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Lactase Activity in Steers Fed Large Amounts of Dried Whey

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LACTASE ACTIVITY IN STEERS FED LARGE AMOUNTS OF DRIED WHEY

BY

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LACTASE ACTIVITY IN STEERS FED LARGE

AMOUNTS OF DRIED WHEY

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

Large amounts of dried whole whey (86% of concentrate mix, 60% of total dry matter intake) were fed to four Holstein steers in place of corn and soybean meal in the control diet to evaluate the extent and site of lactose digestion in the ruminant's digestive tract. Diets consisted of 70% of the dry matter as concentrate mix and 30% as corn silage fed ad libitum as a total mixed ration. Weight gains and dry matter intakes were similar for steers fed dried whole whey or control diets. Samples of rumen contents from steers fed dried whole whey contained more butyrate, less propionate, and less ammonia than from animals fed control diets. No lactose was detected in the rumen or small intestine indicating that it was completely digested. Lactase activity per gram of intestinal tissue was significantly greater in two of fifteen tissue segments and numerically greater in the proximal third of small intestine of steers fed the control diet. Lactase activity per gram tissue protein was similar for both treatment groups throughout the small intestine. Lactase activity was greatest in the proximal third of the small intestine with little activity in the distal third of the small intestine irregardless of diet. Lactase activity of intestinal contents was similar for both treatments, being highest in the duodenum and lowest in the ileum and large intestine. Since no lactase apparently escaped the rumen, differences in intestinal lactase may not be expected. Lactase activity may have been affected by the amount of total

carbohydrates entering the small intestine rather than just the amount of lactose entering. Digestibilities of whey diets were higher for ash and numerically higher for energy and organic matter, while digestibilities of acid detergent fiber and cellulose was numerically lower. Cattle have the capability to consume large amounts of dried whey without digestive disorders or reduced rates of gain.

INTRODUCTION

Large amounts of whey have been successfully fed to ruminants without impairing performance. The chief component of whey is lactose, which comprises more than 70% of the dry matter in whey. Rumen fermentation patterns are altered when feeding lactose, although the amount of lactose which can be fermented in the rumen is not known. Fecal dry matter has been lowered by feeding large amounts of dried whey, indicating some lactose possibly escapes rumen degradation and intestinal digestion. Direct evidence of lactose affecting intestinal lactase is lacking, however, blood glucose concentrations were higher in steers which were adapted to lactose.

The intent of this research was to feed rations sufficiently high in lactose to exceed the ability of the rumen to ferment all of the lactose. This would allow lactose to enter the small intestine for possible induction of lactase to digest this lactose. A second aspect of this research was to evaluate the effect of the high lactose diet on the digestion of feed nutrients and attempt to quantitate the extent and site(s) of lactose digestion in the ruminant digestive system.

LITERATURE REVIEW

Eighty-eight percent of the milk used in the production of cheese results in the by-product whey (27, 67). Liquid whey is mostly (93%) water, but the highly nutritious whey solids are mostly (77%) lactose. When compared to the major grains, dried whey most closely resembles oats in nutrient content, containing 78% total digestible nutrients and 13% crude protein (47). Whey can be fed as liquid, as condensed, or as dried whey. Each have their advantages and disadvantages as a feed source, of which intake, feed handling, or cost of production are often major considerations.

Feeding and Performance

When feeding liquid whey, there were no palatability problems as long as it was fresh (68). Whey over 36 h old became acidic and unpalatable. Getting the animal to consume enough nutrients was also a problem when feeding liquid whey. Studies at Utah (3, 4) and Beltsville, MD, (26, 44) obtained acceptable weight gains and production with dairy cattle consuming up to 30% of their dry matter intake (DMI) from liquid whey. But, when fed more than 30% of total dry matter as liquid whey, gut fill limited DMI, resulting in decreased performance.

When a concentrate containing 40 to 50% of the dry matter as condensed whey was fed alone to cows, consumption of the concentrate was found to be unacceptable (69). By mixing different amounts of molasses with the whey, consumption reached an acceptable level.

The whey to molasses ratio of the concentrate mixtures ranged from 40:10 to 50:50. Dry cows consumed up to 5 kg/day of the 50:50 mixture. When used as a topdressing on silage fed to lactating cows, there were no problems with feed consumption, production, or health. The only disadvantage found was that the lactose had a tendency to precipitate out when high levels of whey were in the mixture. All dried forms of whey are highly palatable (57, 59, 60) and gut fill will not generally limit DMI, but the cost of drying may be a prohibitive factor for it to be used in livestock rations.

Weight gains of steers and heifers receiving 22 and 31% of their dry matter from liquid whey were the same as those fed conventional rations (44, 68). When animals received restricted grain (68) or no grain at all (44), whey consumption increased from 48 to 57% of total dry matter intake, but weight gains were reduced to 0.5 to 1.0 kg/day because of reduced DMI. Feeding 45% of dry matter as dried whey to steers resulted in weight gains of 1.36 kg/day (59). Adding 1 to 4% dried whey to fattening cattle rations increased weight gains 5 to 6% more than those fed control rations (71).

Dry matter content of feces was reduced when rations contained 30% or more lactose as lactose or dried whey (7, 59, 60). Urine output increased 300% when steers were fed 45 to 60% dry whey (60). Increase in mineral consumption increased urination with dried and liquid whey feeding but with no harm to the animal (3, 60).

Metabolism

Rumen fermentation

The effect of whey on rumen fermentation patterns has been well documented (2, 10, 30, 35, 55, 59, 60, 61, 64). Whey exhibits a buffering capacity in the rumen stabilizing the rumen pH when animals are fed a high concentrate ration (38). The mechanism for maintaining the pH is not known, but it is thought to be associated with the balance of minerals (35, 61). The mineral concentration of whey (9.1% of DM) may increase the buffering action of the rumen by stimulating salivary flow.

