36.6	27.5	32.0
23	22.0	31.2	b	1.7	b	b	b	37.7	48.2	35.2
1	16.7	28.4	5.4	1.7	b	b	b	47.4	55.3	43.5
12	9.1	12.2	b	3.3	b	b	b	30.6	34.8	14.7
18	14.7	22.5	b	3.0	2.2	b	b	39.8	38.5	41.4
5	23.1	25.3	b	5.8	b	b	b	72.4	86.1	36.0
16	20.6	16.0	2.0	2.8	b	b	b	44.6	60.2	46.2
24	20.7	19.7	b	2.7	b	b	b	20.2	21.6	57.0
25	32.3	15.2	b	1.1	b	b	b	32.0	41.9	44.9

TABLE 7.--Continued

Calf No.	Sections of Alimentary Tract							
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Feces
26	13.6	20.6	2.0	b	b	49.7	54.5	56.6
17	7.9	20.1	b	2.0	b	37.1	23.5	42.0
4	33.3	12.1	b	2.7	2.8	39.1	44.6	31.0
9	7.5	9.3	b	b	b	25.3	32.4	41.0
20	12.8	24.6	b	b	b	28.7	30.3	39.2
2	9.3	13.3	1.8	b	1.9	67.7	52.7	55.8
11	18.0	4.8	b	b	b	54.3	48.0	61.5
21	14.5	13.3	b	b	b	39.7	39.4	52.3
6	33.5	54.1	1.6	6.3	1.2	60.8	57.9	66.6
14	9.8	8.4	b	b	b	39.8	41.9	52.8
19	19.9	33.6	b	2.1	b	40.0	52.4	33.7
8	33.7	35.9	3.2	3.4	1.2	39.9	37.7	35.0
13	39.8	17.0	4.9	b	b	41.0	44.8	47.2
27	28.5	22.2	2.3	b	1.8	39.9	33.4	42.4

^aSee footnotes of Table 5 for treatments of calves.

^bTrace concentration.

^cNo determination made.

TABLE 8. --Cont Inued

Calf No.	Sections of Alimentary Tract							
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Feces
25	6.8	5.3	b	b	b	15.6	11.9	15.6
26	2.1	5.3	b	b	b	16.3	16.2	25.2
17	2.5	7.0	b	b	b	11.8	7.7	17.4
4	8.1	9.5	b	b	b	23.7	30.3	14.0
9	3.1	4.7	b	b	b	14.7	14.5	25.1
20	5.1	6.1	b	b	b	20.6	19.7	26.9
2	3.4	6.9	b	b	b	13.3	9.7	12.8
11	5.9	b	b	b	b	25.2	21.0	24.7
21	4.0	7.0	b	b	b	15.2	13.5	34.0
6	12.3	16.2	b	b	b	17.7	14.3	18.1
14	4.9	5.2	b	b	b	17.3	17.0	21.4
19	8.5	13.1	b	b	b	21.7	28.2	18.1
8	7.8	11.2	2.1	b	b	15.1	15.2	13.2
13	9.2	4.6	2.1	b	b	26.2	17.7	22.2
27	5.0	4.6	b	b	b	11.1	9.1	16.4

^aSee footnotes of Table 5 for treatments of calves.

^bTrace concentration.

^cNo determination made.

TABLE 9.--Lactic acid concentrations in digesta obtained from alimentary sections and feces of calves

Calf No.	Sections of Alimentary Tract									
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Feces		
Trial I (Micrograms/g wet material)										
2	80.0	b	93.0	940.0	760.0	b	103.3			
5	32.8	b	86.0	780.0	913.3	85.0	55.0			
4	41.6	b	37.6	370.0	470.0	97.5	97.5			
11	30.0	b	26.0	300.0	310.0	57.3	48.0			
6	132.0	b	35.2	600.0	940.0	102.5	67.5			
10	54.0	b	43.6	440.0	483.3	78.0	62.0			
7	64.0	b	42.0	450.0	400.0	175.0	40.0			
8	152.0	b	19.0	340.0	360.0	71.3	40.0			
3	26.0	b	29.0	320.0	240.0	65.0	45.0			
1	36.5	b	56.0	600.0	400.0	52.5	20.0			
9	52.0	b	18.6	460.0	300.0	112.0	58.0			
Trial II (Micrograms/g wet material)										
3	13.0	32.0	168.0	1000.0	560.0	60.0	64.0	100.0		
10	15.6	12.8	84.0	640.0	520.0	60.0	27.2	86.0		
23	14.2	33.0	52.0	370.0	415.0	47.5	34.0	63.3		
1	14.6	30.6	28.6	432.0	460.0	48.8	43.2	76.0		
12	13.0	16.2	144.0	680.0	410.0	25.0	19.0	27.0		
18	12.5	35.1	110.0	700.0	460.0	50.4	40.5	80.0		
5	9.6	12.8	64.0	340.0	400.0	24.0	29.2	34.0		
16	16.5	42.8	164.0	560.0	465.0	58.0	47.0	78.8		
24	10.5	45.2	256.0	540.0	496.0	27.0	16.0	80.0		

