THE EFFECT OF FEEDING PROCESSED RYE GRAIN TO LACTATING DAIRY CATTLE AND THE EFFECT OF RYE BRAN AND FLOUR FRACTIONS ON RUMINAL FLOW AND GASTROINTESTINAL FUNCTION

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BY

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ABSTRACT FOR MICROFILM

Eight lactating Holstein cows (1-3 months postpartum) were fed four diets for 28 days each containing 60% dry rolled extruded or roasted rye or 60% dry rolled barley (control) in the grain mixes using a 4 x 4 latin square design. Total (DM) intake and ADF digestibility were significantly lower ($P<0.05$) for all rye rations. No differences were observed ($P>0.05$) among rations for milk production, 4% fat corrected milk, milk fat level, milk protein level, rumen pH, blood urea nitrogen or blood glucose levels.

Six substrates whole rye (WR), rye bran (RB), rye flour (RF), whole wheat (WW), wheat bran (WB) and wheat flour (WF) were incubated in 40 ml of 39 degree celsius rumen fluid for 3 hours. Each hour the samples were centrifuged and 5 ml of fluid were aspirated and viscosity measured. The pH was adjusted each hour beginning at 6.5, then lowered to 2.5 and then raised to 7.5 to simulate gut physiology. RB and WB fractions were more viscous than RF and WF fractions ($P<0.01$). RF was more viscous than WF ($P<0.01$). WR was significantly more viscous than WW ($P<0.01$).

Four 250 kg Holstein steers were fed four pelleted diets in a 4 x 4 latin square design and cannulated at the rumen, abomasum and ileum. The four diets contained 50% flour and 33% bran in combinations of RBRF, RBWF, WBRF and WBWF fed at 2% of body weight on automatic belt feeders. Each dietary period was 28 days and each diet contained dysprosium chloride as an inert marker used to measure nutrient flow rates. No significant differences in DM intake ($P>0.01$) were indicated for any treatment. The RF diets were lower in ($P<0.01$) apparent methionine absorption values in the small intestine but had equivalent apparent lysine absorption values in the small intestine compared to WF diets.

Diets containing RF showed highest xylose and arabinose flow rates through the ileum and feces ($P<0.01$), had the highest ileal acetate and ruminal and ileal lactic acid contents ($P<0.01$), highest fluid viscosities ($P<0.01$), highest flow of fat through the GI tract and lowest fecal fat digestibilities ($P<0.01$) compared to WF diets. ADF digestibilities were lowest for diets containing RB ($P<0.01$).

ABSTRACT

The effect of feeding processed rye on dairy cattle performance was studied. Eight lactating Holstein cows in early lactation (1-3 months post-partum) were randomly assigned to four diets in a 4 x 4 cross-over design. The four diets contained either 60% dry rolled, extruded or roasted rye or 60% dry rolled barley (control) in the grain mixtures. Grain and forage were fed ad libitum in a 60:40 ratio (DM basis) throughout the experiment. Each experimental period was 28 days in duration with 7 days for diet changeover and 21 days for data collection. Total dry matter (DM) intake was significantly lower ($P<0.05$) for all cows receiving the rye rations. However, no significant differences were observed ($P>0.05$) between rations with respect to daily milk production, 4% fat corrected milk, milk fat, milk protein or lactose content. However, ADF digestibility was significantly lower ($P<0.05$) for cattle fed the rye diets. No significant differences ($P>0.05$) existed among treatments for ruminal pH, blood urea nitrogen or blood glucose levels.

An in vitro experiment was conducted to study the effects on viscosity at three different pH values 6.5, 2.5 and 7.5 which simulate the physiological pH values found in the rumen, abomasum and ileum. The various pH values were adjusted using metaphosphoric acid or sodium hydroxide. A fixed two way statistical analysis of variance of the experiment was conducted. Multiple comparisons were conducted using orthogonal comparisons. There were six treatments, whole ground rye (WR), rye bran (RB), rye flour (RF), whole ground wheat (WW), wheat bran (WB) and wheat flour (WF). Four grams of each treatment were incubated in triplicate

in 40 ml of 39 degrees celsius centrifuged rumen fluid obtained from a cannulated steer adjusted to a 60:40 ratio of concentrate to forage. A three hour incubation was carried out at 39 degrees celsius. At the end of one hour each tube was centrifuged at 40,000 x g, 5 ml aspirated and viscosity measured using a prewarmed viscosity pipette.

A significant difference ($P<0.05$) exists between the rye and wheat bran, versus rye and wheat flour incubation fluid viscosities. The wheat bran fraction showed significantly ($P<0.05$), higher viscosity values across all pH values than wheat flour. Comparisons of wheat flour versus rye flour indicates that rye flour has significantly higher viscosity values ($P<0.01$) at pH values 6.5, 2.5 and 7.5. The comparison of rye bran versus wheat bran showed a significantly higher viscosity for rye bran ($P<0.01$) than for wheat bran at all pH values. Comparisons of whole ground rye versus whole ground wheat indicates that rye is significantly ($P<0.01$) more viscous at any pH value tested. In all cases the whole rye and rye fractions were more viscous than the whole wheat and wheat fractions at pH 2.5 and 7.5.

Four Holstein steers averaging 250 kg were fistulated in the rumen, abomasum and terminal ileum. There were four separate diets fed to the steers in a 4 x 4 latin square design with each period consisting of 28 days. The base of each diet consisted of (1) rye bran, rye flour (RBRF), (2) rye bran, wheat flour, (RBWF), (3) wheat bran, rye flour (WBRF), (4) wheat bran, wheat flour (WBWF). The rations were pelleted and contained approximately 50% flour and 33% bran. All cattle were fed continuously in metabolism crates and received 2% of their body weight in

dry matter of the respective experimental rations. Each ration contained 25 ppm dysprosium chloride added as DyCl3.6H2O for estimation of flow parameters and nutrient digestibilities. The dry matter (DM) intake did not differ ($P>0.01$) among treatments. Average flow of digesta through the whole gastrointestinal tract did not differ ($P>0.01$) among treatments. There was a significant difference ($P<0.01$) in DM flow across all treatments between the rumen and abomasum with significantly more ileal flow of DM from diets containing rye flour (RF). The flow of DM between ileum and feces was not significantly different ($P>0.01$) among treatments.

Diets containing RF had significantly higher ruminal flows of crude protein compared to intake ($P<0.01$). The increased ruminal crude protein flow was associated with significantly reduced ($P<0.01$) crude protein digestibilities and significantly increased ruminal bacterial nitrogen flows. Diets containing RF resulted in significantly higher flows of lysine, arginine and histidine through the abomasum compared to diets containing wheat flour. Diets containing RF had significantly less methionine ($P<0.01$) apparently absorbed between the abomasum and ileum. The diet containing RBRF showed the lowest apparent crude protein digestibility for ileum and fecal measurements. Protein digestion throughout the whole gastrointestinal tract would indicate that protein from diets containing RF are more resistant to protein degradation.

The ADF digestibility was lower ($P<0.01$) and flow of ADF through the abomasum was significantly higher ($P<0.01$) for diets containing rye bran compared to those containing wheat bran. The diets containing the rye bran also showed significantly lower apparent ADF fecal digestibilities

($P<0.01$) than the diets containing wheat bran.

The digestibilities of xylose and arabinose in the abomasum and ileum was significantly lower ($P<0.01$) for diets containing rye flour than those containing wheat flour. The fecal excretion of xylose and arabinose indicates almost 100% fecal disappearance for all treatments. However, fecal excretion of xylose for RF diets was significantly higher than for WF diets ($P<0.01$). The data indicates a significantly higher flow of xylose ($P<0.01$) through the ileum for diets containing rye flour compared to diets containing wheat flour. The total acetate levels for ileal fluid were significantly higher for diets containing rye flour compared to wheat flour ($P<0.01$). The lactic acid content for rumen fluid and ileal fluid were significantly higher ($P<0.01$) for RBRF compared with the other experimental diets ($P<0.01$) indicating increased fermentative activity in these compartments for RBRF fed animals. The diets containing rye flour exhibited the highest ruminal and ileal viscosities ($P<0.01$) while RBRF showed the lowest fecal pH ($P<0.01$). Diarrhea was not detected on any experimental animal at any time.

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INTRODUCTION

A challenge facing producers and feed manufacturers, is to formulate and produce dairy rations which have a consistently high acceptability by dairy cattle. An ingredient with economical value in dairy feeds in portions of North America is rye grain. Rye, is detrimental in animal feed not because of low nutritive value, since rye has an analyzed rating higher than barley and about equal to wheat, but because of possible palatability or other antinutritional problems.

A few workers (McKeon and Egan 1971, Dinusson et al. 1971, Burfening 1973, Ingalls and Phillips 1971) have suggested that an appetite depressing effect may be caused from rye containing as little as 0.06% ergot. Burfening (1973) suggests ergot was the appetite depressing factor which was thought to increase the body temperature because of a direct effect on the hypothalamus which depressed nutrient intake.

However, many other workers contribute reduced feed intake of rye to high levels of 5 - n - alkylresorcinols (Wenckert 1964, Haeberle 1974, Verdeal and Lorenza 1977, Weiringa 1967, Friend 1970, McGinnis 1972, McGinnis 1974, McDonald 1974). Work by Misir and Marquardt (1978) and Haeberle (1974) has concluded that the alkylresorcinol content is not responsible for intake depression and reduced performance in chicks.

The results of many rye feeding studies are conflicting. Winter (1973) and Winter (1975) has concluded that ergot free rye can be included up to 80% in the ruminant ration with no significant reduction in intake. Cave (1974) concluded that rye inclusion up to 40% in the complete feed for dairy cows was acceptable with no loss of performance.

Sharma et al. (1981) found that the dry matter intake was reduced ($P<0.05$) when lactating dairy cows were fed 25, 50 or 75% rye in their grain mixture compared to barley. However, no significant differences were determined on performance of rye fed dairy cows. Sharma et al. (1983) found that alkali treated rye increased the dry matter consumption by 13% compared to untreated rye when fed to lactating dairy cows.

Studies by Misir and Marquardt (1978c) indicate that rye contains an appetite depressing factor in the bran, flour and middlings and a growth depressing factor in the bran. The non-starch polysaccharides could possibly influence ruminant appetite by reducing rate of passage from the rumen because of their highly viscous nature in aqueous solutions (Sharma et al. 1981). As well, the possibility exists that the rumen microbes may not be able to degrade the branched pentosans of rye (Leatherwood 1973, Morrison 1957, Morrison 1979). Therefore the non-starch polysaccharides could by-pass the rumen and enter the small intestine where the absorption of nutrients could be reduced because of non-specific ionic binding of nutrients and gel formation by the pentosans (Mod 1981). The possibility exists that because of larger quantities of fermentable carbohydrates entering the ruminant large intestine the volatile fatty acid concentration increases because of microbial fermentation thereby reducing the true availability of nutrients.

The objective of these studies was to determine if dry rolled rye, extruded rye or roasted rye which contained 0.06% ergot or less, has any detrimental effects in ruminants with respect to milk production. Also to determine which fraction of rye (i.e. bran or flour) may have an effect

in the gastrointestinal tract of the ruminant with respect to nutrient digestibility and compartmental flow rates of nutrients compared to wheat.

LITERATURE REVIEW

INTRODUCTION

Origin, Distribution and Agronomic Features of Rye (*Secale cereale* L.)

Rye is second only to wheat as the grain used most commonly for bread making. Rye, because of its extreme hardiness can grow in areas with sandy, low fertility soils which are generally not suitable for growing other cereal grains. The cool temperate zones of the world are areas where the greatest production takes place, but its also found in semi-arid regions and at high altitudes. Rye enjoys the widest distribution of all cereals (Bushuk 1976).

Rye appears to have originated in Southwestern Asia, the same areas where wheat, oats and barley apparently originated (Deodikar 1963). Rye does not appear to be as old as wheat. Sometime during the first millenium B.C. rye moved from its centre of origin to northern Europe. Rye gradually spread through most of Europe and eventually reached North America in the 16th and 17th centuries. During this period rye reached the fringe of the U.S.S.R. and into Siberia (Bushuk 1976).

Rye, because of its superior winter hardiness is grown as a fall sown annual. Thus, winter rye can be grown successfully in areas where the climate is too severe at present for winter wheat. Spring rye can be grown in areas where the winters are too severe, however, these varieties are inferior in agronomic qualities (Bushuk 1976).

Canadian Rye Production

The production of rye, barley, oats and wheat is almost entirely concentrated in the prairie provinces of Manitoba, Saskatchewan and Alberta. In Canada, 23% of rye is grown in Manitoba, while another 67% is grown in Saskatchewan and Alberta (Ward 1982). In 1981 Canadian rye represented 1.91% of the total cereal grain produced in Canada. Most rye is grown in the prairie provinces primarily because of its winter hardiness. In 1981 Manitoba produced a record 175,100 metric tonnes of rye.

During the last decade there has been an increase in the amount of rye used as animal feed which consumes about 30% of the total production, while exports consume over 40% of total Canadian production (Ward 1982).

Proximate Analysis of Rye and Related Cereals

Great variation exists among cereal grains regarding their proximate analysis especially in the protein content. The composition of four common cereal grains, found typically in North America, are presented in Table 1. One feature of all the major cereals is that they are low in protein and high in N-free extract with wide variations in crude fibre content. Wheat is similar to rye in all aspects except that rye is slightly higher in crude protein content and slightly lower in gross energy content (NAS 1971). Examination of the average composition of cereal grains shows that rye ranks lowest in niacin (1.50 mg/100 g) compared to barley, oats, corn and wheat. The carotene level in rye is considered to be zero as is the case for oats and wheat while barley and

Table 1. Proximate composition, mineral, B vitamin and carotene content of cereal grains (% dry basis)

Component	(1) Barley	(2) Oats	(1) Corn	(1,3,4) Wheat	(1,3,4) Rye
Protein Nx6.25	12.6	12.7	10.4	12.3	12.8
Ether extract	1.1	1.9	4.5	1.8	1.7
Crude fibre	5.0	11.3	2.4	2.5	2.3
Nitrogen free extract	78.3	70.2	81.2	81.4	81.2
Ash	3.1	3.9	1.5	2.0	2.0
Energy Mcal/kg	-	-	-	3.95	3.75
Minerals mg/100 g					
Phosphorus	470.0	340.0	310.0	410.0	380.0
Calcium	90.0	95.0	30.0	60.0	70.0
Magnesium	140.0	140.0	140.0	180.0	130.0
Iron	6.0	7.0	2.0	6.0	9.0
Copper	0.9	4.0	0.2	0.8	0.9
Manganese	1.8	5.0	0.6	5.5	7.5
Potassium	630.0	460.0	330.0	580.0	520.0
Vitamins					
Thiamine	0.57	0.70	0.44	0.55	0.44
Riboflavin	0.22	0.18	0.13	0.13	0.18
Niacin	6.40	1.80	2.60	6.40	1.50
Pantothenic acid	0.73	1.40	0.70	1.36	0.77
Pyridoxine	0.33	0.13	0.57	0.53	0.33
Carotene	0.04	0.00	0.40	0.00	0.00

1 Miller (1958)

2 Crampton and Harris (1968)

3 National Academy of Sciences (1971)

corn have negligible amounts of 0.04% and 0.40% respectively. The mineral content of rye is quite similar to the other grains (Table 1), except that rye is slightly lower in magnesium. The copper levels of rye are 0.9 mg/100 g similar to barley 0.9 mg/100 g and wheat 0.9 mg/100 g but only 22.5% that of oats at 4.0 mg/100 g.

Neither the unavailability of minerals nor the low protein content are a problem in animal nutrition because diets can be supplemented with adequate amounts of minerals and vitamins.

Rye Protein Quality

The amino acid profile of whole rye and whole wheat from two sources is given in Table 2. Of primary importance is the larger ratio of essential amino acids to nonessential amino acids in rye (0.6) compared to wheat (0.5). The amino acid composition of rye protein is considered to be nutritionally superior to that of most other cereals (Hulse and Laing 1974). Primarily this is due to the higher proportion of lysine present in the water soluble proteins (albumin and globulin); which have an improved content of lysine (Bushuk 1976). A comparison of chemical scores for lysine threonine, methionine and tryptophan reveal higher values for lysine and threonine in rye when compared to wheat (Table 3). The data in Table 3 show that in spite of the higher lysine content, this amino acid is still likely to be the first nutritionally limiting amino acid in whole rye when fed to monogastrics. Lysine, methionine and tryptophan content as a percentage of total protein, is inversely correlated with

Table 2. Amino acid composition of whole rye and whole wheat (A)

Amino acids	Rye		Wheat	
Essential (E)	(1)B	(2)C	(1)B	(2)C
Arginine	28.6	26.2	28.8	24.9
Histidine	13.8	13.1	14.3	13.8
Isoleucine	21.9	22.8	20.4	23.9
Leucine	38.5	37.4	41.7	42.0
Lysine	21.2	18.1	17.9	14.5
Methionine	9.1	7.3	9.4	10.5
Phenylalanine	27.6	28.0	28.2	29.7
Threonine	20.9	20.9	18.3	17.3
Tryptophan	4.6	7.6	6.8	9.6
Valine	29.7	30.6	27.6	27.9
Non essential (N)				
Alanine	26.6	23.2	22.6	20.4
Aspartic acid	49.7	40.4	30.8	29.2
Cysteine/cystine	11.9	14.3	15.9	16.2
Glutamic acid	151.1	172.0	186.6	207.0
Glycine	27.1	22.7	25.4	23.5
Proline	58.6	65.0	62.1	69.6
Serine	27.0	26.8	28.7	31.3
Tyrosine	12.0	11.8	18.7	16.7
Ratio E/N	0.6	0.6	0.5	0.5

A g amino acid/100 g sample N

B Canadian varieties

C Average of several samples

(1) Hulse and Laing (1974)

(2) Tkachuk and Irvine (1969)

Table 3. Chemical scores for rye and wheat compared to World Health Organization standards

Amino acid	WHO 1973 standard reference (1) mg/g protein	Rye AA content mg/g protein	Chemical score (2)	Wheat AA content mg/g protein	Chemical score
Lysine	55	37	67	31	56
Threonine	40	37	92	31	77
Methionine & cystine	35	37	105	43	123
Leucine	70	67	96	72	103
Isoleucine	40	39	97	35	88
Valine	50	52	104	47	94
Phenylalanine & tyrosine	60	69	115	81	135
Tryptophan	10	8	80	--	--

(Condensed from Hulse and Laing 1974)

(1) WHO standard based on amino acid patterns of egg and human milk protein and upon estimated amino acid requirements for humans.

(2) The quantity of a particular amino acid present in a foodstuff is expressed as a percentage of the amount present in a standard reference pattern.

total protein although their total amounts as a percentage of the whole meal increases with total protein. Although not specifically reported for rye, there appears to be an effect of fertilizer treatment similar to that of wheat (Hutcheon and Paul 1966). High application of nitrogenous fertilizer raise protein levels in mature wheat grain (Hutcheon and Paul 1966). When nitrogen supplies are limiting an inverse relationship between grain yield and protein content occurs (McNeal 1972, Williams 1966, Munck 1964, Munck 1972). The explanation for this appears to be that higher protein levels are associated with a lower percentage of the water soluble albumin lysine rich groups of protein.

The principle difference between wheat and rye fractions is found in the protein and fibre components (Table 4). Although rye bran contains much less fibre than wheat bran the flour of rye appears to be higher in fibre than that of wheat flour. This difference is due primarily to the fact that rye bran separates less cleanly from the endosperm than wheat bran (Antoniou 1980). Consequently the rye flour contains a higher level of fibre than the wheat counterpart. The protein content of rye bran and wheat bran are similar while the rye flour has a lower crude protein percentage than wheat flour. Kihlberg and Ericson (1964) showed that the first limiting amono acid of four different rye flours was lysine followed by threonine while all other essential amino acids were almost equally deficient. Rye flour protein was superior to wheat flour protein in several tests using growing rats. Sikka et al. (1978)

Table 4. Proximate comparison of rye bran, rye flour to wheat bran, wheat flour (DM basis) (1)

Component %	Rye bran	Rye flour	Wheat bran	Wheat flour
Total N %	3.07	2.05	3.00	2.32
Protein (Nx5.7) %	17.50	11.70	17.10	13.20
Fat	3.40	1.40	4.40	1.30
Starch % (2)	-	78.00	-	72.00
Fibre %	7.60	0.60	11.60	Trace
Ash %	5.20	1.00	6.90	0.50
NFE %	66.40	85.30	60.00	83.60

(1) Antoniou (1980)

(2) Bushuk (1976)

Table 5. Yield of bran, middlings and flour obtained from milling rye and wheat

Fraction	Rye %	Wheat %
Bran	25.4	19.2
Middlings	17.9	9.0
Flour	56.7	71.8

Bushuk (1976)

also compared rye with egg protein and concluded that lysine and threonine were the first limiting and second limiting amino acids respectively. Rye bran contains higher amounts of lysine, histidine, arginine, glycine alanine and sulfur containing amino acids than the flour fraction (Sikka et al. 1978).

The better quality of rye protein over wheat protein was indicated by higher protein efficiency ratios, biological values and net protein retention obtained in rat experiments (Sikka et al. 1978, Knipfel 1979). Using rat bioassays rye was compared to wheat, oats, sorghum, corn and barley. Knipfel (1979) concluded that the biological value for rye was higher than all the rest. However, since rye has a reduced true protein digestibility, the net protein utilization values were equal to the other grains (Eggum 1973). According to Chen and Bushuk (1970), rye differs from most of the other cereal grains in that there is a higher proportion of water soluble (albumins) and salt soluble (globulins) proteins, both of which have a higher content of lysine making rye protein more desirable.

Resorcinols

Rye has not been used extensively as a livestock feed (Sharma et al. 1981). There have been reports of a palatability problem that causes reduced feed intake and reduced weight gains as compared with other cereals (Friend and MacIntyre 1969, Friend 1970, Smith and MacIntyre

1960). This cannot be attributed to major differences in the usual parameters of feed value, such as total digestible nutrients (TDN), digestible energy or protein content, since these compare favorably with other high energy grains (Morrison 1957). Weiringa (1967) conducted experiments feeding Petkuser winter rye to weanling male rats. Growth inhibiting substances known as a mixture of 5-n-alkylresorcinols with odd numbered side chain of 15-23 carbons together with smaller amounts of 5-n-alkenylresorcinols were identified. These studies indicated that these compounds were soluble in petroleum ether and acetone, could be concentrated by solvent fractionation, and isolated chromatographically. These resorcinols are found in the unsaponifiable fraction of rye oil associated with the bran fraction and were shown to depress feed intake because of their very adverse metabolic effects causing general debilitation of the rats rather than because of reduced palatability of rye diets. This same group of chemicals has been found in the non saponifiable fraction of wheat bran (Wenckert 1964). Rye resorcinols and wheat resorcinols have been found to produce the same degree of growth inhibition in rats. However, the lower nutrient valuation of rye was attributed to the fact that rye contains nearly two times more resorcinol than wheat (Wenckert 1964, Evans et al. 1973). The alkylresorcinol content of the spring rye cultivars was found to be higher than for winter rye cultivars; furthermore there was greater resorcinol content in spring cultivars than in winter cultivars; 0.046% to 0.322%

as compared to 0.036% to 0.279% respectively (Evans et al. 1973).