The molar percentage of butyrate in rumen fluid was higher for rations containing whey, while the molar percentage of propionate decreased and acetate usually remained the same (2, 10, 30, 35, 55, 59, 60, 61). Similar molar percentage values for volatile fatty acids were obtained when lactose was fed apart from whey (60, 61, 64).

Rumen ammonia concentrations were lower for animals fed whey rations compared to animals fed control rations (50, 59, 60). Thivend and Ehouinsou (64) showed that feeding lactose with nonprotein nitrogen improved the nonprotein nitrogen utilization in sheep. Rumen ammonia, blood urea, and urinary nitrogen were reduced in sheep when lactose was added to alfalfa hay diets (50). The supplementation may have allowed for a greater use of the ammonia for microbial synthesis.

Poncet and Rayssiguier (50) also showed that organic matter digestibility of the total diet increased from 60.8% for the lucerne hay rations to 70.8% for the lucerne hay and lactose ration; however, organic matter digestibility of the hay portion of the hay and lactose ration decreased from 60.8 to 58.9%. This was indicated by the decrease in acid detergent fiber digestibility from 45.1 to 39.5%. Schingoethe et al. (60) fed rations varying from 10 to 40% lactose fed as lactose or whey to dairy cattle. There was generally an increase in digestibilities of dry matter, energy, and cellulose; a decrease in digestibility of neutral detergent fiber; and no change in digestibilities of nitrogen, ether extract, or acid detergent fiber. Bowman and Huber (10) found a decrease in crude fiber and ether extract digestibilities in cattle receiving a 56% lactose ration.

Metzger et al. (46) worked with high-grain, restricted-roughage rations to determine the effect of whey products on rumen microflora. Grain rations contained dried whole whey, partially delactosed whey, demineralized whey, and lactose. Protozoa numbers were consistently lower with the demineralized whey diet. The genera Dasytricha was the only type of protozoa that varied significantly with the different diets. Dasytricha numbers were lower with the control and dried whole whey diets; none were observed with the demineralized whey diet. Bacteria numbers fluctuated from week to week with no apparent significance. Howard (29) showed that Dashytricha ruminantium, Isotricha intestinalis, and Isotricha

prostoma contained no cellular extracts capable of hydrolyzing lactose. D. ruminantium was found to have a mechanism for fermenting galactose, which led Howard (29) to postulate that the bacteria consumed hydrolyzed lactose, while the protozoa fermented the products obtained.

Homofermentative Lactobacilli are lactose digesters found in the rumen (22, 37). Their end product is principally lactic acid with some acetic acid, ethanol, and CO_2 being produced (66). Lactic acid can then be further used by other fermenting bacteria. Fermentation of DL-(2-^{14}C) lactate by the rumen organism LC-1, a gram negative coccus, showed that the major proportion of total volatile fatty acids formed were butyric and valeric acids (42).

Lactose which escapes digestion in the rumen passes to the lower digestive tract. It can either be digested here or if not, may cause diarrhea due to osmotic properties of lactose. Schingoethe et al. (59, 60) reported that cattle receiving rations containing 30% or more lactose had lower fecal dry matter, indicating that lactose may have been bypassing rumen fermentation.

Intestinal Metabolism

All disaccharidases are located in the mucosa of the small intestine. Disaccharides must first be absorbed by the intestinal epithelium before hydrolysis occurs (70). Lactase, one of the disaccharidases, is found throughout the small intestine with highest concentrations occurring in the jejunum (17, 20, 41, 45, 62).

Huber et al. (36) conducted experiments to determine the effects of varying the amount of lactose in the diet of young calves, 3 to 77 days of age. They found that calves with a greater amount of lactose in the diet also had a greater amount of lactase activity in the proximal third of the small intestine. They also found blood glucose concentrations increased as amount of lactose in the diet increased.

Huber et al. (33) conducted experiments to determine the effect age had on lactase activity in evenly divided segments of the small intestine. One group of calves received a diet of whole milk plus 3% lactose; the other group received a diet of whole milk plus 2.5% sucrose and .5% starch. Calves were sacrificed at ages between 1 and 44 days. They found the diet had no significant effect on the amounts of lactase activity throughout the trial. Peak activity occurred at day one and slowly declined to day 15, then drastically dropped, especially in the final two of the three segments of the small intestine measured.

In another experiment, Huber et al. (34) fed previously weaned 8 mo old steers a liquid diet containing either added lactose or starch via nipple pail in order to bypass rumen degradation. Blood glucose concentrations were higher for the steers fed lactose, indirectly indicating that lactase activity was induced in functional ruminants.

Ekstrom et al. (20) showed that in pigs, lactase activity of intestinal tissues increased up to day 15 after birth and then declined. These findings agree with other data obtained with rats

(39, 43) and pigs (16, 45). In rats there was also an increase in activity up to day 15 after birth and then a sudden decline.

Research by Ekstrom et al. (20) using two breeds of swine, Hampshires and Chester Whites, showed that lactase activity of both breeds were similar up to day 8, but activities in Chester Whites remained higher from then on. This indicated that there is a breed difference and that the amount of lactase activity is a heritable trait.

Fervier and Aumaitre (23) found that in swine, lactose is hydrolyzed by mucosal lactase until a given dietary lactose level. The amounts of lactose fed were 0, 10, and 20% of the diet. They concluded that mucosal lactase is a non-adaptative enzyme and that lactase in the intestinal contents is adaptive. The incorporation of whey into the weaning diet did not prevent the decrease in tissue lactase activity and did not make the animals more tolerant to high lactose diets. Ekstrom et al. (19) found similar results when feeding swine 40% lactose in the diet. Total mucosal lactase activity did not differ between the control and whey diets, while lactase activity in the intestinal contents increased, especially in the cecum. Studies with similar results have been performed on rats (40, 41, 43, 52), pigs (6, 18, 19, 20, 45), and cattle (31, 32, 34).