TABLE 9. --Continued

Calf No.	Sections of Alimentary Tract							
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Feces
25	13.0	43.0	41.0	400.0	350.0	114.0	88.2	42.0
26	12.7	22.8	122.0	540.0	560.0	36.0	22.0	44.0
17	14.0	25.2	78.0	810.0	470.0	40.6	25.0	70.6
4	16.0	26.2	120.0	600.0	400.0	39.0	33.2	41.2
9	8.0	13.0	64.0	360.0	280.0	33.2	20.0	41.0
20	16.5	28.2	100.0	258.0	210.0	54.0	35.5	66.6
2	12.0	30.6	264.0	500.0	380.0	64.0	26.0	64.0
11	14.6	25.2	152.0	580.0	500.0	32.4	29.0	80.6
21	13.5	122.4	89.0	460.0	260.0	27.0	26.5	60.0
6	11.0	17.6	24.8	410.0	292.0	28.8	24.8	45.0
14	10.0	22.5	00.0	440.0	290.9	46.0	32.0	65.4
19	16.5	23.0	42.0	396.0	350.0	39.9	38.0	45.3
8	10.6	12.4	32.0	500.0	300.0	28.8	24.8	42.4
13	17.8	24.0	25.0	360.0	270.0	33.0	32.0	33.2
27	12.5	19.0	54.0	410.0	350.0	32.5	27.0	48.0

^aSee footnotes of Table 5 for treatments of calves.

^bNo determination made.

TABLE 10.--Percentage digestibility of nutrients in sections and the entire (total digestibility) alimentary tract of calves, Trial Ia

Sections of Alimentary Tract									
Calf No.	Rumen	Abomasum	Upper Small Intestine		Lower Small Intestine		Large Intestine	Cecum	Entire Tract
			Intestine	Intestine	Intestine	Intestine			
Dry Matter									
2	86.2	-50.4	-595.0	70.1	51.6*	57.6	81.5		
5	83.5	38.8	-1503.5	45.6	80.4	81.1	82.6		
4	80.4	1.9	-503.2	60.9	58.8	61.4	81.7		
11	82.8	0.7	-449.0	69.8	44.3	47.5	84.6		
6	81.3	-25.5	-391.5	68.8	50.0	49.5	81.9		
10	77.7	19.4	-747.0	70.6	59.5	61.2	81.8		
7	57.8	-18.9	-393.2	77.8	25.6	31.0	59.1		
8	51.4	21.3	-523.8	51.0	75.6	67.8	71.4		
3	58.2	37.9	-560.3	58.2	50.7	48.8	64.7		
*12	55.9	-5.8	-143.2	89.8	13.4	12.2	67.5		
1	69.6	6.8	-507.6	71.3	22.5	17.7	61.7		
9	51.6	32.1	-1314.9	89.6	32.7	37.1	67.3		
Organic Matter									
2	87.0	-48.5	-610.4	72.4	66.5*	56.5	83.6		
5	84.8	42.6	-1628.4	48.8	79.7	80.5	84.2		
4	82.3	2.0	-507.1	62.9	56.0	58.8	82.7		
11	84.7	0.7	-414.7	70.2	41.0	43.5	85.9		
6	82.2	9.7	-553.0	68.1	47.8	47.3	82.8		
10	80.3	23.9	-803.8	71.4	57.3	60.0	83.3		
7	60.0	-21.8	-362.0	77.9	21.9	27.9	61.1		
8	57.3	23.4	-498.6	51.2	73.6	65.8	74.8		
3	60.5	35.8	-524.2	59.8	46.4	45.1	65.5		
*12	60.4	28.6	-245.6	88.7	4.4	6.8	71.1		
1	70.8	4.9	-468.9	72.2	20.2	14.7	64.9		
9	53.9	30.1	-1192.3	89.4	29.7	35.0	69.0		