An average of 36.0 mg of resorcinol per 100 g of Manitoba rye cultivars compared to 17.8 mg of resorcinol per 100 g of wheat cultivars have been shown by Haeberle (1974). Fractionating rye, wheat and triticale into their respective milling fractions of bran, shorts and flour indicates that bran contains the highest levels of resorcinols, with flour containing none. Rye contained the highest resorcinol content, triticale intermediate and wheat the lowest (Verdeal and Lorenza 1977). Other authors have contradicted the growth inhibiting findings of Weiringa (1967). In trials using rats fed milled fractions of rye and barley the studies indicated that rye flour rather than rye bran was responsible for lower feed consumption and growth rates (Friend 1970). McGinnis (1972) found that the acetone extraction, which removed any resorcinol present, did not eliminate the growth depressing effect of rye. In feeding trials with weanling mice, McDonald et al. (1964) fed diets containing up to 160 mg resorcinol/100 gm of diet and found no adverse effects on voluntary feed intake or weight gain. The apparent discrepancy between these findings and Weiringa (1967) may be attributed to the lower resorcinol levels in the diets (McDonald et al. 1974). The diets fed by Friend (1970, McGinnis (1974) and McDonald (1974) had resorcinol levels comparable to those normally present in diets formulated using rye in Western Canada. Weiringa (1967) used higher than normal levels (115 to 2.5%) of rye oil. The levels used in these diets (Weiringa 1967) are 100% higher in resorcinol levels than that of a diet containing 80% rye. From these observations Haeberle (1974) concluded that the

alkylresorcinol content of rye is not responsible for its poor nutritional status. Misir et al. (1978) also showed that not only rye bran but also rye flour and middlings had chick growth depressing activity, which was independent of resorcinol content.

The Polysaccharides of Rye Grain

Very little information is available on the non-starchy polysaccharides in rye grain since most of the work concerning the isolation and characterization of these compounds has been with wheat, barley, corn and rice (Antoniou 1980). In cereal grains, the hemicelluloses, cellulose, glucofructans, pentosans and β-glucans are among the recognized non-starchy polysaccharides (D'Appolonia et al. 1971). Hemicelluloses are defined as that part of the cell wall often containing lignified tissues that can be extracted by dilute alkali but not with water (D'Appolonia et al. 1971, Aspinall and Greenwood 1962, Wilkie 1979). Two main classes of polysaccharides may be recognized, the xylan group, which comprises the water soluble arabinoxylans of cereal grains and the major hemicelluloses compounds of the bran. Cereal fibre is reported to contain as much as 75% hemicellulose (Mares and Stone 1973a). Two general types of hemicellulose reported to be widely distributed are the xylan group and the β-glucan group (Wilkie 1979). The β-glucan group comprises chains of glucose residues with β 1,3 and β 1,4 with a small proportion of β 1,6 linked side units. The water soluble pentosans and β-glucans are also known as cereal gums because of their highly viscous nature and adhesive power (Aspinall and Greenwood 1962). The β-glucans

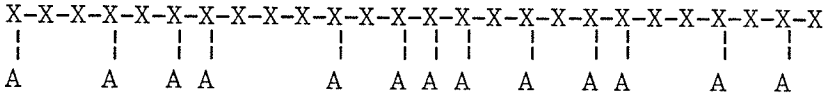
are found mainly in barley and oats. The pentosans are a group of polysaccharides composed mainly of B-D-xylopyranose and arabinofuranose. Mares and Stone (1973a) have determined that the endospermic pentosans contain small quantities of glucuronic acid. The endospermic pentosans which are soluble in water have a composition similar to, but less branched than those pentosans which are insoluble in water (Antoniou 1980). Although the typical gums and the typical hemicelluloses from lignified parts of cereals are distinct in their origin and presumably have different functions, clearly there is no simple relation between chemical structure and solubility characteristics (Antoniou 1980, Antoniou and Marquardt 1981b). If pentosans are to be classified by solubility characteristics, a misnomer exists in that this does not reflect any structure or biological differences (Mares and Stone 1973a). The water soluble and insoluble cereal pentosans are composed of xylose and arabinose (Mares and Stone 1973a). However, Mares and Stone (1973a) and D'Appolonia (1973) have shown that some water insoluble pentosans become water soluble after alkali extraction. Preece and MacKenzie (1952) in comparative studies of the yields of unfractionated water soluble gum like material from a number of cereals have indicated that barley is probably the best source of β-glucans; rye, the best source of pentosans; with wheat in an intermediate position, and oats and corn poor sources of pentosans. Preece and MacKenzie (1952) extracted pentosans in 80% boiling ethanol under reflux to inactivate enzymes. The water soluble pentosans in the eluant were totally precipitated by the addition of Fehligs solution followed by acetone. The sugars were then

hydrolyzed and their contents were examined using paper chromatography. Preece and MacKenzie (1952) and Preece and Hobrick (1953) have reported that rye is very rich in high molecular weight water-soluble pentosans composed of D-xylopyranose and arabinofuranose with small quantities of galactose, glucose and B-glucans. Podrasky (1964) separated glucans and arabinoxylans from gums of rye, wheat, barley and oats by stepwise extraction with either ammonium sulphate or with methanolic borate solutions. Measurement of the ratio of arabinose:xylose indicated that arabinoxylans from rye and barley were more highly branched. Molecular weights and degree of polymerization of the arabinoxylan and glucan components obtained from the different cereal gums can be attributed to the relative contents of the arabinoxylan and glucan components. A comparison of pentosan content is given in Table 6 for various cereal grains. D'Appolonia (1973) suggests that most of the insoluble pentosan found in cereal grains are associated with the bran. Aspinall and Sturgeon (1957) isolated a water soluble gum fraction from rye flour which yielded on hydrolysis xylose 60% arabinose 29% and glucose 5.5%. Using periodate oxidation or enzymolysis Aspinall and Sturgeon (1957), Preece and MacDougall (1958) and Preece and Hobrick (1955) have determined a more exact description of the sequence of arabinose and xylose residues. The arabinoxylan components of wheat and rye contain on the average side chains attached to approximately every second xylose residue (Preece and Hobrick 1955). The arabinoxylan of rye flour has been shown by the above cited authors to contain isolated D-xylose residues, two adjacent D-xylose residues, but not four or more D-xylose residues. According to Aspinall and

Table 6. Total pentosan content of cereal grains

Grain	% Dry basis	Source
Oats	14.0	D'Appolonia (1973)
Wheat	6.0	D'Appolonia (1973)
Barley	10.0	Podrasky and Fantik (1964)
Corn	Trace	Preece and Hobrick (1953)
Rye (Puma)	9.8	Antoniou et al. (1981b)

Greenwood (1982 and Aspinall and Ross (1963) a partial formula for rye flour pentosans may be represented by the following structure where (X) represents xylose and (A) represents arabinose.

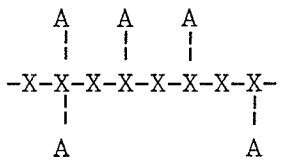


Hemicelluloses and pentosans found in the starchy endosperm or flour portion of cereal grains have received considerable attention (Preece and Hobrick 1955, Antoniou 1980). The term hemicellulose has been used to refer to the water-insoluble pentosans which are located in a layer of material above the prime starch when a slurry of flour and water is centrifuged. Different terms have been used to describe this layer of material including "amylodextrin", "squeegee", "tailing" and "sludge" (D'Appolonia 1973, Antoniou et al. 1981b). The water-soluble gums extracted from flour with water are most often referred to as the water soluble pentosans. The insoluble flour pentosans may be similar in structure and properties to the insoluble pentosans found in bran (Holloway 1980). The insoluble pentosans of rye have been shown to contain 59% xylose, 34% arabinose and 7% glucose with a trace of galactose (D'Appolonia 1973).

Antoniou (1980) fractionated puma rye and found that of the 9.8% total pentosan, (Table 6) 2.1% was soluble while 7.7% was insoluble. Analysis of the hydrolyzed fractions indicated that the water soluble pentosan preparation contained 67.7% arabinose plus xylose, 2.9% galactose, 4.2% mannose and 6.2% glucose with a ratio of xylose:arabinose

equal to 1.39. The water insoluble pentosans extracted with NaOH and then hydrolyzed yielded 48% arabinose plus xylose, 1.71% mannose, 2.42% galactose and 24.06% glucose with a ratio of xylose to arabinose 1.12. Since the ratio of xylose to arabinose for soluble pentosans are 1.39 and 1.12 for insoluble pentosans, this indicates that the soluble fraction is less branched than the insoluble fraction. Holas et al. (1972) have reported similar results with a ratio of 1.32 and 1.17 for soluble and insoluble pentosans respectively.

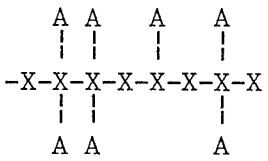
The structure of water soluble wheat pentosans has been elucidated by Perlin (1951a) and Perlin (1951b). The wheat water-soluble pentosans have a slightly different structure than the soluble pentosans of rye. The main chain of water-soluble wheat pentosans consists of anhydro-D-xylopyranose units linked B 1,4. From this chain radiates anhydro-L-arabinofuranose residues at the two or three positions of individual anhydroxylose units. The L-arabinofuranose units are found as alternating isolated and paired branches separated by single unbranched xylose residues. Some xylose units may also be branched doubly at position two and three. A partial structure is given as:



Dea and Morrison (1975) and Perlin (1951b) determined that the molecule has numerous unbranched spaces as well. An unbranched space was composed

on the average of four xylose units every 20-25 xylose residues.

The insoluble pentosans of wheat from the endosperm have been found to be more highly branched and having greater molecular weight compared to the soluble pentosans of wheat. According to Medcalf (1968) half of the xylose residues are doubly branched at the second and third carbon positions and up to four consecutive xylose units can be doubly branched in the main chain. Usually only two consecutive doubly branched xylose units predominate, followed by a singly or doubly branched xylose residue. The structure suggested is as follows:



Montgomery and Smith (1956) have shown that the difference between soluble and insoluble pentosans is probably due to the amount of side chain branching. Perlin (1951a) believed that the pensotan components may become more soluble or less soluble as the incidence of arabinose side chains increases or decreases. Preece and Hobrick (1953) reported that increasing arabinose side chains in wheat increased solubility however the opposite occurs in barley and rye. Rye grains most soluble pentosan components contain the least amount of arabinose. These findings agree with Antoniou et al. (1981b) who found that the insoluble pentosans of rye contained 28.2% arabinose while the soluble pentosans contained 22.6% arabinose. The solubilizing effect of arabinosyl residues are probably

due to their ability to prevent intermolar aggregation of unsubstituted xylose residues. Removal of arabinosyl residues from the arabinoxylan by hydrolysis or enzymolysis produces an insoluble xylan (Antoniou et al. 1981b).

Fractionation of water soluble pentosans by DEAE-cellulose chromatography (Holas et al. 1971, Holas et al. 1972) has indicated that soluble pentosans and the various glycoprotein fractions can be obtained. Neukom (1976) has presented in some detail a hypothetical structure of one of the glycoproteins obtained from wheat flour. This fraction has been shown to be responsible for the gelation reaction that takes place when small amounts of oxidizing agents are added to an aqueous extract of wheat flour. The presence of ferulic acid in this fraction has been implicated in the gelation reaction via esterification between the phenolic acid and the sugar (Painter and Neukom 1968, Neukom 1968). Neukom (1976) has demonstrated a sensitivity of wheat pentosans to oxidation. The results indicate that wheat pentosans contain quantities of ferulic acid, i.e. one residue of ferulic acid to every 50 xylose residues, which can oxidize to diferulic acid and can bind to adjacent arabinoxylan residues vis ester linkages. Protein may also be involved in the gel structure through tyrosine-ferulic acid bindings. This oxidative gelation of pentosans is different than the usual gel formation seen with compounds like starch or pectin in that oxidation occurs without heating or cooling and only when oxidizing agents are present.
The importance of a protein in the gelation reaction has been shown to be an important factor (Painter and Neukom 1968). Upon treatment of the wheat flour gel with the proteolytic enzyme Pronase the gel capacity and viscosity of the slurry decreases rapidly. The high ash

content of wheat flour has been shown to reduce gelatinization and any gel formed will break down spontaneously on standing, thereby reducing viscosity (Neukom 1968). The extractability of rye pentosan depends on their solubility which is affected by conditions, such as temperature, pH, electrolyte concentration and pentosanase activity (Antoniou 1980). Plant pentosanase activity or strong acidic conditions destroy the high water binding capacity and adhesive power of the highly viscous soluble pentosans (Antoniou et al. 1981b). Hydrolytic or enzymatic activity destroys these properties by removing arabinose side chains which are responsible for prevention of precipitation (Howard 1955). Determinations of viscosity at constant concentration of extracted pentosans, showed a progressive decrease with decreasing pH because of enhanced enzymatic activity and reduced pentosan solubility (Drews 1970). Addition of electrolytes especially 2% NaCl tended to stabilize the viscosity probably by inhibiting the plants endogenous pentosanases especially at pH values less than 4.9. At pH levels below 4.9 pentosan solubility and enzyme activity were reduced more rapidly than above 4.0. Reduced enzymatic activity is likely due to either substrate modification or enzymatic inactivation. Soluble rye pentosan extractability also increased from 10% to 15% when the temperature of the extract was increased from 20 to 40 degrees celcius (Drews 1970). According to Table 7 the water soluble pentosans of rye are affected by variety and environmental conditions. Drews and Seibel (1976) reported that the level of soluble pentosans increased above 2.5% in wet years while their viscosity decreased and the reverse occurred in dry years with the soluble

Table 7. Average composition of rye grown in different countries

	Pentosans %	Soluble pentosans %	Soluble pentosans % of total	Starch %	Protein %
Canadian	8.2	1.41	16.4	60.4	12.4
Manitoba (Puma)	9.8	2.10	21.4	-	12.4
Petkuser normal stroh	7.7	1.56	20.2	62.2	11.4
Karshulder roggen	8.5	1.80	21.3	60.2	12.6
Russian (USSR)	8.1	1.39	17.8	60.2	13.4
American	8.3	1.40	17.0	60.2	13.8

Drews and Seibel (1976)

pentosan concentration as low as 1.5%. Data from Table 7 indicates that there is a large variation of total and soluble pentosans compared with starch and protein.

Physiological Effect of Fibre in Animals

The hemicelluloses are a mixture of linear and highly branched polysaccharides comprised of various sugar residues, i.e. arabinose, xylose, glucose, mannose, glactose, ferulic acid and approximately 4% uronic acid. The hemicelluloses are intertwined with lignin and laid down around cellulose fibres with a physical admixture through covalent bonds. Rees (1971) suggests when water is added to certain polysaccharides they swell to form a semi-rigid, jelly like mass which holds all the liquid present. First water is tightly bound through hydrogen bonds and this structure then becomes surrounded by loosely bound water held by dipole attraction and adhesion. As the polymer swells, the spaces in the macromolecules are filled by immobilized water. Each fibre will have a capacity to hold water which is known as the fibre saturation point (Ward 1982). This point will be determined by the chemistry of the macromolecule, electrolyte concentration and pH of the surrounding liquid (Rees 1971). Polysaccharides can form gels with varying water content depending on their chemistry species and anatomical source. Pectic substances and hemicelluloses can form gels while celluloses are more insoluble. Gels can be dispersed by cleavage either mechanically or by enzymatic hydrolysis of the network (Neukom 1967). Dispersion of the tightly packed fibres can also be achieved by the presence of small reactive molecules

i.e. acids (HCL) or detergents (bile acids) (Mod et al. 1981). This produces a polyelectrolyte solution in which the colloidal particles possess charges balanced by the small reactive ions present. These ions will influence the degree of swelling. Polysaccharide gels are essentially carboxylic (weak-acid) cation exchangers (Mod et al. 1981). The more hydrated and more polarizable species are most strongly held: CS+<Rb+<K+<Na+<Li+ (Drews 1971, Mod et al. 1981). Ca ++ and Mg ++ ions are less strongly held than monovalent ions. The fibre matrices apparent capacity for ionic absorption depends on the pKa value of the ionogenic groups present (Antoniou 1980, Antoniou et al. 1981b, Mod et al. 1981). The (weak acid) carboyxlic acid groups become non ionic when the pH drops below the pKa value. However, the pH in the matrix will usually differ from that of the external solution (Mod et al. 1981). For example, Na + ions will tend to displace H + ions thus raising the internal pH. This effect will then increase with the concentration of Na+ in the external phase (Mod et al. 1981).

When a solute molecule is suspended in a phase, interaction with surrounding molecules through such forces as ionic bonds, hydrogen bonds and dipolar interactions occur (Drews 1971). Molecules can be absorbed into the stationary phase and pass this way through the gastrointestinal tract of monogastrics and ruminants (Mod et al. 1981, Drews 1971, Campbell et al. 1983b). Absorption of molecules to the gel surface may occur by such forces as hydrogen bonding, dipole forces and hydrophobic effects (Mod et al. 1981). Exclusion occurs when particles tend to concentrate in one phase or another depending on difference in surface

energy of the particle in the various phases. Since gels act as carboxylic (weak acid) cation exchangers, Mod et al. (1981) reported that alkali soluble rice hemicellulose bound copper < zinc > iron and water soluble hemicellulose bound copper > iron > zinc. When these fractions containing the bound minerals were subjected to hemicellulase, pepsin and trypsin over half of the bound minerals were released indicating that the released mineral should be available for absorption in the lower gastrointestinal tract (Mod et al. 1981). The effect of proteolytic enzymes on mineral binding indicates that protein is involved in hemicellulose binding with protein moieties (Painter and Neukom 1968, Mod et al. 1981). From the results of the study by Mod et al. (1981) some hypothetical models have been developed to explain the copper-fibre interactions and their subsequent release by digestive enzymes. The copper-fibre interaction can be produced because a chelate can be formed between the terminal amino groups of lysine and arginine found in the glycoprotein (Painter and Neukom 1968, Mod et al. 1981).

Treatment with trypsin cleaves the peptide linkages between arginine, lysine and their adjacent amino acids. This enzymatic cleavage destroys the chelate bond and copper is released for possible resorption in the lower gastrointestinal tract. Mod et al. (1981) determined that the water soluble hemicellulose contained 37.7% protein while the alkali soluble hemicellulose contained 4.3% protein.

Eastwood (1973) has reported that the rate of bacterial degradation of fibre is dependent on the degree to which the fibril of cellulose,

hemicellulose and other glycoproteins are opened. The presence of lignin with cellulose can inhibit bacteria from passing into the fibrous mass. The size of the pores in molecular dimensions dictate the permeability of the surrounding molecules. Many bacteria produce extracellular enzymes which may permeate into the gel to act on smaller molecules meshed within the matrix (Eastwood 1973, Nelson and Potter 1980).

The diarrhea associated with feeding some fibre sources may be due to impairment of the digestive and absorptive function of the intestinal mucosa, resulting in increased osmotic pressure in the gut lumen causing water secretion from the body to the lumen to decrease the osmotic pressure (Campbell et al. 1983a). Campbell et al. (1983a) and Holas and Hampl (1973) reported that pentosans in rice possess adhesive power and a high water binding capacity forming very viscous solutions. Neukom (1976) has reported that the viscosity of solutions of rye extracts varies greatly and can be affected by oxidizing and reducing agents. Studies presented by Southgate (1973) and Wolever et al. (1978) suggest that a gel can slow down diffusion of nutrients toward the intestinal mucosa. In a study using human diabetic patients Wolever et al. (1978) found that gel forming fibre sources such as methyl cellulose, wheat bran and guar gum decreased the glucose absorption peak. This peak reduction correlated positively with viscosity. When hydrolyzed gels were fed the glucose absorption peak was high. According to Nelson and Potter (1980), Eastwood (1973), Drews (1970) and Drews and Seibel (1976) binding of

minerals in various fibre and protein sources is dependent on pH, viscosity and enzymatic attack when studied in vitro and in vivo using rats. Nelson and Potter (1980) indicate that more ferrous iron (Fe++) was released when HCl-pepsin hydrolysis was employed rather than HCl alone.

Feeding Value of Rye Grain for Livestock

Cereal grains are incorporated into rations to serve as the major energy, protein and micronutrient sources. Crampton (1933) after reviewing the available literature on the feeding of various cereal grains to cattle, sheep, swine and poultry concluded that animal performance was poorest when rye diets were fed.

Weiringa (1967) after reviewing all the available literature, reported that the feeding value of rye was lower compared to wheat, barley and corn. His studies indicate that the effect of rye was not only due to a palatability problem but also to other physiological effects. In experimental trials using swine, various milling fractions were tested and indicated that rye bran was more harmful than rye flour (Weiringa 1967). The nutritive value was improved if the rye was boiled or steamed (Weiringa 1967, Fernandez 1973b, Misir and Marquardt 1978d). Antoniou (1980) has reported that the antinutritional component found in rye was removed by water extraction and the alkylresorcinols thought to be the antinutritional factor was not the problem when fed to chicks.

Bell and Owen (1973) concluded that rye content in the diets of

swine should not exceed 33%. When swine were fed a diet containing 50% rye compared to 50% wheat, Weiringa (1967) found that the rye fed swine had a 12% growth depression. Friend and MacIntyre (1969) indicated that the effect on growth of pigs fed finisher rations containing 0%, 30% or 60% rye in substitution for barley depends on rye content in the diet, ergot level, sex and ration form. Rye containing 0.20% ergot produced less growth than ergot free rye. Friend and MacIntyre (1969) showed that pelleting of the high ergot rye (0.20%) was more beneficial than pelleting ergot free rye for gilts than for barrows. Apparently pelleting of rye diets improved the feeding value by increasing feed consumption and improving feed conversion. Friend (1970) working with Wistar rats averaging 167 g initial body weight, fed a basal diet in which 42% of the total diet was provided by (a) ground barley, (b) ground rye, (c) barley flour plus rye bran, (d) rye flour plus barley bran. The poorest performance as measured by feed intake, weight gain and nitrogen retention was obtained from the ground rye diet. The rats fed barley flour plus rye bran had the best overall performance. Rye flour, rather than rye bran appeared to elicit lower food consumption and thus overall performance (McDonald 1974, Friend 1970). The results of McDonald (1974) show that addition of rye bran to a wheat based diet at levels equivalent to 30% and 60% of the wheat flour had no adverse effects on weight gain and feed consumption of weanling male mice.

The relative growth depressing effect of rye has been studied by Misir and Marquardt (1978c) using different milling fractions either alone or in combination at the same proportions they would be found in normal milling. From the results they concluded that rye bran contained

primarily an appetite depressing factor while rye flour had a growth depressing factor. However, when rye flour and rye bran were fed together a synergistic effect was evident not only for fecal wetness but also for growth depression. Moran et al. (1970) suggests that the rye content of diets supporting broiler growth from day 1 to 63 days of age could not be more than 13% of the diet. Any further increase in the percentage of rye in the diet resulted in poor growth and fecal stickiness. Misir and Marquardt (1978a) determined that diets containing 15% rye in replacement of wheat resulted in significant growth reduction and appetite depression of broilers.

Consumption of rye by chicks has been associated with sticky wet feces. Fecal material from rye fed birds tends to contain increased concentrations of volatile monocarboxylic acids especially acetic acid (Misir and Marquardt 1978a). The same authors have reported these acids also cause a reduced fecal pH. The growing bird tends to be more susceptible to these adverse effects than mature adult birds (Antoniou and Marquardt 1981, Campbell et al. 1983a, Misir and Marquardt 1978a). The antinutritional factor in rye has been attributed to the high pentosan content of rye which may promote the growth of adverse microflora which may compete with the host animal for nutrients. The unabsorbed nutrients promote the development of deleterious microflora which can be suppressed by antibiotic supplementation (MacAuliffe and McGinnis 1971, Misir and Marquardt 1978b, Marquardt et al. 1979).

Speculation has also been made by Moran et al. (1969) and Preece and Hobrick (1953) as to the nature of the antinutritional factor in rye.