Fischer (24) found an increase in mucosal growth and lactase activity in rats when fed a lactose ration. Adrenalectomized and hypophysectomized rats, when fed the lactose diet, had a decrease in villus height and also weight of the mucosa. This led to the

hypothesis that lactose stimulation of mucosal growth and lactase activity may be a hormone-mediated process. Bustamante et al. (12) found that intestinal lactase activity increased in rats when fed varied amounts of carbohydrates. Those fed higher carbohydrate diets had greater lactase activity in addition to an increased growth of intestinal villi. Bustamante et al. (12) found that increasing the amount of α-saccharides in diets of rats, lactase activity of the small intestine was increased.

Reddy et al. (53) conducted trials using lactose, 70% of diet, as the only carbohydrate in the diets of germ free and conventional rats. At 30 days of age lactase activity in the small intestine increased for both the germ free and conventional rats. At 60 days of age the germ free rats died, apparently from poor utilization of the lactose. This indicated that the conventional rats depend to a large extent on bacterial lactase activity (especially in the cecum) for their survival. Kim et al. (40) estimated that when feeding a 30% lactose diet to rats, as much as 30 to 43% of the ingested lactose was available for fermentation in the large intestine. In (21) approximately 30% and 15% of the lactose ingested by the Hampshire and Chester White breeds of pig, respectively, escaped hydrolysis in the small intestine. Anaerobic incubation of the cecal and colonic contents showed that pigs fed 30% lactose diets produced volatile fatty acids at twice the rate of contents from controls (5.7 vs 3.7 and 5.0 vs 2.7 m moles/10g DM/h for cecal and colonic contents, respectively).

An additional study by Kim et al. (39) found that the pH of pig cecal and colonic contents was decreased when feeding a 40% whey diet as compared to a control (pH of 5.4 vs 6.0). This was attributed to the fermentation by the microflora in the cecum and colon. Fermentation products were mainly volatile fatty acids and lactic acid. In vitro studies (39) estimated the large intestine supplies 9% and 15% of the energy used by the pigs from control and whey groups, respectively. Lactase activity of large intestinal contents increased when whey was fed.

Lactase

Lactase is a tetrameric enzyme containing four identical subunits, each with an active site which may act independently (72). Lactase has a molecular weight of 540,000. Of the 1,170 amino acids/subunit, aspartic and glutamic acids are most abundant, while the sulfur containing amino acids are found in very low proportions (72). Eighty-eight percent of the enzyme is made up of carbohydrates (71% 2-acetamido-2-deoxy-D-glucose and 17% D-galactose). Removal of the bound carbohydrate portion causes a rapid loss in enzyme activity. The function of the carbohydrate is thought to aid in the stabilization of the secondary and tertiary structures (49).

Lactase is one of the two types of β-D-galactosidases found in the intestinal mucosa (17, 49). Lactase is capable of hydrolyzing lactose and o-nitrophenyl galactoside at a pH range

of 5.5 to 7.5. Lactase is found localized exclusively in the brush border of the intestinal mucosa. The second type of β-D-galactosidase is o-nitrophenyl-galactosidase (ONPG). This enzyme is not capable of hydrolyzing lactose and has a pH range of 2.0 to 3.0. The ONPG enzyme is found mainly in the subcellular particles, especially in the lysosomes of the liver, kidney, bone tissue, brain, testis, and gastrointestinal tract (49). This enzyme functions in the nutrition and catabolism of glycoproteins, erythrocyte membranes, and glycolipids.

The active site of β-D-galactosidase contains a sulfhydryl and an imidazole group (49). The imidazole group acts as a nucleophile and the sulfhydryl labilizes the oxygen atom of the glycosidic linkage. Deschavanne et al. (16) found evidence of two different binding subsites on the enzyme, a glucose subsite and a galactose subsite. Alpers and Cote (1) found that lactose hydrolysis was diminished in the presence of glucose, galactose, and fructose, suggesting the rate of <u>in vivo</u> hydrolysis of lactose cannot always be predicted by the isolated measurement of lactase activity.

MATERIALS AND METHODS

Eight Holstein steers weighing 220 to 310 kg were assigned to two treatment rations, a control and a dried whole whey ration. Animals received 30% of their dry matter intake as corn silage and 70% as the respective concentrate mixes fed free-choice as total mixed rations. Compositions of the concentrate mixes are listed in Table 1. Dried whole whey comprised 60% of the total ration dry matter of the dried whey ration. Chemical compositions of the feeds are presented in Table 2. Rations were formulated to meet National Research Council (47) recommendations for protein, energy, calcium, and phosphorus.

Steers were fed the respective rations for 4 to 5 wk, depending on the availability of facilities for sacrifice. Steers were group fed (two steers per group) in boxstalls which were bedded with straw. Groups from both treatments were fed at two different time periods, starting in August and January.

Animals were weighed 3 consecutive days at the beginning and end of trial and once a week during the trial. Feed offered and refused was weighed daily and samples taken weekly. Fecal samples were taken twice each week and pH determined on fresh samples using a conventional glass electrode pH meter. Samples of silage, concentrate mixes, and feces were frozen for later analyses. Samples were oven dried at 57°C for 48 h and ground in a Wiley Mill through a 1 mm screen. Proximate analyses (5) were conducted on dried samples, in addition to acid detergent fiber, lignin, cellulose,

TABLE 1. Ingredient composition of control and whey concentrate mixes fed to steers.[a]

Ingredient	Mix	
	Control	Whey
	(% dry matter)	
Ground shelled corn	87.0	13.5
Soybean meal, 50% cp	9.5	....
Dried whole whey	....	86.0
Limestone	1.5	....
Dicalcium phosphate	1.5	....
Trace mineralized salt	.5	.5

[a]Mixes also contained 8800 IU/kg added vitamin A and 2200 IU/kg added vitamin D.

TABLE 2. Chemical composition of concentrates and corn silage fed.

Measurement	Concentrate		Corn silage
	Control	DWW[a]	
	(%)		
Dry matter	90.1	94.7	41.8
	(% of DM)		
Crude protein	13.9	11.9	8.2
Energy, Mcal/Kg	3.83	3.53	3.47
Organic matter	94.4	91.5	94.6
Ether extract	3.7	1.5	3.4
Acid detergent fiber	4.1	.5	26.4
Lignin	1.3	.1	4.4
Cellulose	2.8	.4	20.6
Acid insoluble ash	.05	.01	1.50
Ash	5.6	8.5	5.4
Lactose	....	54.9	....