TABLE 10.--Continued

Calf No.	Sections of Alimentary Tract							Entire Tract
	Rumen	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum		
			Fiber					
2	35.1	-49.3	43.2	-36.8	15.0*	12.6	34.0	
5	18.7	39.4	72.7	3.6	24.7	25.8	37.7	
4	16.9	19.2	9.5	0.6	12.0	12.3	35.6	
11	17.6	13.2	31.9	11.9	12.5	18.7	29.6	
6	11.6	18.9	13.9	-11.1	21.6	20.3	30.0	
10	16.7	11.5	1.0	4.3	7.2	12.6	33.8	
7	42.9	22.0	58.0	41.9	3.4	3.1	38.2	
8	35.4	16.0	14.0	9.8	27.5	3.7	59.5	
3	47.1	26.4	80.3	-10.4	30.4	25.1	46.1	
*12	32.1	-0.4	1.6	79.3	-14.1	-7.8	52.5	
1	57.3	-4.9	18.9	6.3	13.2	2.8	56.7	
9	35.8	18.5	27.7	14.9	7.9	34.3	47.8	
			Phosphorus					
2	73.9	-111.7	-587.7	71.6	76.8*	63.9	61.1	
5	57.7	86.0	-7723.1	39.4	88.9	88.5	68.6	
4	53.4	59.0	-1534.5	65.8	75.9	78.6	74.2	
11	71.2	22.2	-338.9	73.6	70.2	70.5	83.0	
6	69.5	26.4	-520.3	76.2	64.0	61.5	74.0	
10	67.3	67.3	-401.6	73.5	79.8	56.0	80.3	
7	30.0	19.7	-243.5	86.7	54.6	66.2	59.6	
8	39.4	38.5	-522.2	-6.7	91.4	88.8	77.0	
3	-15.9	68.4	-501.8	69.5	73.7	66.0	52.0	
*12	117.5	55.5	-1243.9	72.2	52.6	86.6	101.7	
1	66.0	41.5	-387.2	83.0	48.3	49.0	63.3	
9	86.9	53.6	-837.6	92.3	75.5	72.9	77.1	

TABLE 10.--Continued

Calf No.	Sections of Alimentary Tract							Entire Tract
	Rumen	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum		
			Calcium					
2	84.8	27.2	-483.2	23.5	30.4*	32.1	66.6	
5	80.2	86.6	-3222.8	35.4	65.4	67.3	80.1	
4	71.4	71.9	-444.2	36.0	50.8	30.3	86.2	
11	87.0	16.3	-338.9	34.5	22.7	31.6	75.6	
6	86.8	29.9	-520.3	63.0	51.7	45.8	90.0	
10	73.5	44.2	-401.6	53.5	2.8	44.0	66.6	
7	44.1	13.6	-243.5	71.7	-21.0	-12.9	43.0	
8	54.4	54.1	-522.2	29.7	68.9	58.5	71.5	
3	35.2	69.9	-501.8	44.5	12.9	21.1	43.2	
*12	68.9	10.6	-34.7	41.8	13.7	-9.5	73.5	
1	71.1	39.2	-387.2	43.4	-26.1	-9.3	38.8	
9	47.1	65.5	-837.6	62.1	37.5	52.2	59.7	
			Ash					
2	76.6	-77.5	-607.6	58.0	87.6*	61.1	52.1	
5	66.0	5.2	-975.0	23.8	84.1	85.0	57.8	
4	62.5	2.6	-476.3	36.6	80.6	79.9	74.0	
11	71.6	23.0	-835.2	64.8	63.8	71.1	73.6	
6	77.6	81.0	-379.4	67.2	67.2	66.3	78.6	
10	53.5	21.1	-498.3	66.9	72.8	68.2	69.7	
7	49.2	18.7	-1144.5	80.5	53.2	52.0	52.9	
8	45.4	-2.6	-722.3	45.2	88.3	79.7	70.6	
3	35.2	61.4	-1472.3	53.7	81.1	76.3	65.8	
*12	66.5	28.0	-1825.9	78.4	29.0	43.9	59.7	
1	66.6	38.5	-1403.8	65.5	34.6	32.0	30.3	
9	47.7	60.6	-2963.0	86.1	54.5	55.2	60.2	

^aSee footnotes of Table 5 for treatments of calves.

*Values estimated according to Snedecor (121).

TABLE 11.--Percentage digestibility of nutrients in sections and in the entire alimentary tract (total digestibility) of calves, Trial IIIa