The carbohydrate nature of the antinutritional growth inhibitor which causes the sticky feces in poultry seems to act similar to the B glucan of barley. Water soaking of rye significantly improved the feeding value of rye similar to water soaking the B glucan of barley (Moran et al. 1970). However, the undesirable sticky feces produced when feeding barley can be overcome by adding a fungal B-endoglucanase which aids in the digestion of the 1 to 3% B glucan present. The action of this enzyme returns the viscous wet feces to a normal consistency. Supplementation with B-endoglucanase failed to improve the nutritional value of rye (Moran et al. 1969, Moran et al. 1970). Cave (1978) using a one to one ratio of whole rye to whole wheat found this combination delayed sexual maturity by 8 days in broilers. Also the birds had a lower mature weight and had high mortality on wheat-rye based diets. Antoniou et al. (1980) found that the utilization of rye compared to wheat diets was consistently depressed, because of reduced feed palatability and nutrient digestibility especially fat, protein and minerals. Fractionation studies of the pentosans in rye indicated 2.1% soluble and 7.7% water insoluble pentosans (Antoniou et al. 1981b). The soluble pentosans and insoluble pentosans having a high arabinose content exhibited antinutritional activity manifested by decreased palatability and reduced nutrient digestibility. The antinutritional activity of the soluble pentosans in chick diets is attributed to the viscosity in aqueous solutions, stickiness, swelling and indigestible nature in the chick gut (Antoniou 1980, Campbell et al. 1983b). Pentosans may exhibit non-specific binding of ionized molecules (Mod 1980). Ward (1982) has also indicated that antinutritional factors

in rye were associated with the bran and flour fractions when fed to chicks. Air classification of rye flour into starch and protein rich fractions demonstrated that the antinutritional factors, evident in poultry feeding, were associated with the starch fraction rather than the protein subfraction. Extraction of the starch fraction with 0.1 N NaOH showed that the extract contained 12% pentosans. Retention nutrients were affected however fat retention was affected the most. Ward (1982) concluded that the evidence of reduced nutrient retention was due to soluble rye pentosans found in the starch fraction. Antoniou and Marquardt (1981a) found that pentosans can be partially degraded by endogenous pentosanases after water soaking which results in improved chick growth.

Antibiotic Studies

The aspect of antibiotic supplementation has been studied by Fernandez et al. (1973). In experiments involving young chicks, procaine penicillin supplementation at 50 ppm significantly increased the growth of chicks receiving rye diets but not wheat based diets. The feces of birds fed water extracted rye was of normal consistency. The lyophilized water extract fed to chicks exhibited the characteristic sticky feces. Graber (1976) and Maurisch (1978) using wheat diets as controls, reported a dramatic increase in weight gain of chicks fed penicillin supplemented rye diets containing 5 or 10% meat meal, replacing an equivalent percentage of fish meal. Penicillin elected greater weight gain in chicks ($P<0.05$), compared to chlortetracycline or zinc bacitracin

supplemented wheat or rye diets. The type of protein (meat meal vs fish meal) as well as the antibiotic used to supplement rye diets combine to influence the nutritional status of rye. Antoniou et al. (1982) found similar results indicating that penicillin improved chick performance, particularly when poor quality protein and fat (tallow or lard) were used in the diet. Antibiotic response was found to be of short duration, since rye diets fed to chicks resulted in better overall performance as the chicks matured (Antoniou and Marquardt 1982). MacAuliffe and McGinnis (1971) indicate that rye diets supplemented with penicillin increased chick growth. Antoniou and Marquardt (1982) showed that chick growth was improved using antibiotic supplemented rye diets because of increased nutrient retention. Optimal penicillin level was found to be 50 ppm by MacAuliffe and McGinnis (1971). Maurisch (1978) using 17 anti-bacterial growth promotants in rye based diets found that there was an improvement in growth and feed efficiency especially when the diets were unbalanced with respect to energy:protein ratio. The improvement was excellent even when a poor quality protein supplement was fed such as meat meal. Misir and Marquardt (1978a) and Misir and Marquardt (1978b) have reported that the optimum level of penicillin is 200 ppm when a poor quality protein such as meat meal is fed while 70 ppm is adequate if fish meal is utilized. The improved nutrient retention of amino acids resulted from feeding penicillin. Antibiotic supplemented rye diets are inferior to unsupplemented corn or wheat based diets (Watner and Thomas, 1978, Scott et al. 1976). This would suggest that the antibiotic is not able to overcome all of the antinutritional

properties of rye (Antoniou and Marquardt 1982).

Possible explanations for antibiotic response have been demonstrated by several researchers (Wagner and Thomas 1978, Barnes et al. 1972, Untawale and McGinnis 1979, Scott 1976). Chicks fed rye based diets have been reported to have increased proliferation of *Clostridium* spore formers in the ileum. The organisms in rye fed chicks have been found to produce quantities of butyric acid and methane gas. When penicillin was added to these diets the levels of butyric acid and methane gas dropped and the levels of succinate increased. The assumption is that penicillin acts on the *Clostridium* by inhibiting their logarithmic growth phase. Untawale and McGinnis (1979) found that replacing corn with rye also increased the viable counts of *Lactobacillus* and *Enterococci* in the ileum. Supplementing penicillin in these diets resulted in a reduction of viable *Lactobacillus* (the predominant organism in normal gut flora) and *Enterococci*. Maurisch (1978) has suggested that antibiotics may have a nutrient sparing effect by inhibiting the growth of bacteria which compete with the host for dietary nutrients and that antibiotic supplementation results in a thinner intestinal wall which may improve nutrient absorption.

Gamma irradiation of rye has been reported to result in considerable improvement in the feeding value of rye (Campbell 1983a, Campbell 1983b, Patel et al. 1980, MacAuliffe et al. 1979). When water extract of rye is subjected to gamma irradiation a subsequent decrease in viscosity of the aqueous solution is evident. Kim et al. (1966) has reported steatorrhea in chicks fed rye diets as a result of excessive deconjugation of bile

salts. The addition of sodium taurocholate a conjugated bile salt or antibiotic supplementation reduces the steatorrhea. The *Enterococcus* bacteria *Streptococcus faecalis* and *Streptococcus faecium* have been reported to deconjugate taurocholic acid and taurochenodeoxycholic acids. Campbell et al. (1983a) conducted several experiments to determine the influence of intestinal microflora when rye diets were fed to young chicks. In a conventional environment dietary rye was found to severely depress growth, amino acid and fat retention and metatarsal bone ash. These conditions could be effectively alleviated by 2.5 M rads of gamma irradiation to the diet and maintenance of birds in a germ free gnotobiotic environment. The addition of sodium taurocholate was found to improve fat retention in conventional birds fed rye to a greater extent than from wheat fed birds. A deficiency of conjugated bile salts might be the contributing factor to the steatorrhea observed in rye fed chicks (Campbell et al. 1983a). Campbell et al. (1983b) has reported an improvement in the nutritive value of rye for growing chicks using graded levels of gamma irradiation. He reported great reduction in the viscosity of rye slurries as well as improved body weight, feed efficiency, fat retention and bone ash, when rye was irradiated from 0-10 M rads. Maximum overall improvement occurred at 6 M rads. After rye was subjected to graded levels of gamma irradiation the viscosity of xylose, arabinose, galactose and mannose were measured in the water extract. The improved performance of chicks coincided with radiation induced damage to rye polysaccharides, as indicated by reduced viscosity and increased concentration of reducing sugars. Campbell et al. (1983a) and Campbell et al.

(1983b) suggest that gamma irradiation depolymerizes the polysaccharide gums, and not only is effective on water soluble pentosans but also on water insoluble pentosans. Campbell et al. (1983a) found that addition of Streptococcus faecium to gnotobiotic birds caused decreased nutrient retention, especially fat, similar to rye fed to conventional birds.

Rye Feeding to Ruminants

The factors limiting full utilization of rye nutrients are probably not simply effects on the palatability but because of more fundamental physiological effects. As discussed earlier, ergot, resorcinols and non-starchy polysaccharides result in lowered acceptability. Ergot has been linked with reduced feed intake, depressed growth rate, diarrhea, lameness and eventually dry gangrene (McKeon and Egan 1971) on the bodies peripheral tissues. Dinusson et al. (1971) suggest that as little as .06% ergot in the ration of fattening cattle could affect feed intake, feed efficiency and lameness (McKeon and Egan 1971). Ingalls and Phillips (1971) conducted a study to test triticale on the growth of calves. Barley based diets containing .07 and 0.28% ergot from triticale or a triticale diet containing .07% to .09% ergot were tested. Data indicated that the calves feed intake and weight gains were reduced and the animals were unable to shed their winter coats on the ergot containing diets. Burfening (1973) has attempted to determine why the ergot alkaloids affect appetite. He concludes that the ergot alkaloids have an effect on the temperature control and appetite centres in the hypothalamus. These effects cause an increase in body temperature and a reduced intake of

nutrients. The results of many rye studies are conflicting. Winter (1973) conducted an experiment at the Charlottetown Research Station and found that up to 60% rye grain in place of barley can be used in high energy grain rations for steer calves with no loss in weight gain or feed efficiency. Winter (1973) also indicated that many producers are reluctant to feed rye grain and most feeding recommendations indicate that rye should make up less than 50% of the grain in the ration for cattle. Winter (1973) indicates that up to 60% rye could be incorporated safely into dairy cow rations with no loss in intake or production. In another study Winter (1975) fed growing steers ergot free rye at 0, 40, 60 and 80% of the ration. Rye replaced barley in the diets, while restricted amounts of corn silage and hay were fed. Animals had free access to the grain mixtures. The rate of gain and feed conversion was slightly less for steers on the rye rations, and, did not change appreciably with increasing levels of rye in the diet. Since these decreases were not found in the previous experiment, no logical explanation can be given except perhaps animals or environmental difference. Therefore Winter (1975) concluded that rye may be included up to 80% in the grain ration for steers with no significant reduction in intake or rate of gain. Goings et al. (1976) conducted a study to determine the acceptability of dairy grain mixes containing rye or feed flavors. Diets containing 10, 20, 30 or 40% rye were fed with or without the addition of commercial dairy flavors. Since rye was considered a product containing unacceptable "palatability" factors, the assumption was that flavour addition would enhance intake by lactating Holstein dairy cows. There was no difference

in acceptance between the control feed which was a 20% crude protein pelleted dairy grain mix and the feed containing 10% rye. The rye was substituted for wheat in the grain mixes and all mixes pelleted. The grain mixes containing higher levels of rye resulted in a depressed intake. They further indicate that the reduction in consumption of rye containing diets was proportional to added rye. When cows were offered the 40% rye diet pelleted with or without flavoring the unflavored feed was preferred. Addition of flavoring did not improve consumption of the 40% rye diet compared to the unflavored feeds in the studies. Schneider and Lantzsch (1971) studied the apparent digestibility of the crude nutrients from 5 different types of rye using groups of 4 sheep. The crude protein content of the 5 varieties tested showed crude protein values ranging from 9-14.5%. The differences discovered in the apparent digestibilities of crude nutrients were not significant. There were no differences between the rye types, with respect to energy availability. However, a difference did exist in the apparent digestible crude protein content which may be due to the different crude protein levels among the varieties.

The greatest scope for increasing utilization of rye in diets is found, when it is realized that the palatability and growth depression effects are less in older animals than in young animals (Antoniou 1980). Sharma et al. (1981) used sixty young Holstein calves (both sexes) to evaluate the nutritive value of rye grain in calf starter diets. Calves were assigned randomly at birth to one of five diets containing 0, 30, 60 and 80% dry rolled or 80% roasted rye for an 18 week growth trial.

Average daily gain and feed consumption were similar during the first 6 weeks, however calves receiving 60% rye consumed less feed and gained slower than the barley control and 80% roasted rye fed groups in the next 12 weeks ($P<0.05$). The apparent digestibilities of the calf diets were measured using 0.3% chromic oxide in the diets for the male calves during the 9th and 10th week of the growth period. Calves fed the 60 and 80% rye diets tended to show lower digestibilities than the barley control group. The 80% roasted rye group showed improved digestibilities of the acid detergent fibre and ether extract but showed slightly reduced protein digestion. In another experiment Sharma et al. (1981) fed twelve lactating Holstein cows four diets containing 0, 25, 50 and 75% rolled rye in the grain mixture along with grass silage. The grain to silage ratio was 60:40 on a dry matter basis and animals were offered feed free choice twice per day. The replacement of barley with rye in the grain mixtures reduced the total dry matter intake of lactating cows ($P<0.05$), however little effect was noticed on milk composition, milk prolactin and average daily milk production.

Morgan and Campling (1978) using British Friesian cattle of different age groups studied the starch digestibility of rolled barley or oats. They concluded that the steers digested more starch from the whole grain than did the dry cows. Orskov (1978) has reported that the consumption of dry matter by growing calves was greater when alkali treated grains were fed compared to heat treated or untreated grains. Sharma et al. (1983) fed either rolled untreated or 3.5% sodium hydroxide treated rye to lactating dairy cattle in diets with concentrate:roughage ratios

65:35 and 75:25. The concentrate contained either 60% rolled rye or 60% whole alkali treated rye. The alkali treated rye tended to increase intake in cows fed by 13% compared to untreated whole rye. However this difference was not significant ($P>0.05$). Milk yield and composition were not altered by the alkali treatment. Molar proportion of ruminan acetic acid tended to increase with the alkali treated rye, however not significantly ($P>0.05$) compared to untreated rye. Other parameters such as dry matter, crude protein and energy digestibility did not differ among treatments. The increase in cellulose and acid detergent fibre digestibility in barley (Sharma et al. 1983) appears to be due to the solubilization of cell wall contents by sodium hydroxide, however this does not appear to be the case with rye.

Intake Control in the Ruminant

Montgomery and Baumgardt (1965a) and Orskov (1972) suggest that when the digestibility of the diet reaches a certain point, the size of the rumen will no longer limit intake. Montgomery and Baumgardt (1965a) show that the daily consumption of dry matter actually decreased as digestibility increased while the intake of energy remained constant. According to Montgomery and Baumgardt (1965a), and Conrad (1966) the expected relationship between digestibility and intake may be positive or negative depending on the logical argument, as follows. They assumed that if animals eat to satiety, the consumption of a less digestible diet must be greater than a more digestible one in order to achieve the required level of digestible calories. Thus, a negative relationship be-

tween the amount of freely chosen feed and the digestibility of the diet can be postulated from their data. Conrad (1966) assumed that poor quality feeds contain factors limiting intake such as bulk or nutrient deficiencies, and developed a positive relationship between intake and digestibility. Conrad (1966) using cattle as the experimental model has shown that the two contrasting concepts operate in regulation of food intake. He readily demonstrated these concepts by the dilution of a poor quality forage with concentrate supplementation. The results state that the point of maximum dry matter intake occurred at about 67% digestibility when alfalfa-concentrate combinations were fed to dairy cattle. Van Soest (1980) suggests that this point may not be fixed, but is dependent upon the density of the diet and the energy demand or set point of the animal. Higher energy demand requires a greater rumen fill or a faster rate of passage such that fill becomes limiting at higher densities of dietary energy (Conrad 1966).

Rumen Microbes

Bacteria are the most important of the symbiotic organisms which break down the higher carbohydrates in ruminants (Bauchop 1979, Russell and Hespell 1981, Baldwin and Allison 1983).

The symbiotic relationship is highly developed in the ruminant since the rumen provides both the capacity and substrate which is most favorable to bacterial activity (Wolin and Miller 1983). In addition to digesting carbohydrates the organisms synthesize other essential nutrients such as B vitamins and bacterial protein (Walker et al. 1975).

The acids and gases which are formed by microbial action in the rumen are the end products of various intermediate reactions (Akin and Barton 1983). Cellulose, pentosans and starch are hydrolyzed to monosaccharides and then fermented. The proportion of the acids formed varies with the nature of the ration, the organisms present, the availability of carbohydrates, lignin content and a host of other factors (Baldwin and Allison 1983). Acetic acid makes up from 66-75% of total monocarboxylic acids found in the rumen, while propionic and butyric acids are found in lesser amounts (Baldwin and Allison 1983, Akin and Barton 1983, Sheppard et al. 1959). Other volatile fatty acids in trace amounts are valeric, isovaleric and isobutyric acids. The actual proportions of each volatile acid varies with type of ration fed. Gas chromatography has allowed researchers to study the rate of production of these acids (Erwin et al. 1961). The isotope dilution technique introduced by Sheppard et al. (1959) is also common. The isotope data showed that when sheep were fed average roughage:grain mix diets the average molar percentages of monocarboxylic acids were in the range of acetic 65: propionic 30: butyric 9. However the ratios of volatile fatty acids and methane production can be altered by dietary manipulation. Feeding high grain diets, for example results in greater proportions of propionate in the rumen. Fermentations favoring propionate formation results in less methane gas production resulting in improved feed to gain ratio in growing animals (Wolin and Miller 1983). The gases formed in the rumen are primarily methane, carbon dioxide and some hydrogen gas (Russell and Hespell 1981). The magnitude of microbial digestion is indicated in studies with cattle

and sheep showing that 40-80% of the dry matter consumed, disappears in the rumen and 80% of the available carbohydrate provides the primary source of energy for both the rumen organisms and the host animal (Beever et al. 1972, Van Soest 1980).

The rumen is buffered very well by bicarbonate in the saliva and is supplied with available nutrients especially non-protein nitrogen (Russell and Hespell 1981). Toxic substances which are potentially lethal to the microorganisms are moved across the rumen wall an example being the volatile fatty acids. Bryant (1959) states that the microflora of the rumen are dense with approximately 10^{10} to 10^{11} bacteria and 10^{6} protozoa per milliliter of fluid. The efficiency of nutrient utilization by ruminants is determined largely by the balance of these fermentation products, and this balance ultimately is controlled by the types of microbes in the rumen. Wolin and Miller (1983) and Bauchop (1979) state that much of the current knowledge concerning the predominant bacteria deals with the population that is free or detached from plant material during blending for 1 to 3 minutes. Electron microscopic studies however indicate that a population of microbes is present that are firmly attached to and within feed particles (Akin and Barton 1983, Akin 1979, Akin 1976). The dynamics and formation of these microcolonies, including factors which affect attachment and colonization within feed particles is not well understood (Akin 1979, Akin and Barton 1983). A third population of microbes are those attached to the rumen epithelia cell. Russel and Hespell (1981), Cheng et al. 1977 and Hungate (1966) conclude that the most important rumen organisms are probably known, however Bauchop (1979)

has reported new organisms not previously identified. These anaerobic fungi have been found to attach to the inner surfaces of hollow stems and broken edges of feed particles in the same way bacteria adhere to plants. Contributions of fungi to rumen fermentation is not known. The rumen environment is one of extreme anaerobiosis and therefore most of the organism inhabiting this fermentation vat are strict anaerobes (Russell et al. 1981, Baldwin 1983, Cheng et al. 1977, Hungate 1966). The most prominent niche occupied in the rumen are the cellulolytic, amylo and dextrinolytic saccharolytic and hydrogen utilizing bacteria (Bryant 1973, Bryant 1963). An extensive list of protozoa is presented by Russell and Hespell (1981). Classification of substrate utilization, fermentative end products, nutrient requirements, percent of total isolates and type of diets in which protozoa and bacterial cells are found are presented by Baldwin and Allison (1983) and Russell and Hespell (1981). Only the most important species are listed, from more than 200 known species and strains.

Cellulose Digesters

Cellulose digesters are the most important bacteria in the rumen ecosystem, at least in the normal state since cellulose would provide the primary energy source (Leatherwood 1973). The cellulose digesters affix themselves to the substrate and secrete extracellular cellulase which hydrolyzes the β (1-4) linkages to cellobiose. Cellobiose is then absorbed into the microbe for further metabolism. The primary cellulolytic microbes in the rumen are *Bacteroides succinogenes, Ruminococcus albus*

and *Ruminococcus flavefaciens* (Leatherwood 1973). These primary cellulolytics are among the most restricted of the rumen microbes in terms of the niche they occupy. They do not ferment monosaccharides, and are thus restricted to utilize disaccharides, trisaccharides and oligosaccharides released during hydrolysis of cellulose as energy and carbon sources (Wolin 1975). Several workers (Wolin and Miller 1983, Baldwin and Allison 1983, Russell and Hespell 1981, Hungate 1966) indicate that *Butyrivibrio fibrisolvens* are cellulolytic. However, very few strains have been found to be actual cellulose digesters and for the most part are considered to ferment soluble sugars and the hydrolyzed polymers of sugars (Hungate 1950). The nutrient requirements for the cellulolytic bacteria are reported to be mainly protein, ammonia, branched chain fatty acids and para-aminobenzoate for growth (Hungate 1966, Russell and Hespell 1981, Baldwin and Allison 1983). Interactions among the cellulolytics with other species of bacteria help supply their nutrient requirements (Forsberg et al. 1981, Pettipher and Lantham 1979a). The cellulolytic bacteria also digest starch, pectins and xylans (Baldwin and Allison 1983 and Prins 1977). The xylan degradation is related to hemicellulose digestion and other complex polysaccharides. Fibre digestion is a slow fermentative process, so these organisms tend to support a sustained fermentation (Hungate 1966, Leatherwood 1973).

Starch Digesters

Since starch varies greatly from diet to diet the amylolytic and dextrinolytic microbial species vary most in numbers from 1-20% of total

isolates (Cheng et al. 1977). Bryant (1977) has stated as well as starch variability the level of soluble sugars across diets varies considerably. The numbers of saccharolytic microbes do not vary as drastically as do numbers of the amylolytic isolates (Baldwin and Allison 1983). The most prominant saccharolytics appear to compete favorably with cellulolytic and amylolytic species for disaccharides and trisaccharides released by the extracellular enzymes of the latter two groups (Russell and Hespell 1981, Forsberg et al. 1981). *Streptococcus bovis*, an organism in the amylolytic group, can result in rapid over growth when ruminants are suddenly switched to high starch diets (Hungate 1966, Allison et al. 1975). The rapid mulitiplication of *Streptococcus bovis* can result in rumen acidosis because of the excessive levels of lactic acid produced followed by a drop in pH (Allison et al. 1975). Baldwin and Allison (1983), Russell and Hespell (1981) and Hungate (1966) report that *Megasphera elsdenii*, a saccharolytic organism found in less than 1% of total rumen isolates has the largest range of end products in the group. They report acetate, propionate butyrate, valerate, caproate, hydrogen and carbon dioxide gas as end products of fermentation of *Megasphera elsdenii*.

The hydrogen utilizers found in less than 1% of total rumen isolates have been reported to produce methane gas, ammonia and propionate as fermentative end products (Baldwin and Allison 1983). The same authors report that the nutrient requirements of hydrogen utilizers and saccharolytic organisms are minimal consisting of ammonia, amino acids and branched chain fatty acids.