[a]DWW = dried whole whey.

and acid insoluble ash, by the method outline by Goering and Van Soest (25). Acid insoluble ash was used as a marker for nutrient digestibility determinations. One gram samples of whey concentrate and feces from steers receiving the whey ration were dissolved in 10 ml of distilled water, then analyzed for lactose by the method of Nickerson et al. (48). Energy was measured using an oxygen bomb calorimeter.[1]

Samples of rumen fluid were taken using a suction strainer apparatus via esophageal tube (51), weekly. Samples were put into 250 ml sample jars containing 0.5 ml of saturated mercuric chloride. Samples were analyzed for pH using the conventional pH meter then strained through four layers of cheesecloth. Rumen fluid samples were deproteinized by adding 2 ml of 25% metaphosphoric acid to 10 ml of sample. After 30 min the samples were centrifuged for 20 min at 12,000 rpm at 3°C using an International Refrigerated Centrifuge, Model B-20. The samples were analyzed for volatile fatty acids by gas-liquid chromatography using a stainless steel column (3.2 mm O.D. by 160 cm) containing neopentylglycol succinate as described by Baumgardt (8). An additional 10 ml of strained rumen fluid was centrifuged 10 min at 5,000x gravity. The supernatant was acidified with 0.5 ml of 0.1 N HCl and analyzed for rumen ammonia by the method of Chaney and Marbach (13).

Steers were sacrificed, approximately 5 h after feeding, at

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[1]Double valve, automatic temperature control, Parr oxygen bomb calorimeter, Parr Instrument Co., Moline, IL.

the conclusion of the trial. Normal slaughtering procedures were followed. The intestines were spread out and the lengths measured. To prevent the flow of intestinal contents during this handling, ties were placed in several locations. Ruminal, abomasal, small intestinal, cecal, large intestinal, and colonic contents were sampled. Small intestinal contents were gently squeezed out of the intestine and pooled according to sections, duodenum, jejunum, and ileum. Samples were immediately chilled on ice, transported to the laboratory for pH determinations, and frozen for later analyses. The analyses conducted were the same as those of the feed and fecal samples. Lactase activity was measured by the method described by Britt and Huber (11).

Fifteen samples of small intestine tissue (8 to 10 cm in length) were taken at evenly divided intervals. Dahlquist's procedure (15) for intestinal mucosa lactase activity was followed. The Bio-Rad protein assay was conducted for the determination of soluble protein (9).

Statistical variables measured were treatment, time, week, and interactions. Analysis of variance was conducted on data as outlined by Steel and Torrie (63). Sum of squares for data analyzed are presented in the appendix.

RESULTS AND DISCUSSION

Rumen Fermentation

Rumen volatile fatty acid (VFA), pH, and ammonia data are listed in Table 3. Rumen fluid from steers fed the whey diet contained a higher molar percentage of butyrate ($P<.01$), and slightly greater proportions of acetate and isobutyrate than steers fed the control diet. Molar percentage of propionate was lower ($P<.01$) when fed whey and isovalerate slightly lower ($P<.05$). Satter and Esdate (56) showed that butyrate was the ultimate end-product of lactate metabolism. The oxidation of lactate to pyruvate resulted in the synthesis of butyrate from acetate to maintain an oxidation-reduction balance. The decrease in propionate has occurred in most (10, 57, 60) but not all studies (50) with feeding large amounts of whey. High butyrate concentrations occurred in all trials where large amounts of whey or lactose were fed (2, 10, 30, 35, 55, 59, 60, 61, 64).

Rumen ammonia was lower ($P<.01$) for steers fed whey which was in agreement with (50, 59, 64). This may indicate that lactose supplies a readily available carbon skelton for bacteria to combine with ammonia in the production of bacterial protein.

Lactase Activity

Lactase was not detected in intestinal contents or feces indicating that all lactose was fermented in the rumen and therefore, not available for possible lactase induction in the small

TABLE 3. Rumen volatile fatty acids (VFA), ammonia, and pH from steers fed whey or control diets.

Measurement	Diet		SE
	Control	Whey	
Total VFA, μmoles/ml	64.5	61.6	.36
VFA	—— (Mole %) ——		
C_2[a]	38.3	43.3**	.96
C_3	43.3	19.4**	1.71
iC_4	.1	.6**	.13
C_4	12.6	30.3**	1.58
iC_5	2.2	1.6*	.17
C_5	3.8	4.6	.39
Ammonia, mg/100 ml	7.9	5.2**	.34
pH	6.6	6.8	.09

[a]Numeral refers to number of carbons in VFA, i means isomer.

*Different from control (P<.05).