Calf No.	Sections of Alimentary Tract										Entire Tract
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum	Dry Matter		
3	83.9	- 3.4	13.9	-497.8	73.0	22.1	25.1	10.8			84.1
10	91.3	-17.5	-41.3	-186.3	-39.7	67.0	12.8	53.9			91.2
23	84.7	-12.9	-20.3	-253.4	62.6	40.0	35.6	- 0.1			84.5
1	82.1	-21.9	14.3	-502.0	69.4	41.0	38.8	6.5			80.9
12	91.6	-12.4	-49.2	-635.1	76.5	48.2	45.4	6.3			92.6
18	76.1	-38.0	- 3.0	-785.2	85.4	52.2	48.9	8.1			80.6
5	81.9	- 8.4	9.7	-239.3	54.9	30.7	34.7	- 7.2			79.9
16	78.0	8.1	17.7	-705.8	61.9	72.6	60.6	-13.5			84.1
24	85.0	-25.1	34.5	-1139.0	72.4	48.1	44.9	40.7			87.2
25	91.7	- 5.8	- 7.4	-203.6	40.8	52.9	53.2	-38.6			89.0
26	86.4	2.6	-19.8	-348.5	65.2	50.8	51.8	-25.8			90.3
17	87.7	-37.5	17.9	-1434.1	86.8	50.7	50.4	16.0			88.3
4	84.2	-14.2	9.4	-1621.6	81.4	61.6	59.8	15.8			83.1
9	87.9	- 7.7	-87.4	-625.3	82.1	43.2	49.7	24.6			86.5
20	83.2	-39.5	-69.7	-481.8	71.0	73.7	52.5	-25.7			77.9
2	78.3	-24.8	-76.4	-342.8	66.0	56.1	55.8	-15.3			63.5
11	80.5	7.2	- 2.5	-2604.5	87.2	73.8	72.4	-13.3			80.8
21	79.7	- 8.6	-176.8	-225.8	60.2	66.2	59.6	21.3			78.9
6	78.4	-21.4	- 6.5	-290.3	66.2	35.9	32.8	31.1			83.7
14	86.1	- 0.5	-22.7	-284.9	28.7	68.9	64.7	- 1.9			85.1
19	76.1	23.6	-54.2	-419.5	68.5	58.9	42.8	-36.8			74.1
8	80.6	- 0.7	-22.9	-647.9	60.0	70.8	69.9	11.8			81.5
13	70.5	8.7	-79.3	-798.9	85.8	51.1	44.9	8.3			72.3
27	81.8	-28.5	-20.7	-1306.8	87.1	53.9	44.3	8.2			78.3

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract									
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum	Entire Tract	
3	87.5	-58.1	28.8	-827.7	68.7	42.1	42.8	25.0	82.4	
10	91.6	-17.5	-13.0	-245.8	-46.8	69.3	22.1	50.2	91.3	
23	86.6	-19.8	10.2	-334.7	63.5	34.4	31.0	1.0	83.9	
1	83.8	-33.0	12.5	-471.0	70.3	39.2	37.6	5.6	81.9	
12	91.9	-15.7	-34.3	-391.5	77.3	45.2	42.8	7.2	82.8	
18	79.6	-60.0	16.6	-947.8	86.2	48.5	45.9	8.8	81.6	
5	83.2	-17.0	13.3	-226.2	54.0	28.9	30.2	-8.3	80.2	
16	80.2	-1.0	19.3	-641.8	62.2	70.4	57.7	-16.0	84.6	
24	86.0	-27.0	33.8	-1038.2	76.9	37.7	35.6	36.4	87.6	
25	92.0	-7.8	-5.3	-193.7	66.3	50.1	51.0	-40.0	89.2	
26	87.4	-3.2	-12.7	-371.4	66.7	48.3	49.6	20.4	90.5	
17	88.5	-48.5	17.8	-45.5	87.2	47.3	47.3	15.2	88.4	
4	84.8	-17.6	20.3	-1250.9	75.1	59.0	57.4	14.0	83.1	
9	88.9	-16.2	-42.4	-791.8	82.6	37.5	46.2	25.5	86.6	
20	83.9	-46.2	-55.7	-465.6	72.5	69.5	45.5	-26.9	78.0	
2	80.2	-34.6	-62.2	-344.4	65.7	53.0	54.2	-16.4	63.8	
11	80.8	5.5	-0.6	-139.5	83.7	76.2	75.1	-14.4	80.7	
21	81.0	-16.3	-138.7	-224.1	83.0	61.6	55.4	21.4	79.2	
6	79.3	-25.0	-4.2	-279.3	66.9	32.8	30.9	29.6	84.0	
14	86.7	-3.6	-7.8	-310.7	58.6	47.6	36.2	-11.8	85.2	
19	77.4	21.3	-46.8	-438.4	70.6	55.6	38.8	-38.2	74.9	
8	81.1	-4.8	-15.6	-625.0	62.5	67.1	66.2	7.5	81.0	
13	70.6	6.9	-55.9	-836.3	85.8	45.0	40.5	28.2	77.9	
27	82.4	-35.0	1.0	-1515.1	88.0	50.0	41.5	3.5	78.2	