Rumen Protozoa

The protozoa found in the rumen are in much smaller numbers than the bacteria (Hungate 1966, Bryant 1959). Protozoa are approximately 100 times larger than bacteria in protoplasmic mass and are found in numbers to be approximately 10^6 protozoa/ml of rumen fluid (Russell and Hespell 1981). Bryant (1977) concluded that the greater size of protozoa relative to bacteria enables the protozoa to comprise up to 50% of the total microbial mass. Lindsay and Hogan (1972) have determined that the problem in assessing the role of protozoa arises when growing protozoa are removed from the bacteria since bacteria are a primary nutrient requirement for protozoa (Coleman 1979, Russell and Hespell 1981, Hobson and Wallace 1982). Protozoa are not considered essential to the ruminant. Bird and Lang (1978) showed that defaunated cattle exhibited greater growth rate than faunated cattle. Hungate (1966) in contradiction has stated that faunated cattle tend to perform better than non-faunated animals. Hungate (1966) states that rumen protozoa have a biological value greater than bacteria and possess a higher intestinal digestibility factor for the host. Welch and Smith (1978) have shown that high grain diets with protozoa present in the rumen, tend to produce higher levels of butyric acid whereas defaunated animals produce more propionic acid. Vogels et al. (1980) have shown that the numbers of bacteria are higher in defaunated rumens suggesting either competition for energy sources or protozoal feeding on bacteria. Vogels (1980) has noted during his microscopic evaluation of protozoa that the *Entodiniomorphs* have bacteria adhering to the body of the protozoa. He speculates that these bacteria

may be methanogens living symbiotically with their host. The *Entodiniomorphs* have been shown to be more tolerant of rumen pH changes and have a regeneration time of 6-15 hours compared with 24-48 hour regeneration time for other genera (Hungate 1966). Wellers and Pilgrim (1974) have determined that selective retention of protozoa in the fibrous mass may be important since liquid turnover time in the rumen is usually between 10-20 hours. Little protein is contributed by the larger ciliate protozoa since their washout time is very slow (Bryant 1977). However feeding high concentrate diets or pelleted diets especially when intake is high, tends to reduce the selective retention of fibre (Welch and Smith 1978) and causes the elimination of protozoa due to reduced particulate retention time in the rumen (Bryant 1977, Vogels et al. 1980).

The *Holotrichs*, genus *Isotricha* and *Dasytricha* utilize carbohydrate substances such as starch and soluble sugars for energy metabolism, but its apparently unlikely that any cellulose or hemicellulose is digested by them (Bryant 1977). The *Entodiniomorphs* genus *Epidinium* and *Entodinia* are able to engulf whole starch granules (Baldwin and Allison 1983) and may be able to digest cellulose and hemicellulose (Bryant 1977, Coleman 1979). The principle fermentation products of protozoa are butyrate, acetate and hydrogen (Vogels et al. 1980, Wolin and Miller 1983). Propionate is generally a minor end product and may be contributed by bacteria that adhere to the bodies of the protozoa (Vogel et al. 1980). The role of protozoa in overall rumen balance tends to remain somewhat unclear. Coleman (1979) reports that the digestibility of the diet is not altered by protozoa and their effect on overall nitrogen metabolism remains unclear.

Bacterial Interrelationships

Many rumen bacteria depend on others to digest, or at least initiate digestion of feed components (Baldwin and Allison 1983). During fibre digestion there is likely some degree of cooperation. The action of one species on one type of chemical bond exposes other susceptible bonds to attack by other species. The cellulose digesters occupy a preferred position on the substrate which enables them to obtain sufficient yield from their digestion to produce fermentative end products (Dehority and Scott 1967, Akin and Barton 1983). They appear to secrete enough cellulase enzyme to provide their non-cellulolytic neighbours with enough disaccharides, trisaccharides and oligasaccharides so they can ferment and excrete end-products which the cellulolytic microbes can use for their own nutrient requirements (Russell and Hespell 1981). The nutritional requirements of the cellulolytic microbes can be very complex (Akin and Barton 1983, Russell and Hespell 1981) for example the *Ruminococcus* and *Bacteriodes* species require branched chain volatile fatty acids, valerate straight chained monocarboxylic acids, biotin, ammonia or a sulfide source (Baldwin and Allison 1983). In addition many organisms may require a broad spectrum of minerals such as Ca, Mg, Na, K, P, Co, S, Fe, Mo, Se, Ni, Mn and Zn (Bryant and Robinson 1961, Caldwell 1966).

According to Wolin and Miller (1983) and Leatherwood (1973) the cellulolytic bacteria begin with the hydrolysis of cellulose to more soluble products. Only a few of the predominant species of microbes that inhabit the rumen produce cellulase. Cellulase produces hydrolytic products which are available for fermentation by both cellulolytic and

non-cellulolytic microorganisms (King 1961). Fermentation of these hydrolyzed substrates results in the production of major end-products of fermentation namely the volatile fatty acids, propionate, acetate and butyrate (Leatherwood 1973). Minor intermediates such as lactic acid and formate are also further metabolized to end products as well (Leatherwood 1973). Hydrogen gas is a major extracellular intermediate and is used by methanogenic bacteria to reduce CO2 to CH4 (Bryant 1979). Succinate also a major extracellular intermediate, is decarboxylated to propionate and CO2 essentially as fast as the intermediate is formed (Wolin and Miller 1983). According to several workers (Wolin 1983, Russell and Hespell 1981, Baldwin and Allison 1983, Hungate 1966) only two cellulolytic microbes produce succinate, namely *Bacteriodes succinogenes* and *Ruminococcus flavefaciens*. No known rumen cellulolytic organism produces propionate directly (Wolin and Miller 1983). Since non-cellulolytic bacteria interact with the cellulolytic bacteria they must be included in any discussion of cellulose degradation. A few of the non-cellulolytic bacteria namely *Megashera elsdenii*, *Selenomonas ruminatium* and *Veillonella alcalescens* can produce propionate directly otherwise the products formed are similar to the cellulolytic strains (Wolin 1981, Wolin and Miller 1983).

The pathway of carbohydrate metabolism by an important cellulolytic bacterium *Ruminococcus albus* are discussed by Wolin and Miller (1983). Carbohydrates are fermented via the glycolytic pathway. Glyceraldehyde-3-phosphate (G-3-P) is oxidized by NAD to form NADH which is used to reduce acetyl-COA to ethanol. Reduced ferredoxin is formed from electrons

produced from pyruvate oxidation. The reduced ferredoxin is then oxidized to produce hydrogen gas (H2). NADH can also reduce ferredoxin and become a source of H2 but this is not important in single culture because the accumulation of H2 inhibits the production of H2 from NADH. Therefore the only way pure culture *Ruminococcus albus* can regenerate NAD from NADH to continue glycolysis is by reducing acetyl-COA to ethanol (Wolin and Miller 1983, Wolin 1974, Leatherwood 1973).

However in the rumen pure cultures of cellulolytic bacteria do not exist, but rather live symbiotically with a multitude of other strains (Leatherwood 1973, Akin and Barton 1983). The coexistence of *Ruminococcus albus* with the methanogens is a symbiotic relationship of interest discussed by Wolin and Miller (1983). The H2 produced by *Ruminococcus albus* from pyruvate and NADH is used by the methanogens to reduce CO2 to CH4 thus removing the inhibiting effect of H2 on *Ruminococcus albus*. Nothing then inhibits the production of H2 from NADH. This is an advantage for *Ruminococcus albus* because this mode is used for regenerating NAD. NADH is no longer available to reduce acetyl-COA to ethanol but rather acetyl-COA formed from pyruvate is converted to acetate. The methanogens therefore do not allow the build up of H2 because of its rapid conversion to CH4 in the rumen. The methanogens sole source of energy comes from the reduction of CO2 to CH4 (Wolin 1981, Wolin and Miller 1983). *Ruminococcus flavefaciens* another cellulolytic bacterium, which is an important succinate producer can be influenced by methanogens (Bryant 1979, Bryant and Wolin 1975). NADH can be oxidized by either the formation of succinate or the production of H2. H2 production from NADH will depend on coexistence with a methanogen and will be at the

expense of succinate formation (Bryant and Wolin 1975, Bryant 1971, Wolin 1976). Pyruvate carbon that would otherwise flow to succinate will flow to acetate and CO2 (Wolin and Miller 1983). *Selenomonas ruminatium*, an extremely important non-cellulolytic bacterium, is very similar to that of *Ruminococcus flavefaciens* and is affected similarly in the presence of methanogens (Wolin 1976, Hungate 1966). Succinate is again the final repository for electrons from NADH, but *Selenomonas ruminatium* decarboxylates succinate to propionate and CO2. The increase in the levels of acetate with a corresponding decrease in propionate levels indicate the presence of methanogens (Wolin and Miller 1983).

The fermentation end products of the saccharolytic bacterium *Butyrivibrio fibrisolivens* (Miller and Jensel 1979) does not appear to be alterable by coexistence with methanogens. Throughout the metabolic pathway, there is no mechanism for oxidizing NADH to NAD and H2 pathways of butyrate formation by *Bacteriodes fibrisolvens* (Bryant and Wolin 1983). Therefore methanogens cannot alter this pathway since there is no H2 available for the reduction of CO2 to CH4. Consequently there is no source of energy for them. Oxidation of NADH occurs only during the conversion of acetoacetyl COA to B Hydroxybutyryl COA in the pathway of formation of butyrate (Bryant and Wolin 1975, Wolin and Miller 1983).

Bryant and Wolin (1975) have studied the coexistence of *Bacteriodes succinogenes* with *Selenomonas ruminatium*. The former is a cellulolytic bacterium (Wolin and Miller 1983) and the latter is a non-cellulolytic species. *Bacteriodes succinogens* ferments cellulose mainly to acetate

and succinate. *Selenomonas ruminatium* does not use cellulose but does grow very well when co-cultured with *Bacteriodes succinogens* in cullulose (Wolin 1981, Wolin and Miller 1983). Therefore the cellulose hydrolysis supports the growth of both organisms. The selenomonad ferments the products of hydrolysis mainly to acetate and propionate (Forsberg et al. 1981, Russell and Hespell 1981, Gorleau and Forsberg 1981). The succinate formed by the cellulolytic bacterium, *Bacteriodes succinogens* is decarboxylated simultaneously to propionate. Therefore no succinate accumulates in coexistence only propionate is produced (Russell and Hespell 1981, Baldwin and Allison 1983). The feeding of non-cellulolytic organisms on the products of hydrolysis produced by the cellulolytic species and the decarboxylation of succinate to produce propionate are very important chemical reactions in the rumen. The production of propionate depends to a large extent on a significant concentration of *Selenomonas ruminatium* the only known non-cellulolytic bacterium known to carry out the decarboxylation of succinate to propionate (Mink and Hespell 1978, Russell and Hespell 1981) in monoculture.

To prove that the cellulolytic bacterium *Bacteriodes succinogenes* and the non-cellulolytic bacterium *Selenomonas ruminatium* coexist with one another, (Bryant and Wolin 1975, Wolin and Miller 1983) grew these bacteria in monoculture and in coexistence in cellulose culture and measured moles of acetate, propionate and succinate produced. Their data showed that *Bacteriodes succinogenes* in monoculture produced 85 moles of acetate and 105 moles of succinate per 100 moles of hexose sugar fermented. *Selenomonas ruminatium* in monoculture on cellulose

media produced no volatile fatty acid activity. In coculture, *Bacteriodes succinogenes* and *Selenomonas ruminatium* are reported to have produced 82 moles of acetate and 138 moles of propionate and zero succinate per 100 moles of hexose fermented (Bryant and Wolin 1975).

Digestive Patterns in the Rumen

The cellulases of rumen microbes present a number of experimental problems. Before any definitive statements regarding their characteristics and mechanisms can be made more work is required to resolve these problems (Leatherwood 1973). Cellulase is the trivial name for the enzyme or enzymes that degrade cellulose to soluble sugars. The enzyme has been assigned the systematic name of β 1-4 glucan 4 glucanohydrolase by the International Union of Biochemistry (Leatherwood 1973). Cellulose degradation by *Ruminococcus albus* organisms in the rumen has been studied intensively by Leatherwood (1973). Using roll tubes and the amorphous carboxymethyl cellulose substrate a proposed mechanism for cellulose digestion was elucidated. Apparently an affinity factor and a hydrolytic factor are necessary for the formation of a complete cellulase complex. These two factors together act as a single entity and hydrolyze cellulose to cellobiose. The hydrolytic factor must be held in position on the insoluble cellulose by the affinity factor in order to hydrolyze insoluble cellulose effectively. Therefore the major role of the affinity factor is that of binding the hydrolytic factor to the cellulose to permit multiple attacks. The resistance of various celluloses to total digestion is increased by the presence of lignin and silica as well as

by degree of crystallinity of the cellulose (Baldwin and Allison 1983, Leatherwood 1973, Gorleau and Forsberg 1981). On the basis of the mechanism proposed by Leatherwood (1973) resistance to hydrolysis could be expected if inert substances were absorbed to the binding sites on cellulose thus blocking the binding of the affinity factor and therefore making an incomplete cellulose entity. Since cellulolytic bacteria also have proteolytic abilities the possibility exists that the products of the proteolytic activity produces protein or amino acids which become inertly bound to the active cellulose binding sites and inhibits the binding of the affinity factor associated with complete cellulase activity (Leatherwood 1973).

Other studies by Pettipher and Latham (1979b) have shown that the ruminococci produce distinct colonies surrounded by clear zones in cellulose sugar media. This suggests an extracellular cellulase is present. The cellulases of *Ruminococcus albus* are active in the hydrolysis of denatured amorphous cellulose but are relatively inactive against crystalline cellulose (Leatherwood 1973). *Ruminococcus flavefaciens* can hydrolyze crystalline cellulose however the cellulase of *Bacteriodes succinogenes* is more active on crystalline cellulose than any of the *Ruminococcus* (Gorleau and Forsberg 1981). Since the cellulase of *Bacteriodes succinogenes* is more active (Gorleau and Forsberg 1981) on crystalline cellulose than the *Ruminococcus*, this may explain why *Bacteriodes succinogenes* is the most prominent cellulolytic organism in rumen contents when animals are fed diets such as wheat straw that are high in crystalline cellulose. Gorleau and Forsberg (1981) suggest that *Bacteriodes succinogens* must come into physical contact with the substrate

in order for hydrolysis to occur. They demonstrated that the cellulase is bound to the outer membrane of *Bacteriodes succinogenes*. Forsberg et al. (1981) however has observed significant quantities of cellulase in the supernatant liquid of centrifuged cultures of *Bacteriodes succinogenes*. Forsberg et al. (1981) suggests that the enzyme is associated with sedimentable membrane vesicles that are released by *Bacteriodes succinogenes* when in close proximity with cellulose fibres. Leatherwood (1973) and Gorleau and Forsberg (1981) show that the levels of cellulase produced by either *Ruminoccus albus* or *Bacteriodes succinogenes* are dependent on the levels of glucose and cellulase present in the media. This would indicate a product feedback mechanism regulating the synthesis of cellulase in these organisms (Leatherwood 1973).

Hemicellulose Digestion in the Rumen

Since 20-25% of the dry matter in forages may be in the form of pentosans (Heald 1953) and 10% or more of the dry matter in concentrates may be in the form of pentosans (Antoniou et al. 1981b) fermentative breakdown of these substances are of considerable importance in the rumen. Furthermore, since pentose sugars are not readily utilized by the animal tissue (Dehority 1973), they will be of greater value to the ruminant if they are converted to microbial fermentative end products (Heald 1951). Other workers (Balevani et al. 1969, Keys et al. 1969) have reported the disappearance of pentosans or hemicelluloses from the digestive tract of both cattle and sheep. Heald (1953) studied the digestion of meadow hay pentosans in cheviot ewes fitted with rumen and abomasal cannulas.

The data suggest 40% of the pentosan digestion occurred in the rumen and omasum.

The results of this and other work implied that the rumen bacteria were producing bacterial pentosanases capable of hydrolyzing the arabinoxylan polymers of hemicellulose (Heald 1953). Howard (1955) studied the in vitro fermentation of water soluble wheat flour pentosans using rumen bacteria. The rumen bacteria were obtained from the rumen contents of sheep fed a forage and concentrate diet. When a pentosan mixture (0.5% solution) was incubated with a suspension of mixed rumen bacteria and washed with toluene, the pentosan was hydrolyzed rapidly. Stripping off of the arabinose side chains and fragmentation of the xylan chain appeared to proceed concurrently. Arabinose, xylose, xylobiose, xylotriose and xylotetraose was detected in the hydrolysates by paper chromatography. No pentosanase activity was detectable in rumen liquor which had been freed of bacteria even after the fermentation of added pentosan (Howard 1955). In another experiment by Howard (1955) pentosan was added to rumen liquor from which the larger organisms, presumably the protozoa had been removed, leaving only the smaller eubacterium. A vigorous fermentation occurred, and 90% of the substrate disappeared during a 4 hour incubation at 38 degrees celcius. Apparently, hydrolysis proceeded more rapidly than the fermentation of the sugars, so that considerable amounts of arabinose, xylobiose, xylotriose and very little xylose were found in the early stages. Thus the overall decomposition of soluble pentosan in wheat flour is limited not by hydrolysis but rather by fermentation, confirmed by carbon dioxide

production, when compared to free glucose.

Howard (1955) implied that there is a substantial accumulation of extracellular polysaccharide associated with the bacteria when incubated in the presence of soluble sugars. This phenomenon was also noted by Leatherwood (1973). Cheng et al. (1977) states that the production of an extracellular slime coat is proportional to the soluble carbohydrate available in the diet and the slime may be overproduced when soluble carbohydrates are available in high concentration. This overproduction results in a cell-cell adhesion among the rumen bacteria with the eventual formation of slime enclosed microcolonies and, in some cases may cause a significant increase in rumen fluid viscosity (Cheng et al. 1977).

A series of hemicellulases exist in the rumen which can be isolated from cell free rumen fluid. Leatherwood (1969) has stated that no free cellulase exists in rumen fluid, but significant soluble hemicellulase is present. These enzymes are capable of hydrolyzing the main chain of xylans in feeds. Hydrolysis takes place at the bond between two unsubstituted xylose residues but very little free xylose is produced. The products are a series of disaccharides and oligosaccharides including xylobiose and xylotriose, with no glycosidase activity detected in the pentosanase preparation (Morrison 1979, Heald 1955). The suggestion has been made that the pentosanases degrade hemicelluloses to fragments which are small enough to be transported across the bacterial membrane for further metabolism (Morrison 1979, Pettipher and Latham 1979b). The pentosanases of bacterial origin have limited capabilities

of hydrolyzing hemicellulose present either in intact or delignified cell walls. Lignohemicellulose complexes isolated from the rumen have shown that polysaccharide-degrading enzymes are unable to attach to plant cell walls without prior action of a wall-modifying enzyme (Gaillard and Richards 1975, Leatherwood 1973). The precise action of the hemicellulase enzyme has not been established, but possibly the affinity fraction may be a non-hydrolyzed protein fraction, part of which makes up the total hemicellulose, and this renders hemicelluloses into a more hydrolyzable form (Leatherwood 1973), Morrison 1979, Karr and Albersheim 1970). The hemicelluloses and ligno-hemicellulosic complexes prepared from grass samples of increasing maturity are hydrolyzed by rumen microbial pentosanases to varying extents (Morrison 1979). The older the plant tissue, the more available the hemicellulose becomes, as a result of older tissue having a lower number of arabinose side chains and therefore a higher proportion of unsubstituted xylose residues. Therefore, with young grass, the proportion of side chains is the major controlling factor, while with older tissue, lignin is the controlling factor in hemicellulose digestion (Morrison 1979).

Antoniou and Marquardt (1981a) state the main effect of rye pentosans is the antinutritional aspect caused by a low xylose arabinose ratio. Wheat and barley tend to have higher xylose:arabinose ratios than rye, making them less viscous in aqueous solution. This makes wheat and barley more susceptible to bacterial pentosanase attack in the colon of monogastrics than rye (Antoniou 1980). Certain other bacterial

pentosanases are useful tools for characterization of pentosans due to their substrate specificity, for example the xylanase from streptomyces sp OMB814 can split a xylosidic bond between two xylose residues provided both units are not branched. This property of the enzyme was used for characterization of wheat water soluble arabinoxylan (Perlin and Reese 1963, Goldsmith and Perlin 1963). The specificity of bacterial pentosanases may also indicate the limited degradation of pentosans in certain feeds (Morrison 1979).

The presence of endogenous pentosanases in rye, wheat, barley and oats was first shown by Preece and Hobrick (1955) who extracted and used them for digestion of the rye arabinoxylans. The enzyme specificity dictates that arabinose units are first to be removed followed by xylose and xylobiose. With the removal of arabinose side chains, the overall solubility of the xylose polymer remaining is decreased. Preece and McDougall (1958) classified cereal pentosanases as being arabinosidases, endoxylanases, exoxylanases and xylobiases. Endoxylanases could hydrolyze pentosans without prior removal of arabinose. Rye and barley had the highest pentosanase activity, which was determined by either measuring the amount of liberated sugar or the decrease in viscosity of pentosan solutions when buffered at pH 3.5 (Preece and Hobrick 1955, Preece and McDougall 1958).

Microbial Attachment to Feeds in the Rumen

Of the major types of microorganisms present in the rumen, the bacteria rather than the protozoa have been found to be the major

degraders of the plant cell wall (Cheng et al. 1977). The major cellulolytic species in the rumen are *Ruminococcus albus, Ruminococcus falvefaciens* and *Bacteriodes succinogenes* (Russel and Hespell 1981, Baldwin and Allison 1983, Akin 1983, Cheng et al. 1977). These organisms have all been reported to degrade cellulose as well as the saccharolytic organism, *Butyrivibrio fibrisolven* (Bryant 1973, Hungate 1966). Many of these cellulolytics produce enzymes active against other fibrous components of the plant cell wall. All the cellulolytics are capable of utilizing polymeric arabinoxylan (Pettipher and Latham 1979b) except *Bacteriodes succinogenes* which degrade cellulose starch and pectins. Many of the non-cellulolytic rumen bacteria degrade xylans and pectins especially *Butyrivibrio fibrisolvens* (Dehority 1967). The synergistic interaction between cellulolytic and noncellulolytic species have been shown to enhance cellulose digestion (Baldwin and Allison 1981, Dehority and Scott 1967).

Akin (1976) has shown the ultrastructure of rumen bacteria attached to forage cell walls, with the aid of electron microscopy. Tropical and temperate forages have been incubated with rumen populations and have shown that the bacteria, especially the *Ruminococcus* species and *Bacteriodes succinogenes*, firmly adhere to plant cell walls during the process of degradation. Akin and Barton (1983) have shown similarly that two major types of adhering fibre digesting bacteria exist. Using transmission electron microscopy they discovered an encapsulated *Ruminococcus* species and an irregularly shaped bacterium, probably *Bacteriodes succinogenes* that adhered tightly to plant cell walls. Using forages of different digestibility incubated with inoculum from a single

source, the *Ruminococcus* and *Bacteriodes* species were the predominant species adhering to the plant cell walls. Minato et al. (1966) found that the *Bacteriodes succinogenes* and *Ruminococcus* species adhered to digesta fibre and that the *Ruminococcus* species adhered more firmly to plant cell walls. Akin and Barton (1983) have shown from electron microscopic studies that rumen bacteria resembling ruminococci were easier to detach from fibre that was shaken with Tween 80, than the other types resembling *Bacteriodes succinogenes*. Pettipher and Latham (1978b) using perrenial rye grass or cotton cellulose studied the adhesion of pure cultures of *Ruminococcus flavefaciens* or *Bacteriodes succinogens*. They found that either in pure culture or in coexistence that the two types of bacterium needed to adhere tightly to the plant cell wall in order to digest and degrade it.

Even though rumen bacteria adhere to and degrade plant cell walls, they are capable to producing extracellular carbohydrases active against the structural carbohydrate polymers. Leatherwood (1969) and Gawthorne (1979) have reported that rumen bacterial cellulases are either held close to the bacteria or adsorbed to the cellulose fibre with little if any free cellulase in the fluid. Akin and Barton (1983) found that streptomycin-treated (1.6 mg/ml) rumen bacterial suspensions lacked fibre digesting activity, as did centrifuged rumen fluid. Therefore the rumen bacteria must directly adhere, or be close to the plant cell wall before digestion takes place (Leatherwood 1969). Actual attachment to the cell wall however may not be necessary for hemicellulose digestion, since hemicellulose digestion occurs in centrifuged rumen fluid indicating the presence of free hemicellulases (Leatherwood 1973).