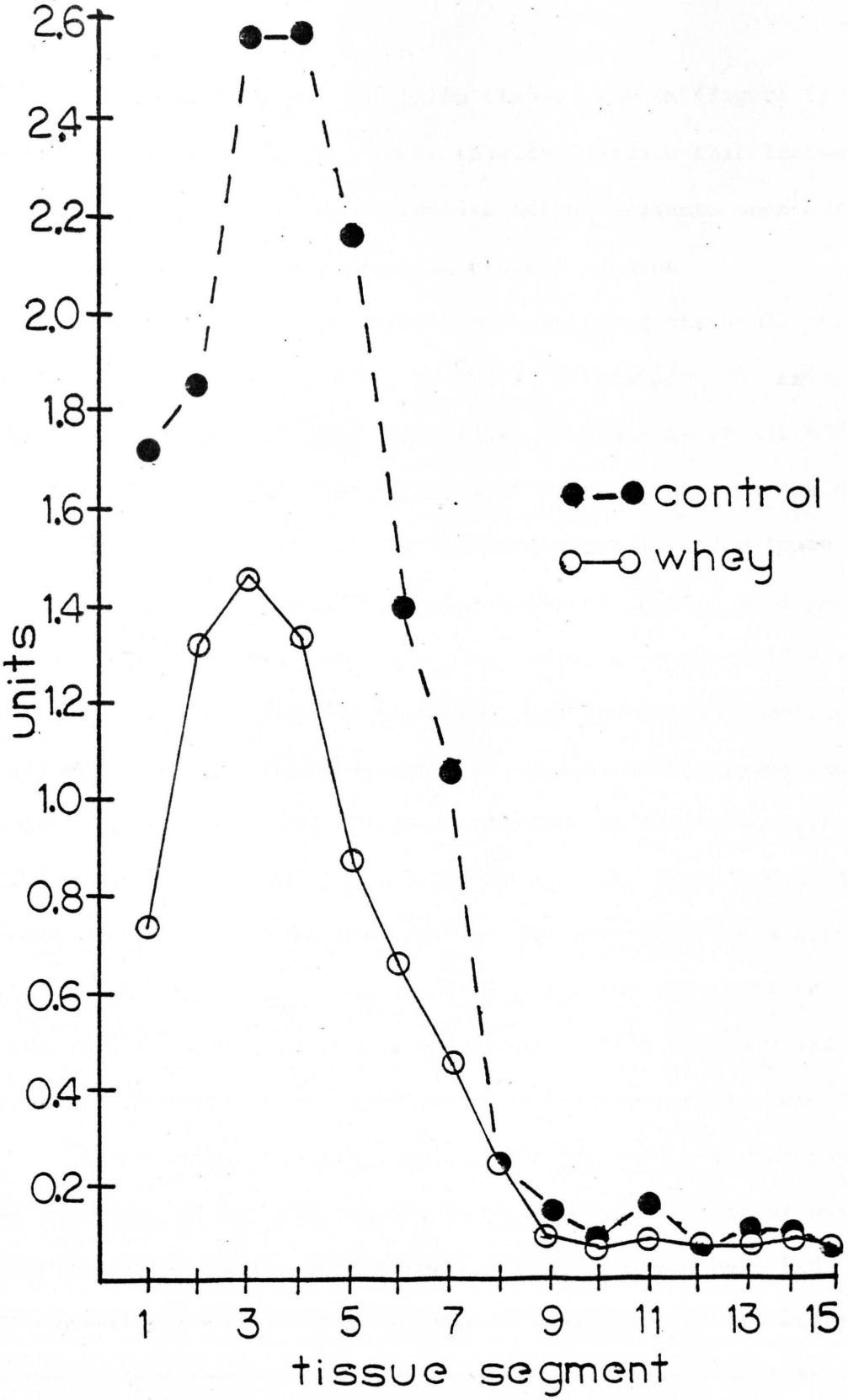
**Different from control (P<.01).

intestine. The lactose assay was sufficiently sensitive to detect 20 µmoles/g of contents (48). However, steers were sacrificed 4 to 6 h after feeding, so it is possible that if lactose was present in the small intestine it may have been digested during that time. Poncet and Raysigguier (50) found less than 1% of the lactose in a 42% lactose diet fed to sheep escaped rumen degradation. Lactose comprised 38% of the diet in this trial.

Mucosal lactase activity (Figure 1) was found in highest concentrations in the proximal half of the small intestine with little activity present in the distal half. These results are similar to those found in other studies (17, 20, 41, 45, 62). Lactase activity was greater ($P<.05$) in segments three and four of the small intestine for steers fed the control diet rather than the whey diet (2.5 vs 1.4 µmoles lactose hydrolyzed/min/g mucosal tissue) and had a tendency to be higher throughout the proximal half of the small intestine. There was also a time and treatment x time affect present for mucosal lactase activity. The two steers fed the control diet in January had over twice as much activity (2.45 µmoles lactose hydrolyzed/min/g mucosal tissue) in the proximal half of the small intestine than the six other steers on the trial (1.05 µmoles lactose hydrolyzed/min/g mucosal tissue).

Tissue protein content of the small intestines remained similar (33.5 mg protein/g mucosal tissue) throughout the small intestine and between all steers except for those fed the control diet in January (52 mg protein/g mucosal tissue). When lactase

Figure 1. Lactase activity of intestinal tissue per gram of tissue (unit = μmoles lactose hydrolyzed/minute/g tissue).