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract										Entire Tract	
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum				
Fiber												
3	38.5	-14.6	-38.0	21.9	-15.2	5.3	-7.0	11.6	28.1			28.1
10	48.3	1.3	-47.0	28.6	-4.9	1.3	7.7	3.2	47.2			47.2
23	38.6	9.6	-171.7	47.0	5.3	7.9	3.9	12.0	37.3			37.3
1	24.8	-4.9	-65.8	26.5	-4.8	10.3	5.8	-0.1	11.8			11.8
12	40.5	7.9	-32.8	25.8	-9.5	5.9	4.1	1.6	44.4			44.4
18	24.4	-84.8	15.5	36.2	-8.4	-	-1.0	-3.2	11.3			11.3
5	28.5	2.5	-18.3	-5.3	10.3	11.7	11.3	-7.2	27.9			27.9
16	43.5	-1.9	-13.7	59.7	-213.6	18.1	12.6	-4.6	33.2			33.2
24	41.1	1.2	13.5	-22.4	-10.6	12.8	0.3	3.2	39.6			39.6
25	55.9	4.9	-18.1	9.2	40.3	5.8	7.1	-31.7	43.2			43.2
26	43.1	4.6	-21.1	10.2	-5.1	15.4	8.3	-1.9	46.8			46.8
17	47.2	-18.3	71.2	55.6	13.3	7.8	14.0	7.6	39.0			39.0
4	61.0	-21.1	0.3	-76.8	19.5	10.8	11.2	6.4	46.3			46.3
9	64.2	-6.2	-87.4	20.3	0.7	0.6	16.5	14.9	51.4			51.4
20	62.0	-51.7	-26.9	-42.9	16.2	45.5	13.3	-41.9	31.8			31.8
2	59.5	-63.2	-21.7	28.9	-40.8	6.5	11.6	-11.7	15.1			15.1
11	61.0	-13.1	-0.6	87.1	-49.3	40.2	40.5	-68.8	21.5			21.5
21	55.1	-1.1	-61.0	22.1	86.6	8.7	-6.5	19.8	45.7			45.7
6	58.1	-19.0	-23.3	-1.7	-12.9	14.2	16.1	27.6	55.7			55.7
14	68.0	-4.6	-26.2	0.2	-11.8	12.3	3.1	-4.1	58.4			58.4
19	54.5	40.4	-125.6	-20.2	8.3	25.6	-	-43.6	28.0			28.0
8	57.9	-4.8	-36.5	4.6	10.5	11.2	4.9	2.2	38.8			38.8
13	43.9	6.9	-34.4	-112.0	35.0	15.1	5.2	19.6	33.0			33.0
27	64.3	-38.9	-32.8	-25.3	6.5	23.4	10.9	-2.9	40.5			40.5

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract										Entire Tract
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum			
3	38.4	11.6	46.6	-3845.1	76.4	66.5	67.9	14.6	26.6		
10	72.4	-75.1	25.1	-674.5	46.9	57.4	-103.3	68.2	79.9		
23	44.5	-15.3	54.5	-1313.6	76.9	55.5	60.0	-29.0	45.6		
1	-20.1	30.5	54.0	-1318.9	77.3	58.7	71.9	37.4	67.7		
12	75.1	-28.0	16.5	-1314.3	85.1	67.4	68.4	-31.2	75.8		
18	-67.3	40.7	56.7	-3617.3	92.8	70.4	71.4	-35.4	53.3		
5	47.2	37.2	35.9	-1004.4	75.2	72.0	60.9	-19.0	60.0		
16	1.0	42.2	56.3	-2802.7	72.9	90.7	82.4	-92.2	65.3		
24	38.8	-85.2	73.1	-2396.8	73.3	71.5	76.9	35.3	62.6		
25	85.9	-42.7	51.7	-672.1	70.5	76.9	80.9	-94.0	81.7		
26	63.2	19.2	-19.9	-586.8	74.3	82.8	86.1	20.4	91.5		
17	69.1	5.1	80.3	-1022.9	94.2	72.4	78.1	-18.4	87.8		
4	21.6	18.9	55.6	-6263.0	82.0	83.5	84.7	40.2	68.2		
9	48.1	39.7	-192.3	-1567.5	91.8	71.0	76.4	13.4	68.5		
20	39.4	1.2	-197.8	-780.9	78.8	87.0	76.3	39.7	73.6		
2	28.1	43.9	-160.9	-935.5	76.9	89.5	90.3	-8.3	72.2		
11	27.3	44.4	50.8	-1138.6	85.9	93.9	94.6	6.0	80.3		
21	27.6	16.3	-369.0	-249.1	96.8	88.2	87.1	-2.2	62.3		
6	39.1	5.3	13.9	-799.3	82.8	53.9	54.4	13.8	69.5		
14	66.5	23.5	2.0	-778.9	81.0	72.6	68.1	-15.1	87.1		
19	36.7	32.0	-29.8	-914.0	92.8	54.8	64.5	-120.3	60.1		
8	41.9	26.4	6.5	-2452.7	89.6	92.1	94.3	-1.3	80.5		
13	4.1	20.6	57.7	-1074.8	88.8	67.1	64.2	23.9	60.8		
27	34.5	6.1	22.8	-498.7	51.5	77.5	74.4	15.5	74.7		