During much of the feeding cycle soluble substrate concentrations are low in the rumen (Hungate 1966, Smith et al. 1956). According to Monod (1949) at low concentrations of substrate, increments of substrate will cause microbial growth rate to increase, and this pattern follows saturation kinetics, typical of enzyme systems. The affinity constant, Ks, is defined as the substrate concentration that will yield half of the maximum growth rate. Since affinity constants of most rumen bacteria are low, affinity usually is determined by end product formation (Russell and Baldwin 1979). Russel and Baldwin (1979) have compared substrate affinities of rumen bacteria and showed that affinity for the same substrate can differ among species and that a species can have higher affinities for some substrates than others. For example the organism *Butyrivibrio fibrisolvens* one of the saccharolytic rumen organisms can utilize cellulose, starch and protein (Baldwin and Russel 1983, Hungate 1966, Russell and Hespell 1981, Russell and Baldwin 1979, Russell and Baldwin 1978). *Butyrivibrio fibrisolvens* has been shown to have high substrate affinities for the soluble carbohydrates of starch and much less affinity for poor quality forages when the two substrates are mixed (Russell and Baldwin 1979). However, *Butyrivibrio fibrisolvens* has been shown to proliferate in the rumen when poor quality forage was fed (Bryant 1962, Hungate 1966, Russell and Baldwin 1978). This would indicate that the rumen bacteria have evolved different strategies of growth and these physiological factors may affect competition among rumen bacteria (Russell and Hespell 1981).

Fermentation of Sugars and Volatile Fatty Acid Production in the Rumen

Fermentation in the rumen, which precedes gastric digestion in ruminants, makes a large proportion of the substrate of structural components of plants available in forms which are directly usable by the tissues of the animal (Baldwin 1963). Carbohydrates, proteins and all other fermentable substrates are converted simultaneously into volatile fatty acids methane, carbon dioxide, ammonia and microbial cells (Leng 1969).

The main routes of substrate metabolism in rumen bacteria are outlined by Baldwin (1963) and Baldwin (1965). Fermentation of sugars is the primary source of energy for the formation of the high energy phosphate bonds of adenosine triphosphate (ATP), that are utilized by the rumen microbes for maintenance and growth (Hungate 1966, Baldwin and Allison 1983, Leng 1969, Baldwin 1963, Baldwin 1965). The primary pathway of hexose fermentation in rumen microbes is the Embden-Meyerhof (E.M.) pathway. Rumen bacteria do not have a complete citric acid cycle, since they cannot oxidize acetate to carbon dioxide and water (Metzler 1977). Portions of the cycle, for example, malate conversion to fumarate and then to succinate tend to operate in reverse compared to aerobic organisms with a normal tricarboxylic acid cycle (Baldwin and Allison 1983). Glucose fermentations based on the E.M. pathway use two ATP's to convert hexoses to triose phosphate and four ATP's are formed during conversion of triose phosphate to pyruvate and NADH2 (Metzler 1977, Hungate 1966). The net products are 2 ATP, 2 pyruvate

and 2 NADH2. According to Joyner and Baldwin (1966) most of the enzymes of the E.M. pathway have been identified in rumen microorganisms using radioisotope tracers, and there is little doubt that this is the major rumen pathway.

The nature of the enzymes involved in hemicellulose degradation are not fully understood (Dehority 1967, Prins 1977, Leatherwood 1973). Dehority (1973) and Baldwin and Allison (1983) suggest that an extracellular hemicellulose can produce a non-specific cleavage of the β 1-4 xylosidic linkages in the hemicelluloses to produce xylose, xylobiose and xylooligosaccharides. The production of xylose from xylobiose comes about via a hydrolytic cleavage from the intracellular enzyme xylosidase associated with non-cellulolytic bacteria (Dehority 1973). The major pathway of xylose utilization appears to involve hexose synthesis (Walker 1965, Dehority 1973, Baldwin and Allison 1983). The pathway involves conversion of xylulose phosphate to two fructose phosphates and one triose phosphate via the reactions of transketolase and transaldolase. The final products of pentose utilization are fructose-6-phosphate and glyceralderhyde-3-phosphate which are then converted to pyruvate via the E.M. pathway (Hungate 1966, Leng 1969).

Howard (1955) has stated that the rate of pentosan fermentation is not dependent on the rate of degradation but rather on the rate of utilization. Dehority (1973) found that many cellulolytic rumen microorganisms were able to degrade various hemicelluloses but were unable to utilize the residues as energy sources. The lack of utilization by a particular strain appeared to be the result of the organisms inability to transport the oligosaccharides across the cell membranes or a lack

of necessary enzymes to ferment these substrates. Dehority (1967) has claimed that in general utilization of pentosan sugars lagged approximately 6 hours behind degradation. Specific strains of rumen bacteria that can utilize cellulose, hemicellulose and pectin have been isolated and are specific only to one substrate (Dehority 1973). With regard to bacterial species Dehority (1963), Kistner (1965), Shane et al. (1969) and Dehority (1973) have shown that hemicellulose digestion takes place when the principle cellulolytic bacteria *Bacteriodes succinogenes, Ruminococcus flavifaciens, Ruminococcus albus* and in some cases *Butyrivibrio fibrisolvens* are present. The principle hemicellulose digesters are *Bacteriodes ruminicola* and *Butyrivibrio fibrisolven.* Dehority (1965) has shown that the difference in the ability of a particular organism to degrade and utilize hemicellulose does not appear to be directly related to the hemicellulose composition, but rather the structure of the hemicellulose may be the main controlling factor (Dehority 1973). Dehority (1965) has shown that *Bacteriodes succinogenes* was an efficient hemicellulose degrader but had virtually zero percent utilization while the cellulolytic ruminococcus were not only efficient hemicellulose degraders but also efficient pentosan utilizers, measured by total organic acids produced. According to Baldwin and Allison (1983) the net ATP yield from fermentation of a pentose sugar via the route described by Hungate (1966) and Leng (1969) would be 1.67 moles of ATP/mole of pentose fermented.

Pyruvate Metabolism in the Rumen

The fate of pyruvate and NADH2 formed from hexose and pentose

fermentation varies depending upon the microbes involved and incubation conditions (Wolin 1976). The main requirement within and among organisms is that of maintaining hydrogen balance in the system. According to Wolin (1975) an important reaction is the interspecies transfer of hydrogen. In this connection the methanogens are most important. The utilization of hydrogen reduces hydrogen concentration, and since hydrogen is a mobile equilibrium, the reaction under favorable conditions will allow the accumulation of hydrogen gas (Wolin and Miller 1983, Wolin 1975). Normal rumen levels of H2 are about 10^{-4} atmospheres and this will favor a net production of hydrogen (Wolin 1975). Thus the result of coexistence between the *Ruminococcus* a hydrogen producer, and *Methanobacterium* a hydrogen utilizer, is a four fold increase in hydrogen production, over and above the hydrogen levels produced if *Ruminococcus* were grown in pure culture (Wolin and Miller 1983, Wolin 1975).

If methanogenesis is active, and as a result the partial pressure of hydrogen gas in the rumen is low, organisms possessing a hydrogenase will release the hydrogen in NADH2 as H2. If the H2 in the rumen environment is high the thermodynamics of the NADH2 > H2 is not favored and then the organisms are forced to reduce pyruvate to lactate or propionate to maintain hydrogen balance (Baldwin and Allison 1983, Wolin and Miller 1983, Wolin 1976). The stimulation and utilization of hydrogen by the methanogens causes a drastic reduction or disappearance of other reduced products such as ethanol, lactic acid, succinate, propionate and formate with an increase in acetate, H2 and CO2 production by the fermentative bacteria (Wallnofer et al. 1966). Two mechanisms have been observed for the conversion of pyruvate to acetate in rumen microbes. The first,

described by Hungate (1966) is the most commonly observed acetate formation pathway in the rumen microbes. The pathway involves the conversion of pyruvate to formate and acetyl-COA as intermediate products. The formate thus released is converted to CO2 and H2, usually by another organism in mixed cultures. Formate is a common product when rumen microbes are grown in pure culture, however, formate is not observed in a mixed culture (Baldwin and Allison 1983). The second mechanism of conversion of pyruvate to acetate has been described by Wolin and Miller (1983). The rumen organisms, *Megasphaera elsdenii, Veillonella alcalescens* and the anaerobic spore forming species of *Clostridia*, have been found to possess a pyruvate-ferridoxin oxidoreductase system that converts pyruvate to reduced ferridoxin, CO2 and acetyl-COA. Oxidized ferridoxin is liberated with the concommitant release of hydrogen. Acetyl-COA is converted to acetate plus ATP by phosphotransacetylase plus acetokinase. The net yield of ATP produced by the conversion of pyruvate to acetate is one ATP/mol of pyruvate (Wolin and Miller 1983, Baldwin and Allison 1983).

Another prominant pathway of pyruvate conversion is the dicarboxylic acid pathway. The pathway described by Baldwin (1965) allows the production of propionate from pyruvate. According to Wallnofer (1966) and Baldwin (1965) there are three possible enzymes which can catalyze the carboxylation of pyruvate. Phosphoenolpyruvate (PEP) carboxykinase which converts PEP plus CO2 and ADP to oxaloacetate (OAA) plus ATP; methylmalonyl-COA carboxytransferase, a biotin containing enzyme that transfers a CO2 unit from methylmalonyl-COA to pyruvate during the

conversion of succinate to propionate; pyruvate carboxylase which converts pyruvate plus ATP and CO2 to OAA plus ADP. According to Wallnofer (1966) the first and second mechanisms are preferred because they accomplish the carboxylation at no net cost in ATP to the cell while the pyruvate carboxylase reaction uses one ATP/mol of pyruvate carboxylated. This is consistent with the results of several workers (Hungate 1966, Baldwin and Allison 1983, Wolin and Miller 1983, Russell and Hespell 1981) who have observed that several cellulolytic bacteria, especially *Bacteriodes succinogenes* produce succinate as an end product, and in mixed culture with saccharolytic organism such as *Selenomonas ruminatium*, the succinate is converted to propionate via the carboxyltransferase reaction possessed by the saccharolytics.

Another pathway important in the conversion of pyruvate to propionate, as observed by Ladd (1959), is the acrylate pathway. This pathway which has been identified in *Megasphaera elsdenii* a hydrogen utilizer, and the saccharolytic bacterium *Bacteriodes ruminicola*, involves the formation of lactate which is converted to acrylyl-COA via the intermediate phospholactyl COA. The acrylyl-COA is then reduced to propionyl-COA via a NADH2-linked crotonyl-COA reductose (Baldwin and Milligan 1964). The acrylate pathway has been found to be most active when ruminants are fed high concentrate diets (Wallnofer and Baldwin 1967).

According to energy calculations by Metzler (1977) the butyrate pathway is less efficient than the propionate pathway. Approximately 3 moles of H2 gas are produced per mole of glucose fermented in the butyrate pathway. Relative to the propionate pathway 22.8% of the total

energy available in glucose is lost as H2 gas in the butyrate pathway (Metzler 1977).

According to Murphy et al. (1982) and Ulyatt et al. (1983) the amylolytic microbes in the rumen produce considerably more propionate than do the cellulolytic organisms, while the saccharolytic and pectinolytic microbes are intermediate in propionate production. Roughage diets high in cellulose, intermediate in soluble sugars and low in starch tend to enhance the numbers of cellulolytic and saccharolytic bacteria with large proportions of acetate formed (Murphy et al. 1982). Diets high in starch result in large number of amylolytic bacteria that compete favorably for soluble carbohydrates and the hydrolytic products of starch and hemicellulose degradation. Thus, propionate production is increased when cereals are fed not only because of the high starch fermentation, but also because the fermentation products formed from other carbohydrates are altered to favor the propionate pathway (Murphy et al. 1982, Russell and Hespell 1981, Wolin and Miller 1983).

Fate of Carbohydrates in the Small and Large Intestines of the Ruminant

While digestion in the small intestine of ruminants proceeds in a manner similar to that of simple-stomached animals, there are important qualitative and quantitative difference in enzyme activities (Nicholson and Sutton 1969). Mammalian tissues do not synthesize specific cellulose and hemicellulose enzymes, therefore research studies have shown, virtually no cellulose or hemicellulose digestion occurs in the small

intestine of ruminants (Beever et al. 1971, Thompson et al. 1972, Beever et al. 1972, Ulyatt and McRae 1974). Data from Hembry et al. (1967) who ran studies using homogenates of intestinal mucosa from mature sheep detected the presence of cellobiase. Later however, Coombe and Siddons (1973) using small intestinal homogenates of milk fed calves concluded from their experiments that the cellobiase enzyme discovered by Hemburg (1967) was identical to the lactase enzyme also shown to be present.

In the small intestine of the ruminant the duodenal enzymes involved in the hydrolysis of alpha linked glucose polymers are the amylases and maltases from the pancreatic juice and intestinal mucosa and oligo - 1,6 glucosidase enzyme of the intestinal mucosa (Armstrong and Beever 1969). The low activities of pancreatic maltase and intestinal amylase relative to pancreatic amylase and intestinal maltase, respectively, suggests a greater importance of pancreatic amylase and intestinal maltase in starch hydrolysis (Hembry et al. 1967, Siddons 1968, Chittenden et al. 1974, McNeill et al. 1974). Isomaltase, an intestinal mucosal enzyme is found mainly in the jejunum and has a pH optimum of 6.0-6.2, (Armstrong and Beever 1969) that hydrolyzes the 1,6 glucosidic linkages (Coombe and Siddons 1973). According to Coombe and Siddons (1973) the distribution patterns of maltase and isomaltase along the digestive tract are similar for adult cows and milk fed calves, being highest in the jejunum.

Studies of pancreatic and intestinal carbohydrase in sucking and grown lambs have indicated that maltase activity may be limiting the capacity for post ruminal starch digestion (Tacu 1972). Mayers and

Orskov (1974) have also emphasized that maltose is likely the limiting enzyme in ruminant small intestinal starch digestion. Walker (1959) found that pancreatic amylase and intestinal maltase of lambs increased much more slowly compared with pigs. No sucrose activity was found in the lamb but developed rapidly in the pig while only lactase activities appeared similar in the pig and lamb. According to Orskov (1973) studies on the postruminal digestion of sucrose in lambs indicated that about 70% of sucrose infused at the abomasum passed the terminal ileum. There was no sucrose activity found in the lambs small intestine and any disappearance of sucrose was due to bacterial fermentation. Orskov (1973) and Orskov and Mayers (1972) studied sucrose activity in sheep and found the enzyme activity negligible, but indicated that sucrose was highly fermentable by rumen bacteria and caecal bacteria, due to an increase in their viable counts, and a sharp drop in pH when grass pellets plus sucrose was fed, compared to grass pellets alone.

Data from Armstrong (1974) for corn and barley indicates that any appreciable amounts of starch which enter the small intestine of the ruminant are removed before reaching the terminal ileum. Armstrong (1974) found that the disappearance of alpha linked glucose polymers that entered the small intestine and again measured at the terminal ileum was 0.85 kg $\pm$ 0.051 for corn, 0.77 kg $\pm$ 0.056 for barley and 0.95 kg $\pm$ 0.050 for oats. According to Armstrong (1974) the maximum starch digesting capacity of a lactating dairy cow in her duodenum and jejunum is approximately 1 kg per day. Armstrong (1974) states that the amylolytic activity is sufficiently low, that on high grain feeding programs large quantities of starch may escape gastric digestion and reach the large bowel where

the starch is either fermented or excreted in the feces.

In order to study whether the physical nature of starch entering the small intestine has any effect on starch digestion Orskov et al. (1969) and Orskov (1973) used two groups of sheep which were infused abomasally with either 350 g/day of raw starch or 350 g/day of pre-gelled starch. The data disclosed that the physical nature of the starch is important since only 22% of raw starch and 47% pre-gelled starch had disappeared by the time the digesta reached the terminal ileum. Mayes and Orskov (1972) examined the effect of age of the animal on the removal of gelled starch from the small intestine of sheep. Lambs from 5-8 weeks of age, 13-16 weeks of age and mature sheep were studied by infusing gelled starch into an abomasal cannula for 28 days. Their data indicates that, in relation to metabolic weight, the mature sheep had a lower capacity to remove starch (33%) from the small intestine while the young lambs could remove 46% of the starch infused. This was due to an insufficient secretion of maltose in the intestine of the older animals rather than to limitation imposed by a relative deficiency of pancreatic amylase. Orskov (1973) states that the digestion of raw starch may, however, be limited both by the concentration of amylase and by the potential rate at which starch is broken down in relation to rate of passage through the small intestine.

Capacity for Absorption of Monosaccharides From the Small Intestine

Net disappearance of starch from the small intestine does not alone

indicate net absorption of glucose, since microbial fermentation occurs in the distal part of the ileum (Mayes and Orskov 1974). The same authors have determined a negative correlation between starch content and pH of digesta at the terminal ileum, and interpret that as evidence of microbial fermentation in the distal ileum. The capacity of the ruminant to remove glucose from the small intestine has been investigated by Orskov et al. (1971). Glucose was infused into the abomasum of sheep starting at 20 g/day and increased to 500 g/day. Using chromium-EDTA as a marker, Orskov et al. (1971) showed that the capacity to remove glucose from the small intestine was limited. Most increments in excess of 300 g/day passed the terminal ileum and provided a substrate for fermentation in the large intestine. White et al. (1971) showed the absorptive capacity for glucose in relation to body weight was seven-fold higher in the rat than in the sheep. White et al. (1971) has also studied the rate of disappearance of glucose from ligated loops of small intestine in anesthetized lambs and adult sheep. Their data showed that the total absorptive capacity of the small intestine of adult sheep was only 25% as efficient as that of lambs less than one week of age. Reid (1950) speculated that when glucose is administered to the abomasum of adult sheep there is a slow rise in blood glucose, however, when administered to a young lamb, a rapid rise in blood sugar occurs. Reid (1950) suggested these results are indicative of an adaptation to intestinal monosaccharide absorption to the amount of carbohydrate entering the small intestine. According to Ballard et al. (1969) hexoses are predominantly absorbed from the small intestine, while volatile fatty acids are mainly

absorbed from the rumen. Ballard et al. (1969) postulates that during forestomach development the site of absorption for products of carbohydrate digestion is shifted to a great extent from the small intestine to the rumen. Ballard et al. (1969) also states that during the period of transition from a pre-ruminant to a ruminant, blood glucose levels, glucose tolerance and glucose utilization rates decrease while hepatic gluconeogenesis increases dramatically.

Disappearance of Carbohydrates in the Large Bowel

When ruminants are given forages such as fresh herbage, dried grass or hay, only trace amounts of soluble sugars can be detected in digesta entering the caecum (Beever et al. 1972, MacRae and Armstrong 1969, Topps et al. 1968, Ulyatt and MacRae 1974). According to Grovum and Hecker (1973) the capacity for fermentation in the large intestine is difficult to access realistically, for when the capacity is exceeded, retention time decreases. Grovum and Hecker (1973) found the contents of the caecum and large intestine to be very similar when sheep were fed either 400 g or 1200 g of lucerne chaff per day, and, that the retention times in the large bowel on the low level of feeding were approximately three times greater than when the high feeding was employed. Orskov and Foot (1969b) investigated the capacity for fermentation of starch in the large intestine by infusion of raw starch via the terminal ileum. The sheep received 900 g of cubed dried grass daily intake. When more than 140 g/day of raw starch was infused most of the excess could be found in the feces which also became extremely liquid and acidic (Wheeler and Noller

1977). Orskov et al. (1971) studying the passage of glucose past the terminal ileum in sheep found that if more than 100 g/day of glucose passed the distal ileum and entered the large bowel, glucose was detectable in the feces. Orskov et al. (1971) also determined that if more than 250 g/day of sucrose was infused via abomasal cannula into sheep that excessive diarrhea resulted and the experimental sucrose infusions had to be terminated in order to maintain healthy sheep.

The site of digestion of high starch diets appears to be influenced by the source of starch (Orskov et al. 1971b). Ruminant experiments carried out by workers (MacRae and Armstrong 1969, Topps et al. 1968, Orskov et al. 1971b) determined that when diets contained a high proportion of barley, only small amounts of starch reached the caecum. However, diets containing a high proportion of uncooked maize, showed a considerable amount of starch escapes rumen fermentation and, while most of this is digested in the small intestine, up to 6% of the digestible starch has been shown to be digested in the large bowel of sheep, (Orskov et al. 1971b), and up to 15% in cattle (Karr et al. 1966). Generally as the intake of maize is increased the proportion of starch digested in the large intestine increased (Orskov 1971b, Karr et al. 1966, Papasolomontos 1977, Russell et al. 1981).

Large amounts of cellulose and hemicellulose the major cell wall carbohydrates, escape rumen digestion and thus become available for fermentation by caecal bacteria (Beever et al. 1971, MacRae et al. 1969, Thompson et al. 1972). Various diets such as fresh herbage, silage, hay, dried grass and cereals, indicate that between 5 and 30% of digestible

cellulose is digested in the large intestine (Ulyatt and MacRae 1974, Thompson et al. 1972, Papasolomontos 1977, Beever et al. 1971). In all experiments where comparisons can be made the proportion of hemicellulose digested in the large intestine was also higher than that of cellulose (Ulyatt and MacRae 1974, Thompson et al. 1972, Beever et al. 1972). Researchers (Beever et al. 1970, Ulyatt and MacRae 1974, Thompson et al. 1972, Beever et al. 1972), indicate the proportion of digestible cellulose fermented in the large bowel when sheep were fed either fresh or dried grass is about 13.5% while approximately 50-60% of the digestible hemicellulose present is fermented in the colon. Two other factors considered by these researchers which can increase the amount of cellulose and hemicellulose fermentaion in the colon are grinding and/or pelleting of forages, and the substitution of forage for a cereal grain. MacRae and Armstrong (1969) studied the cellulose intake and whole gut digestibility of an all hay, 2:1 ratio of hay to barley and a 1:2 ratio of hay to barley. MacRae and Armstrong (1969) concluded that whole gut digestibility of the dietary cellulose decreased from 73% to 61% as the level of barley increased in the diets, but the level of cellulose digestion in the colon increased as the level of barley increased from 12.32% to 47.54%. MacRae and Armstrong (1969) concluded that whole gut cellulose digestibility decreased as the level of barley increased because of increased rate of passage and decreased rumen retention time. The increase in colonic fermentation occurred because more substrate was reaching the area due to increased rate of passage (MacRae and Armstrong 1969). The same reasons appear to affect hemicellulose digestibility (Thompson et al. 1972).

Francis et al. (1978) indicates that most cellulose is digested in the rumen, but a substantial portion of hemicellulose escapes the rumen to be fermented in the lower tract. Francis et al. (1978) believes that the xylan cannot be attached by microbial pentosanases until the arabinosic side chains are removed, and this is accomplished only after the hemicellulose passes through the acidic abomasum and hydrolysis of the arabinoxylan occurs. This action then exposes the xylan so further degradation can occur (Howard 1955). Neilson and Richards (1978) have shown the presence of soluble ligno-hemicellulose complexes in rumen fluid that are resistant to degradation and survive to the feces. Covalent linkage of the carbohydrate to lignin can protect the pentosans from digestion, even in solution. These complexes are soluble in neutral and alkaline solution but may be precipitated by weak acid (Neilson and Richards 1978, McNeil et al. 1975, Holas et al. 1971, Golenkov and Traubenberg 1966, Antoniou 1980).