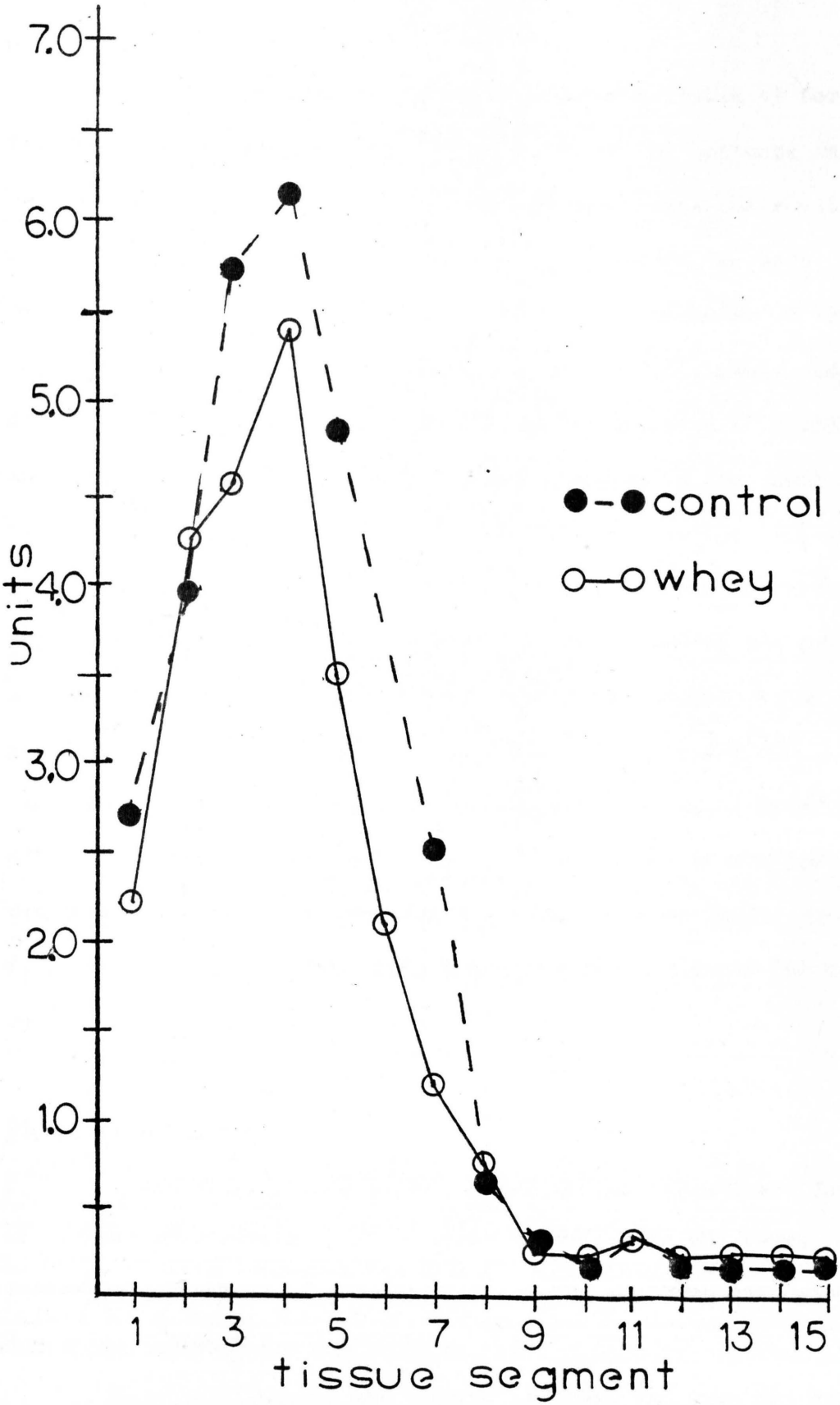

2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
units
control
whey
1
3
5
7
9
11
13
15
tissue segment

activity was expressed per milligram tissue protein (Figure 2), it was similar for all steers. These results indicate that lactase activity is constant in the respective tissue segments when corrections are made for difference in protein content.

The total amount of carbohydrate entering the small intestine is apparently an important factor in determining the amount of lactase activity of the small intestine. Bustamante et al. (12) found that by increasing the quantity of carbohydrates in the diets of rats there was an increase in lactase, sucrase, and maltase activity. They theorized that the carbohydrate effect of disaccharidases might have two steps - the first a nonspecific step affecting both α and β-disaccharidases, and the second involving a specific principle, affecting either α or β-disaccharidases exclusively. Huber et al. (36) found an increase in tissue lactase activity when the amount of lactose, as well as, total carbohydrate content of the diet were increased and fed as a liquid via nipple pail. In another trial by Huber et al. (33) the carbohydrate content of the diet was held constant (3% lactose or 2.5% starch + .5% sucrose added to milk) and no difference in lactase activity was found.

Since starch is approximately 50% digestible in the rumen (14) and most, if not all, of the lactose fed in this trial was fermented in the rumen, steers fed the whey diet may have had less total carbohydrates entering the small intestine than the steers fed the control diet. This could explain the greater lactase activity of the steers fed the control diet.

Figure 2. Lactase activity of intestinal tissue per milligram of tissue protein (units = μmoles lactose hydrolyzed x 10^{-2}/ minute/mg tissue protein).


7.0
6.0
5.0
4.0
3.0
2.0
1.0
units
●-●control
○—○whey
1
3
5
7
9
11
13
15
tissue segment

Lactase activity of intestinal contents (Table 4) for both treatment groups was similar. The lactase of the contents was derived from either lactase sloughed from intestinal microvilli or was a combination of sloughed tissue and bacterial lactase. The bacterial lactase could possibly be from bacteria passed down from the rumen or from bacteria established in the intestines. Lactase activity of the contents was highest in the duodenum (2.5 µmoles lactose hydrolyzed/min/g contents) and declined to the level of the ileum where it remained throughout the large intestine (.04 µmoles lactose hydrolyzed/min/g content). The level of activity corresponds with tissue lactase activity, being greatest in the duodenum and then declining through the rest of the intestine. Rumen lactase activity was numerically but not statistically greater for steers fed whey. Using feed intake as an indication of daily rumen dry matter and assuming lactase activity in the rumen is constant, the rumen was capable of hydrolyzing 4.7 kg of lactose daily. Steers fed the whey diet in this trial only consumed 3.2 kg of lactose daily.

Digestive Contents

There were no differences found in the dry matter (Table 5) of intestinal contents. If lactose was bypassing the rumen, a decreased dry matter of intestinal contents may have been expected due to an increase in osmolarity.

Fecal dry matter was similar for both the whey and control

TABLE 4. Lactase activity of digestive contents from steers fed control or whey diets.

	Diet		SE
	Control	Whey	
	(units[a])		
Rumen	.02	.18	.082
Duodenum	2.71	2.34	.688
Jedunum	.55	.85	.211
Ileum	.03	.05	.011
Cecum	.02	.04	.016
Large intestine	.01	.07*	.011
Colon	.03	.02	.005

[a]1 unit = 1 μmole lactose hydrolyzed/min/g contents.

*Different from control ($P<.05$).

TABLE 5. Dry matter % of intestinal contents.

	Diet		
	Control	Whey	SE
Duodenum	9.97	11.07	.99
Jejunum	7.62	8.25	.96
Ileum	9.64	8.99	1.36
Decum	10.56	12.31	1.48
Large intestine	9.07	12.09	2.16
Colon	11.15	13.69	1.41

steers (19.9 vs 18.0% DM). Schingoethe et al. (59, 60) found fecal dry matter to be reduced when steers were fed a 30% or more lactose diet. Ash content of the feces was higher in (60) than in the present study (14.8 vs 12.6% of fecal DM) which may have caused a greater osmolarity in intestinal contents and a decreased fecal dry matter.