Phosphorus

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract									
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum	Entire Tract	
3	85.9	-63.9	69.6	- 915.6	83.4	-303.6	-266.5	- 4.0	50.4	
10	93.1	-96.2	40.7	- 100.1	-466.2	66.0	72.9	38.2	81.2	
23	74.7	62.7	6.6	- 472.5	48.5	41.0	- 37.4	9.0	86.1	
1	63.3	18.3	12.5	- 216.6	33.3	- 22.7	- 7.7	10.2	39.5	
12	92.4	-62.8	20.9	- 220.0	43.1	- 10.6	- 7.9	19.4	84.2	
18	65.2	66.9	-136.9	- 474.0	71.6	28.5	22.0	7.9	70.1	
5	82.4	- 2.9	75.6	- 430.1	58.5	- 80.1	-192.1	-176.6	52.5	
16	92.1	-34.0	78.6	-3931.5	88.9	-216.2	-219.5	55.7	85.9	
24	97.0	22.4	83.6	-18870.5	79.4	- 92.0	- 38.9	79.2	94.2	
25	97.3	- 1.5	- 80.4	- 181.6	81.3	-196.3	-186.7	18.2	89.1	
26	92.7	- 2.3	-126.6	10.2	32.7	- 55.0	- 23.8	59.4	93.5	
17	95.0	9.0	37.5	24.1	74.7	- 91.3	- 69.0	-16.8	80.1	
4	79.8	-75.9	84.6	-1553.9	40.3	- 13.8	16.4	14.0	60.3	
9	86.5	- 9.8	- 74.3	- 226.3	67.3	- 11.9	12.5	- 3.9	67.3	
20	79.5	-114.4	- 28.6	- 197.6	48.0	- 73.9	27.5	-114.8	51.2	
2	73.8	10.3	-196.2	15.6	24.9	3.9	12.0	-57.8	33.0	
11	76.9	18.4	88.7	- 672.5	88.6	11.8	32.5	-24.6	78.8	
21	78.8	1.1	-310.7	3.4	94.7	7.3	- 8.9	45.8	78.0	
6	70.8	-10.5	16.0	68.1	22.3	- 12.0	-21.5	73.1	89.2	
14	88.5	-37.8	44.9	- 122.6	17.7	- 5.8	- 9.0	-27.1	79.0	
19	72.6	51.1	-179.7	4.5	24.6	- 35.2	-72.7	27.5	71.8	
8	80.1	-43.1	22.5	- 370.9	75.7	- 39.4	-25.3	0.5	65.0	
13	58.4	72.6	-1064.8	29.3	82.7	-249.1	-352.4	70.6	84.0	
27	95.2	-35.0	-245.2	- 317.7	49.0	- 1.0	-24.8	38.4	70.6	

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract										Entire Tract
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum			
3	60.7	49.3	- 40.2	-1384.3	62.7	68.6	67.9	31.6	66.5		
10	84.2	-15.2	-400.2	- 14.3	17.5	30.7	-84.7	79.3	87.5		
23	60.2	44.6	-542.8	- 48.4	57.9	72.3	63.9	-15.0	71.6		
1	43.1	46.3	- 60.3	- 437.0	64.3	52.2	46.1	16.8	62.2		
12	84.5	18.0	-265.5	- 206.0	68.6	69.5	64.6	- 3.1	85.8		
18	- 1.8	55.9	-293.5	- 364.7	82.5	73.3	65.8	1.5	62.2		
5	54.2	58.9	- 63.4	- 423.3	63.0	48.3	73.9	-70.5	47.7		
16	32.5	64.2	- 22.0	-1359.4	60.3	84.1	78.0	7.9	75.2		
24	66.0	- 7.6	41.1	-1992.9	43.0	74.6	69.1	66.7	78.0		
25	87.3	12.3	- 38.6	- 293.6	58.7	69.4	66.8	-19.2	84.2		
26	69.2	42.5	-108.6	- 191.8	51.8	69.5	68.8	15.6	86.9		
17	72.6	43.6	11.6	- 194.1	83.2	71.4	68.2	26.1	85.7		
4	72.8	21.2	-174.5	- 695.4	69.3	81.2	76.7	38.5	83.6		
9	68.9	58.0	-1022.5	- 204.5	79.9	78.4	73.8	17.2	83.9		
20	68.3	30.4	-367.0	- 703.5	65.7	92.2	81.0	- 3.0	77.1		
2	32.2	46.4	-302.0	- 331.1	67.4	78.5	68.3	5.5	58.3		
11	70.4	34.2	- 52.9	- 417.6	75.8	94.6	93.6	8.2	81.3		
21	45.1	53.3	-929.5	- 158.7	95.0	88.5	80.3	23.0	71.0		
6	57.2	18.7	- 35.0	- 463.0	60.5	57.8	49.0	48.3	77.2		
14	61.9	35.6	- 5.4	- 617.0	51.5	79.9	70.5	5.7	83.3		
19	50.3	48.8	-190.5	- 312.9	48.0	78.2	67.4	-25.9	56.8		
8	74.5	32.5	-132.5	- 781.9	46.9	84.7	84.3	49.8	85.5		
13	65.6	29.7	-383.8	- 571.3	82.6	78.9	66.9	28.9	79.4		
27	73.1	22.8	-314.0	- 568.3	78.4	71.5	57.1	42.1	79.5		