Microbiology of the Ruminant Large Intestine

Ulyatt et al. (1975) has determined that bacteria are present throughout the alimentary tract of ruminants, and while the majority of rumen bacteria are destroyed in the acidic abomasum, a characteristic microflora exists in the duodenum, with the number of viable bacteria increasing distally, with largest numbers in the large intestine. According to the data published by Ulyatt et al. (1975) anaerobic viable bacteria counts of 1.5×10^6/g of wet duodenal contents of sheep increased to 2×10^9/g in the caecum and colon when fed fresh pasture and lucerne

pellets. Mann and Orskov (1973) also found that caecal contents of sheep fed dried grass pellets contained on the average 1 x 10^9 viable anaerobic bacteria per gram of wet sample. Ulyatt et al. (1975) determined the viable aerobic bacteria throughout the intestine and discovered that these bacteria increased in viable number in the same pattern as did the anaerobic bacteria. The differences between the two types of bacteria in population numbers show that the aerobic viable bacteria are consistently one hundred fold less throughout the entire small and large intestinal tract of sheep compared to the anaerobic bacteria.

While some bacteria occur in the small intestine Ulyatt et al. (1975) and Mann and Orskov (1973) indicated that the major site of fermentation and volatile fatty acid production (VFA) in the intestinal tract is in the caecum and colon. According to Holdeman et al. (1976), in his studies of the major organisms of the lower gastrointestinal tract of humans, the main genera include *Ruminococcus, Bacteriodes, Eubacterium, Streptococcus* and *Fusobacterium.* Bryant (1974) during his studies of the bacteria from the human colon found that the nutritional requirements of these bacteria are similar to those of the rumen. Bryant (1978) determined that in vitro cultures of caecal and fecal organisms from man were optimally grown on rumen fluid media. Mann and Orskov (1973) found when sheep were fed conventional type diets the predominant caecal and colonic microflora were gram negative rods belonging to the genera, *Bacteriodes, Butyrivibrio* and *Fusobacterium.* Other bacteria isolated in the ruminant colon by Mann and Orskov (1973) were *Streptococcus bovis, Streptococcus faecalis, Selenomonas* and *Micrococcus* all of which, individually form a

low proportion of the total flora found in this area of the gut. Caecal contents of sheep fed dried grass pellets or lucerne pellets and fresh hay have been found to have cellulolytic bacterial counts of 1×10^8 bacteria per gram of wet caecal contents (Ulyatt et al. 1975, Mann and Orskov 1973). According to the latter workers caecal digesta has very high cellulolytic activity, equal to or greater than that of rumen digesta activity.

According to Parra (1978) the environment of the large intestine is more constant and less influenced by dietary pulses compared with the rumen. Parra (1978) states that food proteins and other easily digestible dietary components do not ordinarily reach this section of the digestive tract in ruminants. However, like the rumen, the pH of the cecum will drop if an excess of rapidly fermentable carbohydrate is supplied, in which case the buffering capacity is overwhelmed with resultant diarrhea (Orskov et al. 1972). The pH regulation in the lower gut is dependent upon the transit of free volatile fatty acids across the gut wall and the secretion of bases into the lumen (Orskov et al. 1972). The diffusion of sodium bicarbonate and urea into the bowel offer respectively, buffering capacity and a source of nitrogen for microbial growth (Orskov et al. 1972). In studies where sheep were fed grass pellets, grass pellets plus sucrose or had sucrose infused postruminally, the pH, bacterial numbers and fecal N were measured by Orskov et al. 1972). The results indicated that sheep infused with 250 gms sucrose post ruminally had the greatest pH drop in the caecum from 6.9 for sheep fed grass pellets to 5.6 for the sucrose infused sheep. The viable bacterial count in the cecum were

the highest increasing from 0.7 x 10^8/ml of wet digesta for the grass pellet fed sheep to 18 x 10^8/ml of wet cecal contents for the sucrose infused sheep. The fecal N excretion was 10.9 g/day for sucrose infused sheep compared to 8.9 g/day for the grass pellet fed sheep. Ulyatt et al. (1975) and Faichney (1969) state that fermentation and microbial growth in the cecum and colon are capable of yielding up to 17% of the total volatile fatty acids available to the animal, however, little evidence exists that any microbial protein is available to the animal so far down the gut. Therefore, the level of highly fermentable substrate entering the large bowel has a profound effect on the fecal N excretion and the total energy absorbed (Orskov et al. 1972). According to Kern et al. (1973) and Kern et al. (1974) feeding steers diets containing all timothy hay, timothy hay plus oats, clover, or clover plus oats, the cecal and colon volatile fatty acids were very similar in molar percentages to that of the rumen except for slightly more acetate and slightly less butyrate. The average molar percentage of acetate:propionate:butyrate were 79:13:3 for the cecum of the four experimental diets and 74:15:9 for the rumen analysis. Significant levels of branched chain volatile fatty acids are present in the cecum and colon of ruminants, especially isobutyrate indicating greater conversion of protein to volatile acids (Orskov et al. 1970). These data are in agreement with others (Faichney 1969, Packett et al. 1966) all of whom studied volatile fatty acid production in the cecum of ruminants.

Gastrointestinal Markers in Ruminant Nutrition

The use of markers for studying digestive function has been extensively reviewed by Kotb and Luckey (1972) and MacRae (1974). The following discussion considers the use of specific markers used in the study of digestion, absorption and retention of nutrients in the ruminant.

Criteria for Evaluating Markers

Kotb and Luckey (1972) suggested that before a substance qualifies as an effective gastrointestinal marker eight factors should be met. The marker should be inert with no toxic, physiological or psychological effects 2) have no appreciable bulk 3) be neither absorbed nor metabolized within the gastrointestinal tract 4) have no influence of gastrointestinal secretion, digestion, absorption, normal motility or excretion 5) mix intimately with the usual food and remain uniformly distributed in the digesta 6) have no influence on the microbial population in the gastrointestinal tract 7) have physiochemical properties which make it discernible throughout the gastrointestinal tract 8) have qualities that allow ready, precise quantitative measurements. Before selecting any marker these criteria should be reviewed. Unfortunately few if any substances employed as markers meet all these criteria perfectly.

Liquid Phase Markers

Polyethylene glycol (PEG)

Polyethylene glycol (PEG) compounds are manufactured through the

reaction of ethylene oxide with water, ethylene glycol or diethylene glycol to furnish functional groups for the propagation of the reaction. The process results in a mixture of diols of different chain lengths. Polyethylene glycols having an average molecular weight ranging from 200 to 600 are fluids, and those ranging from 1,000 to 10,000 are solids of increasing firmness (Kotb and Luckey 1972).

Analysis of PEG is based on a precipitation from aqueous solution with subsequent gravimetric techniques (Sperber et al. 1953) or turbidimetric techniques (Hyden 1955). The turbidimetric method modified by Corbett et al. (1958) and Ulyatt (1964) is faster and more accurate, however, the analysis is still a tedious non specific and relatively insensitive method of analysis.

Sperber et al. (1953) reported the use of PEG as a reference substance in ruminant studies of digestion. They found that the polymer with mean molecular weight 4,000 was not degraded in the gut or absorbed and more than 90% was recovered in the feces. Downs and MacDonald (1964) have indicated difficulty in achieving complete recovery of PEG in the feces with no significant amount detected in the urine. Clark et al. (1972) obtained a lower recovery of PEG from the ruminal liquid phase when sheep and cattle were fed cottonseed hulls rather than lucerne hay as a fibre source. In vitro studies by Clark et al. (1972) suggest that 109 mg of PEG was being retained per gram of cottonseed hulls.

Hyden (1961) has given a full mathematical treatment of the principles involved in the use of soluble markers to measure rumen volume and flow rates. Hyden (1961) states that PEG was satisfactory in

estimating rumen volume and that PEG was distributed throughout 95% of the rumen liquid phase. Other workers (Sinha et al. 1970, Bauman et al. 1971) demonstrated that using PEG as a reference substance the approximate weight of rumen contents, rumen volume and approximate fill could be calculated.

Till and Downes (1965) suggested the use of tritium labelled PEG to overcome analytical difficulties. Tritium was not lost by exchange reactions and only 2 to 3% of tritium was recovered in the urine of sheep. Neudoerffer et al. (1973) has reported some dissatisfaction with tritiated-PEG in cattle experiments because they found more than 50% of PEG associated with the particulate phase of digesta.

Chromium Ethylenediamine Tetraacetic Acid (Cr-EDTA)

The complex of radioactive Cr with EDTA (51 Cr-EDTA) has been suggested by Downes and McDonald (1964) as a substitute for PEG. Fifteen comparisons were made of the ratio of disappearance of radioactive Cr-EDTA and PEG-4000 from the rumen. The results showed that most (85-91%) of each dose of radioactive Cr-EDTA was recovered in sheep feces excreted during the first 9 or 10 days. Some radioactive Cr, but always less than 4.7% of the dose appeared in the urine. Hogan (1964), Weston and Hogan (1967) and Binnerts et al. (1968) showed that less than 5%, but generally around 3% for sheep and less for cattle, is absorbed and excreted in the urine. All workers seem to agree that Cr-EDTA is a satisfactory soluble marker in spite of the slight absorption and subsequent excretion in the urine. The estimation of radioactive Cr is

simple, accurate and specific in comparison to PEG.

Hogan (1964) found radioactive Cr-EDTA distributed evenly throughout the digesta water leaving the reticulum in sheep and no absorption onto the particulate material. Warner (1969) found under certain conditions that some radioactive Cr-EDTA complex became bound to particulate matter in the rumen in sheep for undefined reasons. Warner (1969) could not demonstrate this phenomenon in vitro and suggested that the binding of radioactive Cr-EDTA requires the presence of some specific microbial activity along with remastication during rumination.

Problems of radioactive waste disposal associated with use of radioisotopes in food producing animals can be overcome by using atomic absorption spectrophotometry for measuring nonradioactive Cr-EDTA (Binnerts et al. 1968) or instrumental neutron activation analysis (INAA) (Kennelly et al. 1982). MacRae (1974) reported that non-radioactive Cr-EDTA had been used for many rumen volume and digesta liquid-phase retention time studies in sheep given a variety of herbage diets. MacRae (1974) estimated Cr by X-ray fluorescent spectrophotometry.

Goodall and Kay (1973) found that in 32 comparisons, rumen volume estimations obtained with Cr-EDTA were 15.2% greater than those obtained using PEG in sheep. Goodall and Kay (1973) state that the difference may be attributed to the fact that only 92% of the rumen water was available to PEG whereas 99% was available to Cr-EDTA. Warner and Stacey (1968) indicated that Cr-EDTA entered 95-98% of the water in the rumen without adversely affecting the rumen microflora. Poppi (1980) observed that rumen liquid volumes in cattle fed all forage diets were 15.8% lower when measured by dilution of Cr-EDTA as compared to manual

emptying and measurement. These differences between observed and estimated volumes may suggest that Cr-EDTA binds to solids (Warner 1969).

Cobalt Ethylenediamine Tetraacetic Acid (Co-EDTA)

Co-EDTA is currently receiving attention as a liquid phase marker (Uden et al. (1980). During their study either Co-EDTA or Cr-EDTA were tested as liquid phase markers in cattle and sheep. The total fecal recovery for cobalt or chromium was in excess of 90%, 82 hours after administration. In the same study cobalt and chromium were detected in the urine at upwards of 3% of the dose given. These values correspond with that of Underwood (1977) and Kennelly et al. (1982) who fed pigs 48 mg/day cobalt as Co-EDTA for an 8 week period. The urinary cobalt concentration which was not detectable prior to administration of Co-EDTA rose to an average of 0.92 µg/ml. These values indicate an absorption rate of 5.8%.

Therefore, Cr-EDTA and Co-EDTA are equally useful as liquid phase markers (Goodall and Kay 1973, Uden et al. 1980, Kennelly et al. 1982). Kennelly et al. (1982) using instrumental neutron activation analysis (INAA) studied Cr-EDTA and Co-EDTA as liquid markers in rumen fluid samples and found these markers to give similar results. According to Kennelly et al. (1982) the only reason to use Co-EDTA instead of Cr-EDTA in marker studies analyzed by INAA are simply because Cr must be irridated for 1-2 hours, cooled for 15 days and counted for 20 minutes, whereas, Co can be irradiated for 45 seconds or less, cooled for 30 seconds and counted for 60 seconds. Kennelly et al. (1982) indicated that the limits

of detection for activated Cr and metastable Co using a Ge(Li) detector on the neutron activator is 0.87 mg/kg and 1.02 mg/kg of freeze dried rumen fluid compared to 10 mg/kg on the atomic absorption spectrophotometre (Williams et al. 1962).

Based on stability constants with EDTA, metals other than Cr ++ or Cr +++ should have equal or superior utility for liquid phase marker experiments. The stability constants for Cr ++ and Cr +++ are 14.0 and 23.0 respectively while for Co ++ and Co +++ the stability constants are 16.0 and 41.0. Even though Co has higher physical affinity for EDTA than Cr, Kennelly et al. (1982) believes that the stability of Cr-EDTA is slightly better than Co-EDTA in the gastrointestinal tract. He bases this on the fact that slightly more Co is excreted in the urine than Cr indicating greater absorption from the gut.

PEG, CrEDTA and CoEDTA were examined by Teeter and Owens, (1983) to more fully understand the behavior and similarity of water soluble markers (WSM). In general, there was no significant difference between the WSM in estimating rumen volume or dilution rates, suggesting that all three markers are biologically similar. This is in contrast with Goodall and Kay (1973) data which suggests that PEG consistently yielded lower rumen volume estimates than CrEDTA.

In general all the markers tested by Teeter and Owens (1983) underestimated rumen volume when compared to total evacuation by an average of 4%. Teeter and Owens (1983) relate this to a number of factors including that WSM are being absorbed and that WSM are being bound to particulate matter. Warner (1981) suggested that CrEDTA binds to ruminal

particulate matter under conditions yet undefined, and this binding could cause an overestimation of dilution rate. Teeter and Owens (1983) also observed an increase in dilution rate four hours after feeding, however, whether the increase is due to an increase in rumen volume or to an increase in liquid flow is unknown. Earlier results by Warner and Stacey (1968) agree that there is an increase in dilution rate immediately after feeding.

Particulate-Phase Markers

Kotb and Luckey (1972) and MacRae (1974) have reviewed the use of particulate phase marker extensively. MacRae (1974) suggested the need to find a particulate marker which would closely associate itself with the particulate-phase of digesta during its transit through the gastrointestinal tract.

The Lanthanon Series

The rare earths are neither rare nor earths. They are as abundant as many commonly known elements. They are termed earths because they were first identified as a mixture of oxides that resembled the alkaline oxides (Kyker 1962).

The rare earths (lanthanons) comprise fifteen elements (atomic numbers 57 through 71) from lanthanum through lutetium (Kyker 1962). According to Haley (1965) problems of purity made study of the rare earths difficult until the mid 1950's when remarkable strides were made in their chemical separation using ion exchange techniques.

The chemical properties of the rare earths, their metabolism and involvement in biochemical systems are quite similar (Luckey et al. 1975). Solubility of the rare earths salts may be expressed as nitrates> chlorides> bromides> iodides> acetates> perchlorates> sulfates> phosphates> carbonates> fluorides> hydroxides> oxides where the nitrates to the sulphates are relatively soluble and the phosphates through the oxides are very insoluble in water (Venugopal and Luckey 1975). The solubility products of lanthanon hydroxides are in the range 10^{-19} to 10^{-24} molar (Venugopal and Luckey 1975). Poor solubility confers adsorptive capacity since adsorption to some material is inverse to the solubility function. The adsorptive effects of the lanthanon series occurs at concentrations less than the molar solubility of the hydroxides otherwise known as radiocolloidal concentrations (Kyker 1962).

The soluble rare earth salts upon entering the rumen, are thought to hydrolyze, and form a product that yields insoluble hydroxides which would be adsorbed onto feedstuffs (Lascano and Ellis 1979). The specific nature of binding between rare earths and feed residues in ruminant digesta has not been investigated. Some observations (Ho 1977, Kearns et al. 1978) suggest that binding is by coordinate covalent bonds in which the rare earth acts as an electron pair acceptor (or acid) and various ligands of feedstuff constituents act as the election pair donor (or base). According to Bell (1977) the rare earths act as acids which form most stable coordination complexes with bases such as R NH2, OH, ROH constituents of organic molecules.

Rare Earth Markers as Particulate Markers

The use of rare earth elements for estimating particulate phase digesta flow has been discussed by Ellis (1968), Hartnell and Satter (1979) and Crooker et al. (1982).

One of the most distinguishing properties in addition to being essentially undigestible and unabsorbable by livestock, is that rare earth markers possess an affinity for particulate matter, and therefore might be expected to flow through the GI tract closely associated with feed particles (Ellis 1968). This affinity would reduce variation in concentrations of fecal markers attributed to the differential flow rates of feed particles and markers from the reticulum-rumen (Corbett et al. 1958, Corbett et al. 1959).

Although rare earth markers have a high affinity for particulate matter, movement of marker among different particulate fractions has been observed. Faichney and Griffith (1978) have shown an exchange occurring between large and small particle fractions, thus underestimating retention times. Hartnell and Satter (1979a) observed that when rare earth markers were applied to grain and hay particles, an average of 92.6 and 99.0% remained associated with the original grain or hay particles, respectively. In subsequent experiments, Hartnell and Satter (1979b) found that the concentrations of markers on stained hay particles were fifteen times greater than that found on stained grain samples. Differences between the affinities of hay and grains for markers can be explained by the fact that grains are more readily digested than hay. Upon digestion the released markers may be reabsorbed onto hay

particles, or form insoluble hydroxides and get entrapped by hay particles or the markers may be engulfed by bacteria that get entrapped in hay particles (Hartnell and Satter 1979b).

Crooker et al. (1982) observed significant marker movement. Incubating four feeds with one of two markers, in polyester rumen bags for 12 hours, Crooker et al. (1982) observed increases in marker contamination on feed residues, when compared to initial levels.

Crooker et al. (1982) suggested that the difference between the two studies could be related to the specific binding capacity of feeds for markers. Feed particles have a specific binding capacity for markers and when excess markers are added, weak binding sites would occur. During rumen fermentation, dissociation would occur at the weak sites accounting for most of the observed marker movement (Crooker et al. 1982). Dissociation of strong binding sites can occur under acidic conditions, as found in the abomasum (Crooker et al. 1982).

The use of radioisotopes in digestion trials has gained considerable attention (Kennelly et al. 1980), however, the use of radioisotopes necessitates the complete collection and approved disposal of feeds and feces, as well as, eliminating experimental animals at the end of the experiment (Young et al. 1976). These problems can be eliminated by the inclusion of nonradioactive stable isotopes, which can be activated after the samples have been collected (Young et al. 1976). The basic principle of activation is that the stable isotope undergoes a nuclear transformation when immersed in an intense flux of neutrons to produce a radioactive nucleotide which emits radiation of characteristic

energies (Young et al. 1975).

Instrumental neutron activation analysis (INAA) to determine concentration of markers in feed and digesta provides a degree of sensitivity not available to other methods such as mass spectrometry and atomic absorption (Kennelly et al. 1980).

Marker Techniques

Marker technique will be considered in relation to the method of administration and sampling (Faichney 1975). Markers can be given continuously or as a pulse dose. Samples are taken from sections of the tract at successive times or the animal can be slaughtered and then the digesta collected (Faichney 1975, Warner 1981).

Continuous infusion with time sequence sampling requires that the animal be cannulated at different points along the GI tract (Warner 1981). The technique is used primarily to measure flow rate, however, volume and mean retention times for a particular section of the GI tract can be determined when samples are taken after infusion of markers has stopped (Faichney 1975).

CHAPTER 1

Measurement of the Effect of Rye and Wheat Fractions in Fluids at Various pH Values on Viscosity using an In Vitro Rumen Fluid System.

Introduction

According to Antoniou (1980) a comparison of soluble and insoluble pentosans would suggest that the water-soluble pentosans depressed overall chick performance slightly more than insoluble pentosans, and this effect could be related to the higher viscosity of soluble relative to insoluble pentosans. Lindas and D'Appolonia (1972), who worked with wheat, reported that acidic conditions caused hydrolysis of the sensitive arabinofuranose side chains, which resulted in the precipitation of the xylan backbone and a loss of viscosity of the soluble pentosans. According to Wilkie (1979) pentosans can be denatured through conformational changes induced by drying or in the presence of minerals like calcium or magnesium (Blake et al. 1970).

Dea and Rees (1973) studied the denaturation of sugarcane arabinoxylans and concluded that reduced viscosity of fluids was associated with the conversion from a random coil to an ordered ribbon-like conformation which caused aggregation and precipitation of the pentosans. Holas and Hampl (1973a) demonstrated that endogenous pentosanase and microbial degradation of rye pentosans was apparent during the leavening process of dough.

Antoniou (1980) fed ethanol boiled rye which was partially extracted of the soluble and insoluble pentosans and determined that this treatment did not improve chick performance compared to birds fed raw rye. Antoniou (1980) postulates that lack of chick performance may be attributed to inactivation of endogenous cereal pentosanases and microbial sterilization after extraction and therefore pentosan hydrolysis did not take place.

The results of most pentosan studies, (Lindas and D'Appolonia 1972, Antoniou 1980, Wilkie 1979, Blake et al. 1970) indicate that the majority of pentosans possess antigrowth activity and are not readily extracted from rye. Antoniou (1980) reports of the insoluble pentosans only those having a high concentration of arabinose (ratio of xylose to arabinose approaching 1:1) were able to cause growth depression in chicks and rats. The soluble pentosans are reported to have a ratio of xylose to arabinose of 1.39:1. Antoniou (1980) concludes that pentosans having a relatively high content of arabinose relative to xylose possesses antigrowth activity and significant antinutritional activity. Casier and Soenen (1967) have indicated that the antigrowth activity of pentosans could be attributed to their gummy properties, high viscosity in aqueous solutions and their ability to absorb large volumes of water with concomitant swelling. Casier and Soener (1967) also report non-specific nutrient binding capacity, reduced feed palatability and the associated high viscosity reduced nutrient digestibility. Ward (1982) reported that treating rye by soaking in water or HCl, and malting or adding NaCl generally improved the nutritional quality, whereas soaking in NaOH,

autoclaving or sprouting generally decreased the nutritional quality. Ward (1982) showed that rye flour extracted in 0.1N NaOH, had viscosity values 3.23 times higher than water extracted rye flour. The rye bran extracts showed less viscosity than rye flour extracts. However, the rye bran extracted in 0.1N NaOH showed 2.98 times more viscosity than the water extracted rye bran. The increase in viscosity from NaOH treatment may partially represent the extraction of previously insoluble pentosans. The insoluble pentosans are known to be very viscous in nature (Golenkov and Traubenberg 1966), are bound in the cell wall structure (McNeil et al. 1975), and are extracted with dilute alkali (Holas et al. 1971, Antoniou 1980). Ward (1982) has shown that the nutritional quality of rye flour was improved after soaking in 0.1N NaOH for 40 hours. Ward (1982) indicates that rye flour extracted in 0.1N NaOH at zero time is 63 percent more viscous than rye flour extracted in 0.1N NaOH for 40 hours. Aspinall and Greenwood (1962) have also reported a very slow degradation of rye flour arabinoxylan in dilute alkali.

Materials and Methods: Chapter #1

In order to study the effects of viscosity at three different pH values which simulate the physiological pH value found in the rumen abomasum and ileum, a fixed two way analysis of variance in vitro experiment was conducted. Multiple comparisons were conducted using orthogonal comparisons (Snedecor and Cochran 1980).