Intestinal contents were measured for pH (Table 6). Both dietary treatments had similar affects on pH throughout the intestines and the feces. If lactose was entering the intestines, it may have been expected to reduce the pH of the contents by exceeding the buffering capability of the pancreas. Harrison (28) found that due to the large volume of chyme entering the duodenum, the buffering action of the pancreatic buffers were slower to act than that of monogastrics. A reduction of pH in the intestine may be caused by an increase in microbial fermentation products. Lactose might be metabolized directly by bacteria or hydrolyzed to glucose and galactose by the lactase present in the contents and then further metabolized by bacteria. The lactic acid and volatile fatty acids produced in the fermentation process would reduce the pH of the contents. Kim et al. (39) found the pH of pig cecal and colonic contents reduced and fermentation products increased when fed a 40% whey diet. Since lactose was not detected in the intestines in this trial, the similarities in pH were expected.

Nutrient Digestibility

Apparent digestibilities of both diets were measured using

TABLE 6. pH of intestinal contents and feces.

	Diet	
	Control	Whey
Duodenum	6.24	6.18
Jejunum	6.67	6.78
Ileum	6.96	7.08
Cecum	6.52	6.55
Large intestine	6.46	6.48
Colon	6.37	6.52
Feces	6.10	5.92

acid-insoluble ash as the indicator. Thonney et al. (65) found acid-insoluble ash recovery rate ranged from 90 to 106% of the dietary acid-insoluble ash thus, making it a reliable indicator. There were no differences in digestibilities of nutrients (Table 7) between treatment groups with the exception of higher ash digestibility ($P<.01$) when fed whey. Rayssiguier and Poncet (52) found that adding lactose to alfalfa hay diets of sheep increased apparent absorption of calcium, magnesium, and phosphorus, especially in the rumen. Schingoethe et al. (60) showed an increased sodium and potassium absorption with trends of an increased magnesium absorption when steers were fed increasing amounts of whey or lactose. The increased absorption resulted in an increased urinary excretion of those minerals. The exact mechanism for increased mineral absorption in the rumen has yet to be explained. Rayssiguier and Poncet (52) speculated that an increase in water intake and osmotic changes might increase the amount of ruminal fluid; reabsorption of the greater volume of water might result in an increased mineral absorption.

There was a time of feeding effect for the digestibility of all nutrients. Digestibilities of both diets were greater when fed to steers started in January than when fed to steers started in August. However, steers started in January were observed on several occasions consuming straw used for bedding while this was not observed with the August group. This straw would cause a greater acid-insoluble ash content of the feces, causing the

TABLE 7. Apparent digestibilities by steers fed whey and control diets.

Measurement	Diet		SE
	Control	Whey	
	%		
Dry matter	81.3	83.7	.80
Energy	82.0	84.2	1.97
Organic matter	82.3	84.4	1.89
Crude protein	76.6	75.4	2.28
Ether extract	85.8	85.3	1.20
Acid detergent fiber	55.6	54.8	4.10
Cellulose	61.1	60.4	4.05
Ash	63.6	76.7**	2.39

**Different from control (P<.01).

digestibility values to be greater than anticipated.

Lactose has been found to affect the digestibility of fiber components in ruminant diets. Decreases in digestibility of acid detergent fiber (50), neutral detergent fiber (60), and crude fiber (10, 58) have been reported. In this trial digestibilities of acid detergent fiber and cellulose were slightly lower for the whey than for the control diet, although these differences did not approach statistical significance.

Other researchers observed increased digestibility of dry matter (60), energy (60), and organic matter (50) when lactose or whey was fed to cattle or sheep. Digestibilities of these components were numerically higher in the trial when whey was fed, but differences from steers fed the control diet did not approach statistical significance.

Feed intake and weight gains are presented in Table 8. Dry matter intake averaged about 2.9% of body weight for both treatments. Steers had no apparent digestive or health problems when fed the 60% dried whey diet.

TABLE 8. Weight gains of steers fed whey and control diets.

	Diet	
	Control	Whey
Starting body wt, kg	264	288
Weight gain, kg/day	1.19	1.22
Feed intake, kg DM/day	7.6	8.5
DM intake/gain	6.36	6.60

SUMMARY AND CONCLUSION

The results of this study show that cattle have the capability to consume large amounts of dried whey without digestive disorders or reduced rates of gain. Microorganisms in the rumen of steers apparently have the capacity to ferment most, if not all, of the lactose in the 60% whey diet. The fermentation of whey in the rumen resulted in increased proportions of butyrate, but decreased proportions of propionate and ammonia in rumen contents. The decreased rumen ammonia may indicate that microbial protein synthesis was stimulated when dried whey replaced corn and soybean meal in the diet.

It appeared that lactase activity was affected by the amount of total carbohydrates entering the small intestine rather than just the amount of lactose entering. Steers fed the control diet had greater lactase activity than the steers fed the whey diet. Lactase activity was greatest in the proximal third of the small intestine with little activity occurring in the distal third, irregardless of diet. Lactase activity of intestinal contents was similar for both diets. Lactase activity of contents was greatest in the duodenum and declined to low levels found in the ileum and large intestine. Digestibility of ash was higher for steers fed the whey diet and was numerically higher for energy and organic matter. Digestibilities for acid detergent fiber and cellulose was numerically lower for steers fed the whey diet.

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APPENDIX TABLE 1. Sum of squares for rumen volatile fatty acids, ammonia, and pH.