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract										Entire Tract	
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum				
3	26.4	83.5	44.8	-10778.0	81.8	83.8	88.2	99.8	99.9	99.8	99.9	99.9
10	83.7	-31.7	57.2	-2049.2	99.9	-68474.0	-182005.0	99.8	99.9	99.8	99.8	99.7
23	14.7	98.3	-125.6	-7393.5	50.2	91.3	86.0	38.3	93.5	38.3	93.5	93.5
1	-13.5	88.9	23.4	-746.3	99.9	-13588.0	-7244.0	97.2	99.6	97.2	99.6	99.6
12	82.6	-7.6	61.1	-243.6	33.2	64.1	77.1	45.3	97.3	45.3	97.3	97.3
18	-81.0	92.7	-135.8	-2011.0	85.4	87.9	79.0	69.3	96.4	69.3	96.4	96.4
5	-5.3	83.1	-80.3	-866.1	80.0	76.6	99.9	53.8	93.3	53.8	93.3	93.3
16	-32.2	91.5	59.2	-14531.9	70.0	90.3	97.0	40.8	88.4	40.8	88.4	88.4
24	57.0	74.5	67.3	-19949.9	53.7	73.4	80.9	98.6	98.7	98.6	98.7	98.7
25	82.6	51.8	61.7	-4353.3	71.7	96.9	86.5	-76.3	96.2	-76.3	96.2	96.2
26	15.4	81.3	-83.5	-225.0	4.2	79.2	78.4	57.9	92.2	57.9	92.2	92.2
17	33.6	67.0	44.0	-244.5	81.3	59.9	58.0	65.9	89.2	65.9	89.2	89.2
4	76.9	-45.0	99.4	-387171.9	75.1	96.9	99.0	-20.0	92.4	-20.0	92.4	92.4
9	36.8	52.8	-365.3	-383.6	93.8	96.0	60.0	-616.6	88.1	-616.6	88.1	88.1
20	34.4	76.6	-1483.0	-764.2	88.0	94.9	80.2	86.3	98.2	86.3	98.2	98.2
2	-55.6	68.4	92.2	-5623.9	41.4	81.7	21.3	-34.1	68.6	-34.1	68.6	68.6
11	23.3	80.0	-30.6	-840.7	95.7	40.1	84.2	44.9	72.9	44.9	72.9	72.9
21	-31.5	91.9	-3500.3	-239.0	99.0	70.8	20.3	66.3	87.6	66.3	87.6	87.6
6	74.4	40.8	84.8	-15670.0	99.9	-29916.0	-39824.5	60.3	82.7	60.3	82.7	82.7
14	-6.7	62.2	3.2	-179.9	57.9	97.7	89.3	-88.5	92.5	-88.5	92.5	92.5
19	16.2	83.0	-395.3	-334.4	60.0	77.3	73.5	17.7	77.1	17.7	77.1	77.1
8	65.8	13.5	8.1	-4755.1	80.9	88.5	87.5	73.7	92.4	73.7	92.4	92.4
13	78.7	52.4	-180.6	-9376.9	99.9	-535.0	-994.7	-14.0	77.7	-14.0	77.7	77.7
27	14.3	-177.3	89.5	-6772.4	83.9	87.0	68.0	58.9	85.3	58.9	85.3	85.3