Rumen fluid was removed from a cannulated steer adjusted to a 60% concentrate 40% roughage ration, strained through 3 layers of cheese-

cloth and emptied into a 39 degrees celsius prewarmed thermos. The rumen fluid was taken to the laboratory and centrifuged at 4,000 x g at 39 degrees celsius for 5 minutes using a Sorvall Superspeed Centrifuge. There were six treatments, whole ground rye (WR), rye bran (RB), rye flour (RF), whole ground wheat (WW), wheat bran (WB) and wheat flour (WF) (Table 1.2). The rye contained less than .05% ergot. The bran and flour fractions were obtained commercially from Maple Leaf Mills, Winnipeg, Manitoba and ground through a 1 mm screen. Proximate analysis were carried out by the Standard AOAC (1980) methods and presented in Table 1.1. The three pH values tested were 6.5, 2.5 and 7.5. Four grams of each treatment ingredient was added to 40 ml of centrifuged warmed rumen fluid using 50 ml plastic in vitro centrifuge tubes and incubated at 39 degrees celsius. Each treatment was measured 3 times at each pH value with the initial pH adjusted to 6.5. After the end of 1 hour of incubation each tube was centrifuged at 39 degrees celsius at 4,000 x g for 5 minutes and 5 ml of fluid was aspirated and the viscosity was measured using a 5 ml prewarmed viscosity pipette. Viscosity was defined as outflowing time in seconds from a 5 ml viscosity pipette. Then the 5 ml was returned to the original tube, the centrifuge plug thoroughly mixed and the pH dropped using metaphosphoric acid to 2.5 in each tube. Again each tube was incubated at 39 degrees celsius for 1 hour and viscosity measured on the same 5 ml of centrifuged fluid and then returned to the original tube. NaOH was used as the final procedure to raise the pH from 2.5 to 7.5. Again each tube was incubated at 39 degrees celsius for one hour, centrifuged and 5 ml of rumen fluid

Table 1.1 Proximate analysis of whole rye (WR), rye bran (RB), rye flour (RF), whole wheat (WW), wheat bran (WB) and wheat flour (WF)

	Treatments (DM basis)					
	WR	RB	RF	WW	WB	WF
Total N %	2.21	2.75	1.87	2.64	2.72	2.13
Crude protein %	13.80	17.20	11.70	16.50	17.00	13.30
Fat %	1.68	3.30	1.38	1.90	4.40	1.29
Crude fibre %	2.60	7.50	0.58	2.80	11.60	Trace
Ash %	1.85	5.20	1.00	1.80	6.83	0.50
Nitrogen free extract	79.90	66.00	85.60	76.00	60.00	83.60

aspirated and viscosity measured and recorded. Distilled water was used as a control but was not included in the statistics.

Results

The results of the viscosity experiment (Fig. 1.0) indicate a significant interaction between treatments and pH ($P<0.01$) (Table 1.2). An orthogonal comparison of rye bran, wheat bran versus rye flour, wheat flour, indicates a significant difference ($P<0.01$) between the viscosity of flour and bran fraction (Appendix 2). The wheat bran fraction showed significantly higher viscosity across all pH values than did the wheat flour fractions. A comparison of rye flour versus wheat flour indicates a significantly higher viscosity value at all pH levels for rye flour than wheat flour ($P<0.01$). Both flour fractions decreased in viscosity as pH changed from 6.5 to 2.5 and then increased in viscosity as pH changed to 7.5. The rye bran and wheat bran viscosity values showed a significant difference ($P<0.01$) with rye bran showing a consistently higher value than the wheat bran fraction (Table 1.2 and Fig. 1.0). A comparison of whole rye versus whole wheat shows that whole rye has a significantly higher ($P<0.01$) viscosity in vitro value than whole wheat. In all cases the viscosity values at pH 2.5 and 7.5 for the rye was more viscous than the wheat fractions. The trend for rye flour, wheat flour, whole wheat and wheat bran was a decrease in viscosity from pH 6.5 to 2.5 and a general increase as the pH was raised to final pH 7.5. Only whole rye and rye bran showed consistent increases in viscosity as pH changed from 6.5 to 2.5 and finally back to 7.5.

Table 1.2 Average viscosities* of rye and wheat fractions in rumen fluid measured in vitro at different pH values (seconds)

pH	Treatment					
	WR	RB	RF	WW	WB	WF
6.5	123.8	139.6	163.7	116.3	125.0	116.7
2.5	158.0	160.3	143.2	114.3	115.3	107.7
7.5	173.1	168.0	159.2	125.3	148.8	117.1

SE treatment x pH interaction 12.50.

Standard error of pH equals 2.03.

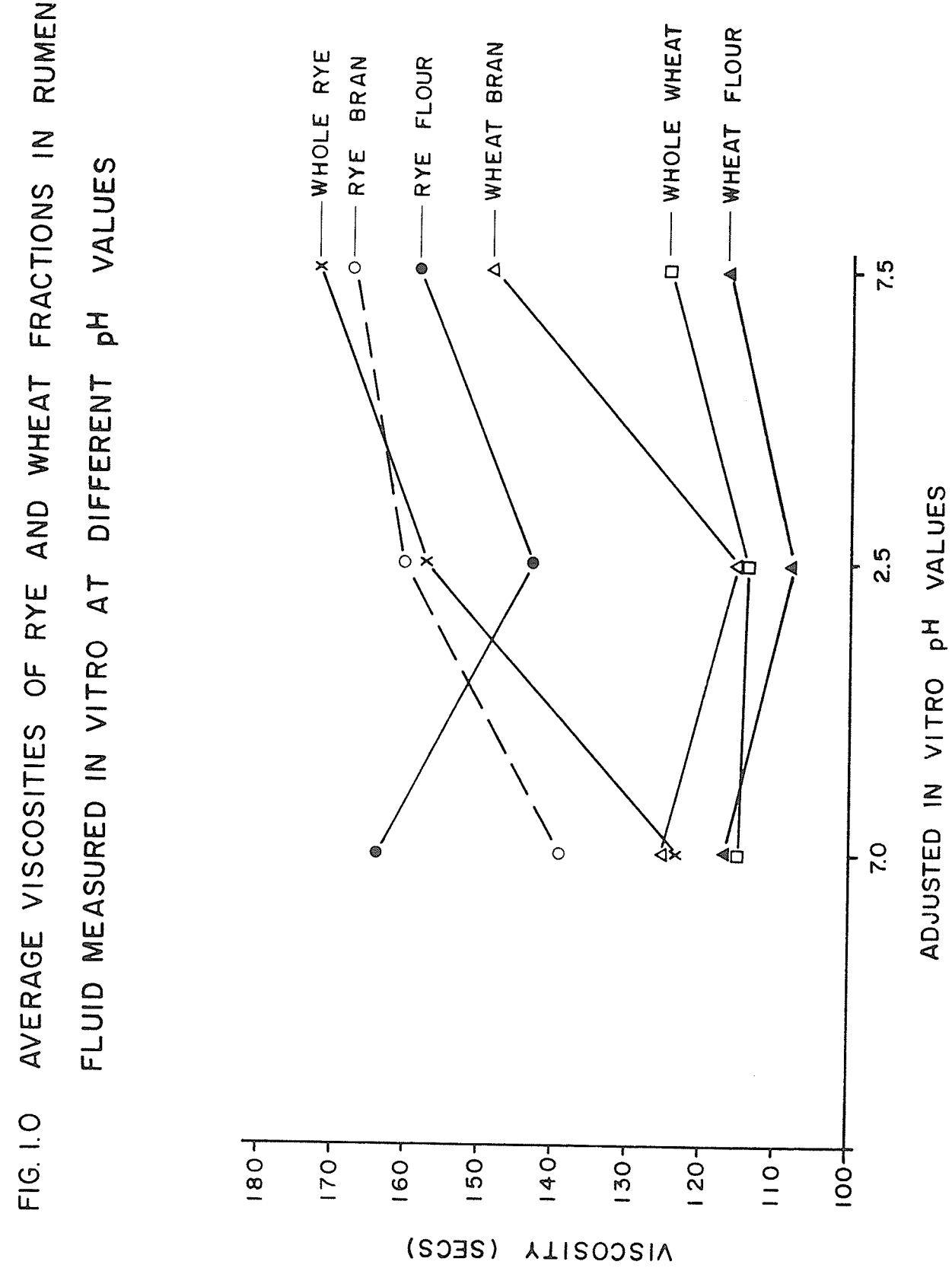
Standard error of treatments equals 4.16.

*Viscosity measured as outflowing time in second from a 5 ml viscosity pipette.

*See Appendix 2 for statistical analysis.

*Distilled water 83.0 seconds ±0.4.

FIG. 1.0 AVERAGE VISCOSITIES OF RYE AND WHEAT FRACTIONS IN RUMEN FLUID MEASURED IN VITRO AT DIFFERENT pH VALUES



Discussion

Data from Antoniou (1980), Neilson and Richards (1978), Holas et al. (1971) and Ward (1982) have shown that the nutritional value of rye can be improved by extracting with dilute acid at pH 2.0. They postulate that the extract contains hydrolyzed or partially hydrolyzed soluble pentosans. These extracts showed lower viscosity values than NaOH treated extracts. The cannulated steer from which the rumen fluid was taken for the viscosity experiment had an average rumen pH value of 6.5. After incubation for 1 hour the pH value was decreased to pH 2.5, using metaphosphoric acid to simulate the pH change and viscosity change as feed passed through the abomasum. All treatments showed a decrease in viscosity except for rye bran and whole rye which showed an increase. The most probable reason for this increase in viscosity in rye bran and whole rye is due to the acidic conditions hydrolyzing the fibre fractions and releasing the highly viscous insoluble pentosans associated with these fractions. A general trend of all treatments as the pH was raised from 2.5 to 7.5 using NaOH was for the viscosity to increase. As pointed out by several workers (McNeil et al. 1975, Holas et al. 1971, Antoniou 1980, Golenkov and Traubenberg 1966), sodium hydroxide or dilute alkali will aid in the extraction of the highly viscous insoluble pentosans thereby increasing the total viscosity of the aqueous solution. Therefore from the in vitro analysis when whole rye or whole wheat enter the rumen the viscosity of the solutions will be similar, however when the digesta enters the abomasum, the viscosity of whole rye would be significantly ($P<0.01$) more viscous than whole wheat, and as digesta

passes from the abomasum to the ileum where a basic pH occurs physiologically the whole rye will again be significantly more viscous than whole wheat ($P<0.01$). Antoniou (1980) has reported that pentosan can absorb large quantities of water. The adsorption of large quantities of water and the formation of a carbohydrate gel could result in lower intestinal digestion, increased volatile fatty acid formation from increased lower gastrointestinal fermentation from increased lower gastrointestinal fermentation and reduced net energy available to the ruminant (MacRae and Armstrong 1969, Topps et al. 1968, Orskov et al. 1971b, Karr et al. 1966).

CHAPTER 2

Feeding of Processed Rye Grain to Lactating Dairy Cattle

Introduction

Limited information is available on the feeding of processed rye (Secale cereale L) grain in lactating dairy cow rations. Sharma et al. (1981) fed young Holstein calves starter rations containing 0, 30, 60, 80% rye and 80% roasted rye replacing barley for 18 weeks. Average daily gain and feed consumption were similar during the first 6 weeks. Calves receiving 60% rye consumed significantly less feed ($P<0.05$) and gained slower ($P<0.05$) than the barley control and 80% roasted rye fed groups in the final 12 weeks. Feed efficiency was not affected ($P>0.05$). Roasting of rye appeared to improve the digestibilities of acid detergent fibre, ether extract, but reduced protein digestion in calves over 10 weeks of age.

Sharma et al. (1981) fed early lactating Holstein cows four diets containing 0, 25, 50 and 75% rolled rye in the grain mixtures replacing barley. The replacement of barley with rye in the grain mixture reduced ($P<0.05$) dry matter intake by lactating cows, but had no significant effect on milk production or milk composition.

Sharma et al. (1983) fed alkali treated rye 35 g NaOH/kg grain and rolled rye to lactating cows whereby rye constituted 60% of the concentrate. Alkali treated rye did not differ significantly from rolled rye with regard to dry matter intake, milk composition, milk yield or

digestibility of dry matter, crude protein and energy. Alkali treated rye tended to increase the molar percentage of acetic acid and decrease propionic acid although not significantly ($P>0.05$). Digestibility of whole barley grain has been improved by treatment with dilute sodium hydroxide solutions (Orskov and Greenhalgh 1977). Orskov et al. (1978) suggests that the deleterious effect of rolled barley or other cereal grains on digestion of cellulose in accompanying roughages, and consequently on dry matter intake, can be overcome by feeding either heat treated or sodium hydroxide treated whole grains.

Balch et al. (1952) and Balch et al. (1955) reported that the level of fat in milk could be lowered by low roughage diets and steam rolled or flaked grain. Storry and Rook (1965) indicate when cows were changed from a diet low in flaked maize to a diet high in flaked maize that milk fat dropped from 4 percent to 1.5 percent. Brown et al. (1970) found digestibility of various feed components and milk production to be similar for pelleted and for steam processed and rolled sorghum and barley based concentrates.

Cows fed steam rolled corn produced more milk ($P<0.05$) with a lower fat test ($P<0.01$) than cows fed cracked corn (Oklahoma Feed Manu. Assn. 1964). Comparable amounts of fat corrected milk were produced by both groups. The cattle fed the steam rolled corn tended to have higher dry matter intake than those fed cracked corn. Arizona workers (Schuh et al. 1971) concluded that pressure cooking was similar to steam processing and flaking sorghum grain for dairy calves. Schuh et al. (1970) reported that daily gain, feed efficiency and intake were not significantly

different for calves fed steam flaked barley or steam rolled barley. Morrill et al. (1970) found increased blood glucose levels after feeding expanded grain sorghum to calves but no significant increase on weight gains. Morrill et al. (1970) reports that steam rolling or heat processing grains for dairy calves did not tend to improve performance unless the control ration was unpalatable or not readily consumed in adequate quantities by the calves.

McNeill et al. (1971) found a significantly greater total digestion of starch by steers with reconstituted and steam flaked sorghum grain as compared to micronized and dry ground sorghum grain. Ruminal digestion of the starch was also significantly greater for the reconstituted and steam flaked grain as compared to dry ground and micronized grain. Ruminal digestion of starch from steam flaked grain was significantly greater than with reconstituted grain. Holmes et al. (1970) observed no effect of processing on overall starch disappearance from the gastrointestinal tract when pressure cooked sorghum grain was compared to sorghum grain which had been steamed at atmospheric pressure for 8 min. prior to rolling.

Materials and Methods

Eight lactating Holstein cows all beyond 2nd lactation (1-3 months postpartum) were randomly assigned to four concentrate mixtures in a 4 x 4 crossover design. The four concentrate mixtures contained either 60% dry rolled, extruded or roasted rye or 60% dry rolled barley (control)

in the grain mixtures (Table 2.1). The rye used in the concentrate mixtures contained less than .06% ergot. Each experimental period was 4 weeks in duration, including one week for changeover to new diets and three weeks for collection data. Grain and forage were fed in a 60:40 ratio (DM basis) throughout the experiment. The forage portion of the diet contained 2 kg long hay fed to each cow during the afternoon milking and the remainder of the forage (corn silage) was fed along with the grain in the morning. Feed intake, weighbacks and milk yields were recorded throughout the experiment.

Extrusion of rye grain was done in a Brady extruder at approximately 150 degrees celcius whereby the whole rye grain was converted into thin wafers. Roasting of the whole rye grain was done commercially using a Brink Meyer Open flame roaster. About 20% of the grains were popped and charred due to the open flame.

Ruminal fluid samples were collected in the third week of each trial via speculum and rubber stomach tube, to determine pH and ammonia nitrogen (N) levels. Immediately after collecting the samples, pH was measured in the strained rumen fluid with a glass portable pH meter (Photo volt model #126). A few drops of mercuric chloride solution was added to stop fermentation. Rumen fluid samples were centrifuged, with the supernatant liquor being transferred into small vials and stored at -20 degrees celsius until further analysis. Ammonia N in rumen fluid was analyzed with a specific ion (ammonia) electrode (Orion Research Model 95-10, Cambridge, MA). Total feces was collected daily on plastic sheets for 5 days in the last week of each period for determination of apparent digestibility of experimental diets. Urine and feces were

Table 2.1 Ingredients and chemical composition of experimental concentrates fed to lactating Holstein cows (Experiment 2)

	Treatments			
Ingredients	Dry rolled barley	Extruded rye	Dry rolled rye	Roasted rye rye
Rolled barley	60	-	-	-
Rolled rye	-	-	60	-
Extruded rye	-	60	-	-
Roasted rye	-	-	-	60
Oats	15.0	15.0	15.0	15.0
Soybean meal	15.5	15.5	15.5	15.5
Molasses	3.0	3.0	3.0	3.0
Salt	1.0	1.0	1.0	1.0
Dicalcium phosphate	1.0	1.0	1.0	1.0
Limestone	1.0	1.0	1.0	1.0
Tallow	3.0	3.0	3.0	3.0
Premix*	0.5	0.5	0.5	0.5

*Premix - vitamin A-2 x 10^6 IU, vitamin D3-1 x 10^6 IU, vitamin E-5 x 10^3 IU, 908 g MgO, 25 g ZnO, 25 g MnO·H2O, 2.6 g KI, 50 mg, cobalt chloride per 500 kg mixed grain.

separated by using a urinary indwelling catheter connected to a plastic jar containing toluene as a preservative.

Tail vein blood samples were collected at the same time rumen samples were taken. The blood was removed from each animal into heparinized vacutainers, centrifuged and analyzed for glucose and urea nitrogen according to standard Technicon methods with an auto analyzer.

Dry matter in feed and fecal samples was determined by drying at 60 degrees celsius to a constant weight in a forced air oven. Gross energy in feed and feces was determined by a Parr adiabatic oxygen bomb calorimeter. Crude protein and ether extract were analyzed according to methods of AOAC (1975) standard procedures. Acid detergent fibre and acid detergent insoluble nitrogen were estimated according to the nethods of Goering and Van Soest (1970). The standard error for dry matter intake, milk constituent, blood data and rumen pH were calculated using 8 animals while the standard error for the digestibility data was calculated using 4 animals.

Data were subjected to analysis of variance and Duncan's multiple range test was used to detect significant differences among treatment means. Each Latin square had a missing value due to death of one animal in period 4 and therefore was calculated according to the equation.

$$X = \frac{t\,(n\,\bar{Y}i.. + \bar{Y}.j. + \bar{Y}..k - 2\,\bar{Y}...)}{(t-1)\,(nt-2)}$$

where

t = number of periods = number of treatments.

n = number of observations per treatment cycle.

n is some multiple of t and nt = number of observations per column.

nt = total number of observations/column.

$Y_{i..}^{'}$ = sum of items in the row with missing value.

$Y_{.j.}^{'}$ = sum of items in the column with missing value.

$Y_{..k}^{'}$ = sum of items in the treatment with missing value.

$Y_{...}^{'}$ = sum of all observations.

(See Appendix #1 for calculation details).

Results

At the start of the experiment, the grain and forage ratio was 60:40 on a DM basis, with the proximate analysis of the experimental ingredients given in Table 2.2. Total DM intake was significantly ($P<0.05$) higher for the cows receiving the barley control diet than those fed the three rye diets (Table 2.3). Roasting or extruding of rye grain slightly improved the daily DM consumption by the dairy cows as compared with the dry rolling of the grains. No significant ($P>0.05$) differences were observed in daily milk production, 4% fat correct milk and milk composition of the cows receiving the four experimental diets. However, daily milk production and 4% FCM tended to be lower for the cows fed the three rye diets as compared to the barley control cows. Milk fat content was not significantly ($P>0.05$) depressed for the cows receiving the extruded rye diet compared with the other three treatments (Table 2.3). Other milk constituents were not affected by feeding processed

Table 2.2 Chemical composition of experimental ingredients (% DM)

	Dry rolled barley	Extruded rye	Dry rolled rye	Roasted rye	Hay	Corn silage
Crude protein	18.9	17.1	18.3	17.0	13.6	8.0
Ether extract	4.9	4.6	5.6	5.4	1.5	6.7
Acid detergent fibre	9.4	5.6	6.9	6.2	40.9	33.5
Energy Kcal/kg	4.50	4.55	4.52	4.51	4.49	4.44
Calcium	1.04	0.81	1.04	0.93	1.09	0.22
Phosphorus	0.81	0.72	0.84	0.86	0.14	0.24

Table 2.3 Effect of feeding processed rye grain to lactating Holstein cows on feed intake, milk yield and milk composition (Experiment 2)

	Treatments				
Parameters	Dry rolled barley	Extruded rye	Dry rolled rye	Roasted rye	SEM
DM intake (kg/day)	20.0[a]	17.7[b]	16.9[b]	17.9[b]	0.4
Milk yield and composition					
Milk yield (kg/day)	25.8	24.3	22.4	23.6	1.08
4% FCM (kg/day)	23.7	21.9	20.8	20.1	1.2
Milk fat (%)	3.69	3.18	3.72	3.47	0.11
Milk protein (%)	3.19	3.31	3.25	3.24	0.06
Lactose (%)	4.65	4.55	4.63	4.61	0.05
Solids - not fat (%)	8.91	8.84	8.88	8.83	0.05

[a,b]Means in a row with different letters are significant at ($P<0.05$).

rye in the concentrate mixtures to lactating Holstein cows.

Apparent digestibilities of DM, CP, EE, and energy were not different ($P>0.05$) among the four treatments (Table 2.4). However, acid-detergent fibre digestibility was significantly ($P<0.05$) higher for the cows fed rolled barley (control) diet than those cows receiving the three processed rye diets. Fecal dry matter content was slightly lower for the cows receiving the rye diets than the barley fed cows, however, the differences were not significant ($P>0.05$) among the treatments (Table 2.4). Ruminal pH, blood plasma urea N and glucose levels were not different ($P>0.05$) among the four treatments (Table 2.4).

Discussion

Studies conducted by Winter (1973) and Winter (1975) concluded that ergot free rye can be included up to 80% in the ruminant ration with no significant reduction in intake. Sharma et al. (1983) concluded that alkali treated rye increased the consumption of rye non-significantly by 13% compared to untreated rye when fed to lactating dairy cows. Sharma et al. (1981) found that the dry matter intake was reduced ($P<0.05$) when lactating dairy cows were fed 25, 50 or 75% rye in their grain mixture compared to barley. However, no significant differences were determined on production parameters of rye fed dairy cows. Sharma et al. (1981) measured the weight gain and feed consumption of weaned calves from 7-18 weeks of age fed either 0, 30, 60, 80% dry rolled or 80% roasted rye. The dry matter intake and ADG were different ($P<0.05$) among the five dietary treatments. Calves receiving the 60% rye diet

Table 2.4 Effect of feeding processed rye grain diets to lactating Holstein cows on apparent digestibility of nutrients, blood plasma urea N, glucose levels, rumen pH and fecal dry matter (Experiment 2)

Parameters	Dry rolled barley	Extruded rye	Dry rolled rye	Roasted rye	SEM
Apparent digestibility (%)					
Dry matter	86.55	86.98	86.40	85.52	0.35
Crude protein	89.43	86.87	87.02	85.75	0.89
ADF	75.07[a]	71.63[b]	72.44[b]	70.76[b]	0.52
Ether extract	92.31	90.07	92.57	91.60	0.88
Energy	86.64	86.28	86.24	85.25	0.29
Fecal DM (%)	16.88	15.26	15.89	16.00	0.40
Blood constituents					
Urea N (mg/100 ml)	24.36	19.28	21.88	19.11	1.49
Glucose (mg/100 ml)	80.06	83.12	84.68	78.37	2.52
Rumen pH	6.98	6.56	6.70	6.73	0.11

[a,b]Means in a row with different letters are significant at ($P<0.05$).

consumed less ($P<0.05$) feed and had less weight gain compared with those fed the barley control (0% rye) or 80% roasted rye diets and similar amounts to those receiving the 30 and 80% rye diets. Sharma et al. (1981) shows regression analysis of average daily gain was negatively correlated to rye content in calf diets ($r = -0.911$).