Source of variation	Degree of freedom	C_2[a]	C_3	iC_4	C_4	iC_5	C_5	Total VFA, µM/ml	Ammonia mg/100 ml	pH
Total	31	753.3	6051	11.92	3636	25.27	77.16	95.66	117.0	10.75
Treatment	1	202.6**	4573**	2.06**	2512**	3.05*	4.97	0.66	58.2**	0.33
Time	1	29.3	101	0.28*	19	4.88**	2.90	33.60**	6.4*	6.05*
Trt x time	1	35.7	60	1.16**	193*	0.04	8.11	8.05	6.9*	0.00
Week	3	138.0*	159	2.94**	68	5.61*	6.26	0.51	5.4	0.86
Trt x week	3	21.6	173	1.42**	306*	0.53	12.28	0.82	12.3	0.03
Time x wk	3	9.2	27	0.80*	31	0.28	2.54	3.08	3.1	0.43
Trt x time x wk	3	76.8	114	2.22**	88	1.22	1.74	4.70	1.8	0.12
Error	16	240.1	844	1.03	419	9.65	28.37	36.24	22.9	2.94

[a]Numeral refers to number of carbons in VFA, i means isomer.

*Significant (P<.05).

**Significant (P<.01).

APPENDIX TABLE 2. Sum of square for lactase activity in intestinal mucosa.

Source of variation	Degrees of freedom	Segment 1	Segment 2	Segment 3	Segment 4	Segment 5	Segment 6	Segment 7	Segment 8	Segment 9	Segment 10	Segment 11	Segment 12	Segment 13	Segment 14	Segment 15
Total	7	3.614	3.641	9.469	12.865	8.781	9.298	4.067	0.190	0.015	0.005	0.071	0.003	0.006	0.008	0.005
Treatment	1	1.950	0.572	2.453**	3.088*	3.251	1.059	0.673	0.000	0.005	0.000	0.009	0.000	0.001	0.000	0.000
Time	1	0.138	0.980	1.320*	2.344	0.186	0.300	0.238	0.013	0.000	0.001	0.008	0.001	0.000	0.000	0.000
Trt x time	1	0.235	1.066	5.233**	6.038**	3.328	2.216	0.054	0.018	0.000	0.000	0.003	0.002**	0.001	0.006**	0.002
Error	4	1.292	1.023	0.463	1.396	2.016	5.724	3.102	0.159	0.010	0.003	0.051	0.000	0.004	0.001	0.003

*Significant (P<.05).

**Significant (P<.01).

APPENDIX TABLE 3. Sum of squares for lactase activity/mg tissue protein.

Source of variation	Degrees of freedom	Segment 1	Segment 2	Segment 3	Segment 4	Segment 5	Segment 6	Segment 7	Segment 8	Segment 9	Segment 10	Segment 11	Segment 12	Segment 13	Segment 14	Segment 15
Total	7	16.64	13.66	43.54	44.50	49.68	46.88	25.84	2.174	0.055	0.079	0.473	0.106	0.079	0.068	0.090
Treatment	1	0.36	0.14	2.74	1.03	3.95	4.15	3.81	0.054	0.005	0.013	0.002	0.024	0.006	0.009	0.031
Time	1	0.39	0.89	1.64	0.15	3.30	0.01	3.33	0.361	0.006	0.007	0.228	0.026	0.007	0.000	0.008
Trt x time	1	2.06	2.82	35.87**	27.57*	27.45*	11.57	0.03	0.266	0.000	0.014	0.002	0.029	0.026	0.030	0.026
Error	4	13.83	9.81	3.29	15.75	14.97	31.16	18.68	1.492	0.044	0.045	0.241	0.027	0.039	0.029	0.023

*Significant (P<.05).

**Significant (P<.01)

APPENDIX TABLE 4. Sum of squares for protein content in intestinal mucosa.

Source of variation	Degree of freedom	Segment 1	Segment 2	Segment 3	Segment 4	Segment 5	Segment 6	Segment 7	Segment 8	Segment 9	Segment 10	Segment 11	Segment 12	Segment 13	Segment 14	Segment 15
Total	7	1102	1553	621	1029	1064	1119	1175	1585	1349	1938	1987	850	1249	628	1230
Treatment	1	559*	378	217	327	181	135	224	580	291	221	394	226	448	142	647*
Time	1	155	797*	40	167	489	333	431	335	394	249	772	171	183	111	226
Trt x time	1	207	151	3	215	0	138	59	1	126	1	6	7	65	138	44
Error	4	181	227	362	319	394	514	462	669	538	1467	815	446	552	238	313

*Significant (P<.05).

APPENDIX TABLE 5. Sum of squares for lactase activity in intestinal contents.

Source of variation	Degrees of freedom	Duodenum	Jejunum	Ileum	Cecum	Large intestine	Colon
Total	7	11.37	1.369	0.008	0.005	0.012	0.002
Treatment	1	0.27	0.180	0.001	0.001	0.006*	0.000
Time	1	3.24	0.304	0.005*	0.000	0.001	0.000
Trt x time	1	0.30	0.174	0.000	0.000	0.002	0.001*
Error	4	7.57	0.711	0.002	0.004	0.002	0.000

*Significant ($P<.05$).

APPENDIX TABLE 6. Sum of square for digestibility of nutrients.

Source of variation	Degrees of freedom	Dry matter	Energy	Crude protein	Organic matter	Acid detergent fiber	Lignin	Cellu-lose	Fat	Ash
Total	31	353.9	2599	5798	3735	11,842	15,149	13,262	2653	6050
Treatment	1	18.2	39	12	33	5	903	4	2	1381**
Time	1	56.3*	411**	2545**	1509**	1728*	2800**	3009**	1426**	1532*
Trt x time	1	0.0	370*	453*	203	838	2148*	1508*	22	758**
Week	3	15.2	534*	1078**	699*	3133*	2475	3414**	623**	757
Trt x wk	3	52.1	84	168	32	474	609	429	27	40
Time x wk	3	48.6	343	299	227	1378	1171	1090	107	106
Trt x time x wk	3	8.0	15	65	43	333	333	268	9	57
Error	16	155.7	803	1179	989	3951	4710	3540	435	1419

*Significant (P<.05).

**Significant (P<.01).