TABLE 11.--Continued

Calf No.	Sections of Alimentary Tract										Entire Tract
	Rumen	Omasum	Abomasum	Upper Small Intestine	Lower Small Intestine	Large Intestine	Cecum	Rectum			
3	77.7	-	123.1	-	960.0	65.5	74.5	71.7	29.2	Water	
10	37.9	-	142.1	-	412.9	27.9	82.8	51.0	19.9		
23	69.6	-	113.2	-	859.0	59.3	79.5	72.8	20.3		
1	79.1	-	134.5	-	956.8	66.0	73.9	71.5	30.1		
12	31.2	-	178.9	-	642.5	70.6	78.2	72.3	17.5		
18	81.3	-	376.4	-	1162.9	81.4	86.0	80.6	25.6		
5	72.7	-	109.4	-	469.0	58.6	68.0	68.9	9.3		
16	86.0	-	452.3	-	938.6	65.5	90.6	90.3	21.8		
24	62.0	-	382.8	-	1040.2	39.3	82.0	73.3	77.4		
25	56.7	-	138.2	-	653.8	32.5	87.8	83.5	-21.2		
26	79.3	-	280.3	-	375.3	47.9	80.1	76.8	40.7		
17	71.7	-	97.8	-	2606.8	81.6	78.6	76.1	42.3		
4	51.1	-	40.0	-	3385.2	74.7	86.5	83.5	32.4		
9	67.8	-	782.2	-	540.1	77.4	84.3	80.1	37.1		
20	56.3	-	1043.1	-	631.2	65.9	95.3	90.0	-	3.3	
2	67.6	-	562.4	-	237.6	63.4	82.5	71.0	19.7		
11	78.3	-	152.7	-	6608.9	84.3	94.2	92.8	-	1.2	
21	79.5	-	2430.0	-	177.5	46.4	91.5	83.5	48.7		
6	48.8	-	150.1	-	551.6	60.5	68.6	60.9	58.8		
14	66.6	-	213.2	-	428.0	15.6	89.4	84.8	17.9		
19	74.4	-	567.0	-	282.2	48.4	83.7	76.0	-	1.4	
8	57.5	-	103.0	-	1663.7	45.4	90.8	88.0	36.4		
13	75.7	-	726.4	-	1384.1	82.5	88.9	82.7	22.5		
27	62.5	-	259.8	-	1885.7	77.5	88.4	78.8	22.9		

^aSee footnotes of Table 5 for treatments of calves.

TABLE 12.--Percentage of the net energy required for maintenance and growth supplied by the volatile fatty acids absorbed from the rumen and cecum of individual calves

Calf No.	Per Cent Net Energy to Meet Maintenance and Growth from					Total	VFA from Cecum					Total
	VFA from Rumen						VFA from Cecum					
	Acetic	Propionic	Butyric	Total	Acetic		Propionic	Butyric	Total			
3	13.2	8.1	2.7	24.0	4.4	1.6	4.1	10.1				
10	24.5	---	---	24.5	---	---	---	---				
23	28.0	20.0	6.5	54.5	4.8	3.9	2.4	11.1				
1	21.0	18.4	5.4	44.8	6.6	---	2.1	8.7				
12	20.4	5.9	---	26.3	8.4	7.9	1.9	18.2				
18	80.0	30.3	10.6	120.9	3.1	1.3	---	4.4				
5	42.3	28.6	8.7	79.6	25.2	23.4	15.0	63.6				
16	41.1	41.2	17.9	100.2	5.2	4.3	1.4	10.9				
24	95.8	34.7	10.7	141.2	2.5	1.3	---	3.8				
25	126.3	158.6	31.9	316.8	---	---	---	---				
26	38.7	19.1	2.6	60.4	6.0	5.2	---	11.2				
17	11.3	7.3	3.1	21.7	---	---	---	---				
4	66.5	119.0	13.3	198.8	28.2	5.7	12.4	46.3				
9	11.2	8.3	4.3	23.8	4.1	1.3	---	5.4				
20	20.7	9.8	9.1	39.6	1.3	0.6	---	1.9				
2	11.9	9.2	3.3	24.4	6.7	8.8	1.7	17.2				
11	42.8	92.2	---	135.0	2.0	---	1.0	3.0				
21	28.9	27.7	5.6	62.2	3.2	2.2	---	5.4				
6	44.5	18.5	12.4	75.4	3.4	2.0	0.6	11.4				
14	26.2	21.7	13.0	60.9	7.7	4.0	1.9	13.6				
19	14.4	12.3	9.1	35.8	22.8	11.1	9.2	43.1				
8	41.4	43.3	10.5	95.2	7.5	3.2	2.2	12.9				
13	105.1	166.6	50.1	321.8	14.2	5.5	2.1	21.8				
27	44.5	47.3	10.1	101.9	---	1.3	---	1.3				

TABLE 13.--Analysis of variance on the percentage apparent total digestibility of dry matter estimated by the total collection method, Trial II

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Square	F
% Fiber (F)	1	653.13	653.13	8.53
Phosphorus level (P)	3	31.47	10.49	0.15
F x P interaction	3	210.03	70.01	1.01
Sub-total	7	894.63		
Error	16	1105.78		69.11
Total	23	2000.41		

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