The literature (Winter 1983) appears to indicate that in the beef studies, using up to 80% rye in the ration, there was no reduction in intake. However the dairy data indicates that using up to 75% rye in the grain mix (Sharma 1981) results in a significant reduction in intake but no differences in milk yield compared to dry rolled barley. At higher levels of milk production the intake effect may become more critical. The difference in the beef and dairy responses could be a function of the absolute amount eaten by the dairy cow resulting in a highly viscous rumen. The finishing beef animal will consume 2.2-2.4% of body weight (Orskov 1982) while the mature dairy cow in early lactation will consume 3.7% of body weight in dry matter (Sharma 1981).

Factors which could influence appetite and growth rate in young animals include the soluble non-starch polysaccharides especially the pentosans (Baker 1931), pectins (Wagner and Thomas 1977b) or pectin-like compounds (Misir and Marquardt 1978b). Misir and Marquardt (1978c) indicated that rye contains at least two detrimental factors, an appetite-depressing factor located in the bran and a growth depressing factor in all fractions of rye (bran, flour and middlings). The data (Table 2.3), shows a significant difference ($P<0.05$) in dry matter intake for dairy cattle receiving the rye based experimental rations and a decrease ($P<0.05$) in acid detergent fibre digestibilities for the rye fed cattle

(Table 2.4). Other digestibilities of dry matter, crude protein and energy for the rye rations tended to be lower compared to the barley control ration. The nutrient digestibilities appear to be high. All data were checked and no explanation is apparent. Sharma et al. (1981) showed no differences ($P>0.05$) in digestibilities of dry matter, crude protein, acid detergent fibre fat and energy for rye fed calves, however, calves fed 60% and 80% rye ration tended to show lower digestibilities of nutrients.

Part of the reason for variability in rye experiments could be because of variety and environmental conditions. Drews and Seibel (1976) have shown that the level of the soluble pentosans of rye can increase above 2.5% while their viscosity decreases. Drews and Seibel (1976) also report that in very dry years the levels of soluble pentosans can be as low as 1.5% but they are much more viscous in nature. Therefore a large variation of total and soluble pentosans can exist and depends on environmental conditions.

Other reasons for variability could be due to microbial hemicelluloses (Leatherwood 1973) and endogenous plant pentosanases (Drews 1970). Data from Drews (1970) show that as the pH of an aqueous solution approaches 4.9 the pentosan solubility is reduced and pentosanase activity is enhanced especially as the temperature approaches 40 degrees celsius. Reduced acid detergent fibre digestibility could be due to the fact that rumen pH normally ranges around 6.5, thereby maintaining a very viscous fluid, and the endogenous rye pentosanases are not functioning at maximum potential because of the high pH.

The tendency for reduced digestibilities of rye grains could be due to the fact that pentosans have an ability to adsorb large quantities of water and swell forming a gel (Antoniou 1980, Holas et al. 1971, Rees 1971). Polysaccharide gels are essentially carboxylic cation (weak acid) exchangers (Mod 1981). The monovalent ions such as potassium and sodium are more strongly held than the divalent ions such as calcium and magnesium (Antoniou 1980, Mod et al. 1981). When pentosans of rye enter the small intestine of the ruminant they are exposed to increasing pH values, which will increase the viscosity (McNeill et al. 1975, Golenkov and Traubenberg 1966, Holas et al. 1971). The polysaccharide gels formed at the ileal-cecal junction could be responsible for increased viscosity in this gastrointestinal compartment which bind nutrients such as monovalent and divalent minerals as well as protein through tyrosine-ferulic acid binding (Neukom 1976) so that their excretion is increased and digestibility reduced. Painter and Neukom (1968) have shown that wheat flour pentosan will undergo a gelation reaction but because of the high ash content will cause spontaneous breakdown of the gel. Perhaps feeding a slightly higher mineral content in diets for ruminants would result in reduced viscosity of pentosans when ingested.

Under the conditions of this experiment including rye as 60% of the grain mixture for lactating dairy cattle resulted in a significant ($P<0.05$) reduction in feed intake. Although milk yield was not affected by diet ($P>0.05$) there was a trend for lower milk production with the dry rolled rye diet.

CHAPTER 3

Determination of the effect of rye bran and rye flour in comparison to wheat bran and wheat flour on gastrointestinal flow and compartmental digestibility of nutrients.

Introduction

In the past, feeding of rye to dairy cattle has been avoided not because of low nutritive value as compared to other cereal grains but because of low palatability (Sharma et al. 1981). The presence of ergot alkaloids influence the palatability of the rye grain and consequently have an appetite reducing effect (Burfening 1973, Ingalls and Phillips 1971, Dinusson et al. 1971, McKeon and Eagen 1971).

Winter (1973) and Winter (1975) concluded that ergot free rye can be included up to 80% in the ruminant ration with no significant reduction in intake. Sharma et al. (1981) found that the dry matter intake was reduced ($P<0.05$) when lactating dairy cows were fed 25, 50 and 75% rye in their grain mixture compared to barley. However, no significant differences were determined on performance of rye fed dairy cows. Sharma et al. (1983) concluded that alkali treated rye increased the consumption of rye non-significantly by 13% compared to untreated rye when fed to lactating dairy cows.

Misir and Marquardt (1978c) indicate that rye contains an appetite depressing factor in the bran, and a growth depressing factor in all fractions when fed to chicks. The depressed performance of chicks fed

on rye has been attributed to the presence of highly viscous pentosans in rye (Antoniou and Marquardt 1981a, Ward and Marquardt 1981) that depress retention of most nutrients (Marquardt et al. 1979, Antoniou et al. 1980). Antoniou and Marquardt (1981a) have postulated a direct effect of gut viscosity, however there is considerable evidence to suggest that the effect may be mediated in part by excessive microbial activity in the intestines of chickens fed rye (Campbell et al. 1983). MacAuliffe and McGinnis (1971) and Marquardt et al. (1979) have demonstrated that growth rate, nutrient retention and bone mineralization of chicks fed on rye are considerably improved by addition of dietary antibiotics. The bacterial species most often implicated in the antibiotic response of chicks is *Streptococcus faecalis* (Huhtanen and Pensack 1965, Elyssen and De Somer 1967). Excessive bacterial deconjugation of the bile salts taurocholate and taurochenodeoxycholate (Coates et al. 1981), has been implicated with the resultant steatorrhea seen in rye fed birds (Kim et al. 1966, Coates et al. 1981, Campbell et al. 1983a).

The objective of this experiment was to determine if ergot free rye bran and rye flour have any major effect in the gastrointestinal tract of the ruminant with respect to nutrient flow rates and nutrient digestibility.

Experimental Design

Four Holstein steers averaging 250 kg in weight, were fistulated in the rumen abomasum and terminal ileum (approximately 10 cm proximally from ileal-cecal junction). Steers were between 6-8 months of age at

the beginning of the experiment. The abomasal and ileal fistulas were fitted with flexible silicon T-shaped cannulas. The flexible silicon tubing was purchased from New Brunswick Scientific Inc., Edison, New Jersey. Each T-shaped cannula measured 14 cm along the horizontal base, and 14 cm on the vertical barrel extension. The horizontal and vertical barrel portions were adhered together using silastic adhesive 734 RTV Dow Corning and allowed 96 hours to set. Plastisol plugs 15 cm long were prepared to prevent leakage and accumulation of material in the barrel of each cannula. The rumen fistulas were each fitted with a standard Bar Diamond flexible cannula (Bar Diamond, Inc., Parma, Idaho). Cattle were weighed at the end of each experimental period and average daily gain was calculated and recorded.

Four test diets were fed to steers, in a 4 x 4 Latin square design. The base of each diet consisted of combinations of rye bran, rye flour, wheat bran and wheat flour (Table 3.1, 3.2). The combinations of flour and bran were incorporated into complete pelleted rations containing approximately 50% flour and 33% bran. The diets consisted of (1) rye bran, rye flour (RBRF) (2) rye bran, wheat flour (RBWF) (3) wheat bran, rye flour (WBRF) and (4) wheat bran, wheat flour (WBWF). Analysis of the diets are given in Table 3.2. All diets contained 8 - 10% Alfa Floc B-N-B 40 grade cellulose added as a fibre source and 1% sodium bicarbonate buffer. Each experimental period was 28 days long, beginning with a 7 day adjustment period where cattle were gradually switched from one diet to another. During this period of time cattle were fed twice daily in individual stalls. On day 8 cattle were moved from individual stalls to raised metabolism crates and fed continuously using four automatic

Table 3.1 Composition of rye and wheat fraction rations fed to cannulated Holstein steers for measurement of gastrointestinal nutrient flow rates

	Treatments			
Diet	RBRF	RBWF	WBRF	WBWF
Rye bran	334	333		
Rye flour	500		512	
Wheat bran			342	342
Wheat flour		500		512
Alfa floc*	99	95	86	83.5
Sodium bicarbonate	10	10	10	10
Molasses	29	29	29	29
Dyna-K	6.0	10		1.5
Limestone	7.0	5.0	6.0	4.0
Dical	5.0	8.0	5.0	8.0
Salt	5.0	5.0	5.0	5.0
Vitamin premix+	5.0	5.0	5.0	5.0
	1000	1000	1000	1000

#Each ration also had 25 ppm DyC13.6H20 added as a rare earth marker in a separate premix.

+Provided per kilogram of diet: 3500 IU vitamin A, 1750 IU vitamin D, 10 IU vitamin E, 44 mg ZnO, 45 mg MnO.H20, 0.3 mg CoC12, 1.6 mg KI, 116 g MgO.

*Alfa Floc - B-N-B -40 grade
Lee Chemical Company, Toronto.

Table 3.2 Nutrient analysis of rye and wheat fraction rations fed to cannulated steers for measurement of gastrointestinal nutrient flow rate. (% DM)

	RBRF	RBWF	WBRF	WBWF
Crude protein %	9.76	13.70	11.31	13.52
Ether extract	1.92	1.33	2.4	1.54
ADF	9.7	8.5	12.74	11.40
ADF-N	0.54	0.52	0.46	0.48
Sodium %	0.51	0.45	0.52	0.55
Potassium %	0.87	0.93	0.79	0.79
Magnesium %	0.26	0.27	0.36	0.34
Energy Kcal/kg	3.84	3.84	3.93	3.90
Xylose %	5.97	5.62	6.32	5.97
Arabinose %	2.90	2.88	4.20	3.80
Lysine %	0.35	0.31	0.39	0.36
Methionine %	0.17	0.24	0.22	0.24

belt conveyors. The belt conveyor was set to operate for one minute every 45 minutes and would deliver approximately 208 grams of feed each running minute. All cattle received 2% of their body weight in dry feed per day. Each animal had access to fresh clean water at all times. Each ration was sampled daily for the last six days of each period and composited for chemical analysis. There were no feed refusals at any time throughout the entire experiment.

Nutrient digestibility and flow parameters through the rumen, abomasum, ileum and feces were assessed using Dysprosium (Dy), a particulate marker, added as 25 ppm DyCl3.6H2O (ICN Pharmaceuticals, Plainview N.Y.) according to the methods outlined by Kennelly et al. (1980).

The marker DyCl3.6H2O was ground through a 1 mm screen. One to two kg of the same constituent of the ration was ground in a similar manner to the same mesh size as the DyCl3.6H2O powder. Twenty-five grams of DyCl3.6H2O was mixed with 1 litre of water, heated gently and stirred continuously until all crystals were dissolved. Then the litre of liquid was added to 1 kg of ground ration. The two components were mixed thoroughly and dried to a constant weight. Then the premix was washed with 6 litres of water and redried. Then the prepared premix was added to the experimental diet.

An attempt was made to measure fluid flow using Co-EDTA according to Kennelly et al. (1982). Instrumental neutron activation analysis resulted in large discrepancies from expected concentration of cobalt in the fluids under continuous infusion. Kennelly et al. (1982) indicates that Cr-EDTA may be more stable in the gastrointestinal tract.

Materials and Methods

Calculation of digesta flow through the gastrointestinal tract

The digesta flow parameters were measured using the continuous infusion, time sequence sampling method as described by Faichney (1975).

Hydrated dyprosium chloride added to the diets as DyCl3.6H2O was used to determine the flow of solid digesta through the gastrointestinal tract using the following equation:

$$\text{Dry matter (flow)} = \frac{\text{Dry matter intake/day} \times \frac{\text{Concentration of Dy}}{\text{g of dietary DM}}}{\frac{\text{Concentration of Dy}}{\text{g of digesta DM}}}$$

The flow of all other nutrients, such as electrolytes, amino acids and sugars at each cannulated site, was determined by multiplying the concentration of nutrient in the digesta at each sampling site times the flow of digesta dry matter.

Digestibility of Nutrients using Dysprosium

Beginning on day 15 through day 22 grab samples of feces were collected 3x daily via the anal route from all steers in the metabolism crates. The fecal material was weighed and pH recorded according to Russell et al. (1981) and frozen. Urine for N balance was also collected but not used because of contamination in the collection bottles from

leaking rumen cannulas when the animals laid down. The daily fecal samples were composited and subsampled at the end of each experimental period. After subsampling feces was freeze dried, ground and stored for chemical analysis. Digestibility of nutrients was calculated using the indicator ratio method (Kennelly et al. 1980).

Compartmental Digesta Collection

Beginning on day 23 of each experimental period rumen, abomasal, ileal and fecal samples were collected. Samples were collected 3 times per day starting at 8:00 A.M., 4:00 P.M. and 12:00 midnight for 5 days. Beginning with the feces (via anal route collection), then ileal, abomasal and rumen (cannula collection) the samples were frozen and stored for compositing and sub-sampling later. Approximately 400 ml of rumen digesta was collected in four 100 ml plastic disposable containers at each collection schedule. Abomasal digesta was collected in three x 100 ml plastic containers at each collection schedule. No absolute amount of ileal digesta was collected at each collection schedule because of the variable flow of material in the compartment. All samples were subjected to immediate pH testing composited and then frozen. Total fecal collection was not used because of significant fluid losses from the rumen, abomasal and ileal cannulae which resulted in inaccurate fecal excretion weights. All rumen volumes were determined by manual emptying and sub-sampled so total rumen dry matter could be calculated. This value was equated with abomasal flow of dry matter to calculate rumen turnover.

Chemical Analysis

A 100 ml subsample of all composites was freeze dried to determine total dry matter. Other digesta samples from sub-sampling were centrifuged using a Sorvall Superspeed RC2-B Automatic Refrigerated Centrifuge at 4,000 x g for 5 minutes. Five hundred ml of each liquid phase and three x 100 g of each particulate fraction was freeze dried. All samples were ground and stored for chemical analysis after freeze drying. Viscosity of rumen, abomasal and ileal fluid was determined from centrifuged fluid samples (4,000 x g for 5 minutes) using a 5 ml pre-warmed viscosity pipette and recorded.

Volatile fatty acids (VFA) in the rumen, abomasal and ileal fluid were determined by gas chromatography according to the methods of Erwin et al. (1961). Rumen, abomasal and ileal samples were analyzed for ammonia level using an ammonia electrode Model 95-10, Orion Research, Cambridge, MA.

Lactic acid analysis on fluids was carried out using a Gilford 240 narrowband width spectrophotometer set at Ultraviolet 340 nm. Lactic acid is converted to pyruvic acid by added lactate dehydrogenase resulting in the reduction of an equivalent amount of NAD. The increase in absorbance at 340 nm is proportional to lactic acid concentration (Sigma Chemical, St. Louis, MO).

All viscosity data were determined by a viscosity pipette and all rumen volume data were determined by manual emptying.

Dry matter (DM), ether extract (EE), and total nitrogen on feed, compartmental particulate samples, compartmental fluid samples and feces

was determined according to the Association of Official Analytical Chemists (AOAC) (1980). Acid detergent fibre (ADF) and acid detergent fibre nitrogen (ADF-N) was determined according to the methods of Goering and Van Soest (1970). Gross energy was determined by Parr Adiabatic Oxygen Bomb Calorimetry. The four rations, and particulate phases of the fecal, ileal, abomasal and ruminal digesta were acid hydrolyzed and analyzed for amino acids and diaminopimelic acid (DAPA) el Shazley et al. (1966), using a Beckman Model No. 116/119 Amino Acid Analyzer with sample injector port.

Analysis of Na and K was determined using atomic absorption spectrophotometry.

One gram samples of feed and the freeze dried solid phases of rumen, abomasal, ileal and feces were sent to the Slowpoke facility at the University of Alberta, where concentrations of metastable dysprosium (Dym) were estimated using instrumental neutron activation analysis (INAA) (Kennelly et al. 1980). Samples were irradiated at a neutron flux of 10^{11} $n/cm^2/sec$ for 45 sec allowed to cool for 30 sec and were counted for 60 sec using a (Geli) gamma ray detector coupled with a 4096 channel analyzer (Nuclear Data Inc., Shaumberg, ILL). The radiation released from 165 Dym emits at an energy level of 108 Kev and has a half life of 75.42 with a standard error of 0.36 secs.

Gas liquid chromatographic analysis

This analysis was to measure xylose and arabinose and was similar to the procedures reported by Antoniou (1980). The samples to be

analyzed (10 or 20 mg) were weighed into pyrex hydrolysis tubes. My-inositol (1 mg) and/or erythritol (1 mg) were added as internal standards. Sulfuric acid (1.75 ml of 0.571 N) was added to each tube containing digesta samples and to tubes containing standard amounts of glucose, galactose, mannose, arabinose and xylose (see below for preparation of standards). The samples were autoclaved at 123 degrees celsius for exactly 20 minutes, removed and immediately cooled at room temperature. The samples were then neutralized with 0.4 g of barium carbonate and then centrifuged at 20,000 x g for 10 minutes. The samples were decanted into hydrolysis tubes and 10 mg of sodium borohydride in 0.5 ml of 1 N NH4OH (made fresh just before use) was added and the samples allowed to stand for 16 hours at 5 degrees celsius. Glacial acetic acid was then added dropwise until gassing stopped and the samples were evaporated to dryness. Methanol (1 ml) was added to the dried sample and the sample redried. This was repeated two additional times. Acetic anhydride (1 ml) was added and the samples were heated in an oven at 96 degrees celsius for 16-18 hours. The samples were evaporated to dryness in the presence of 1 ml portions of toluene. This was repeated three times after which the samples were stored dry at -20 degrees celsius until analyzed. Just before analysis the samples were dissolved in approximately 0.5 ml of ethyl acetate and were filtered through a teflon milipore filter (type FH, Millipore Corp., Bedford, Massachusettes). The filter was washed with 0.1 ml portions of ethyl acetate which were combined with the original filtrate. The samples were made up to exactly 1 ml with ethyl acetate and immediately injected into the gas-liquid

chromatograph (Varian Aerograph Series 1200). The alditol acetates were separated on a glass column (180 x 0.2 cm) containing 3% Silar (10 c polsilozan polymer containing phenyl and cyanoalkyl functional groups, Applied Science Labs, State College, PA) coated on 100/120 mesh Chromosorb W.H.P. (Chromatographic Specialties, Brockville, Ontario). The peaks were detected by a hydrogen flame ionization detector. Column temperature for the Hewlett Packard G.L.C. was programmed between 150-210 degrees celsius with 2 degrees celsius/minute increase in temperature and thereafter held at 210 degrees celsius until the final peak was eluted. Injection post temperature was 215 degrees celsius and detector temperature was 230 degrees celsius. Gas flow rates (ml/min) were 46 for hydrogen, 32 for nitrogen and 150 for air. Electrometer attenuation was set at 1 with a range of 10^{-11} amps/m.u. Peak areas were calculated either by integration (Columbia Scientific Industries, Model 38) or by a manual method (peak height x peak width at 1/2 peak height). Standards for G.L.C. were prepared as follows: 4 mg/ml of xylose, arabinose, glucose, mannose, and galactose were dissolved in water. The samples (0.25 ml, 0.50, 0.75 and 1 ml) were placed in hydrolysis tubes and treated by the same procedure as the unknown samples above except they were not hydrolyzed. The procedure was initiated at the sodium borohydride step.

Statistical analysis

All data was subjected to Latin square analysis of variance according to Snedecor and Cochran (1980). Then all flow and fluid data was

subjected to randomized complete block analysis using the last period from each latin square to test treatments across digestive tract locations plus any interactive effects because the flow data in the last period contained homogeneity of variance. This was not true in other periods possibly because of cannula leakage. Treatment means and location means were tested using the Student Neuman Keuls S.N.K. multiple range test to determine significant differences (Snedecor and Cochran 1980).

Results and Discussion

Nitrogen retention

It was not possible to measure nitrogen retention because of cannulae leakage which resulted in digesta fluid contamination of urine samples in some cases.

Flow of digesta

The mean percentage recovery of dysprosium on the feces of Holstein steers was 92.98 with a standard error of 2.17 for the four treatments. The recovery of dysprosium did not differ among the treatments.

Dietary intake was set at 2% body weight and did not differ significantly among treatments (Table 3.3) with the average intake of dry matter being 4.94 kg/day (SEM .075). Variable response in intake has been reported when rye was included in the diet. Winter (1973) has reported that up to 80% rye may be included in the grain ration of growing steers with no significant reduction in intake or feed efficiency

when compared to barley. However, Goings et al. (1976) has shown that dairy cattle fed diets containing 10, 20, 30 or 40% rye had proportional decreases in feed intake. Sharma et al. (1981) fed dairy calves 60 to 80% rye diets and showed reduced feed intake and digestibilities especially in the higher percentage rye diets. Sharma et al. (1981) in another experiment showed significantly ($P<0.05$) reduced feed intake in dairy cows fed rye in their grain allotment at 25, 50 and 75% of the grain mixture. Orskov (1978) and Sharma et al. (1983) have shown a non-significant increase in feed intake for cattle fed alkali treated rye. The trend of dry matter flow measured at rumen, abomasum, ileum and feces (Table 3.3) indicates that there is a significant difference ($P<0.01$) in flow between rumen and abomasum among all treatments while the flow between ileum and feces did not differ significantly among any treatment. Throughout the thesis, rumen flow in g/day has been used. This might better be expressed as % of intake rather than flow rate. Steers receiving RBWF had the lowest flow of rumen dry matter at 1857 g/day and differed significantly from the other three treatments ($P<0.01$) all having flow rates greater than 2130 g/day (Table 3.3). There was no difference among treatments regarding excretion of fecal dry matter ($P<0.01$).

The flow of dry matter as presented in Table 3.3, indicated that significantly more dry matter was flowing through the ileum for diets containing rye flour. Since the dry matter flow from the ileum to the feces is not significantly different ($P<0.01$) for any treatment, rye bran or rye flour does not appear to contribute to significant large bowel

Table 3.3 Dry matter intake and flow of dry matter through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, kg/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	4.947^{a}	4.947^{a}	4.935^{a}	4.917^{a}
Rumen	2.297^{BAb}	1.857^{Cb}	2.422^{Ab}	2.130^{Bb}
Abomasum	1.639^{Bc}	1.40^{Dc}	1.779^{Ac}	1.567
Ileum	1.195^{Bd}	1.052^{Dd}	1.401^{Ad}	1.065^{Ce}
Feces	$1.261^{A}d$	1.047^{Ae}	1.373^{Ad}	1.222^{Ad}

The standard error of diet equals .075 g.

The standard error of locations equals .067 g.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.4 Intake and flow of energy through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, Mcal/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	19.057^{a}	18.992^{a}	19.392^{a}	19.207^{a}
Rumen	10.443^{Bb}	8.522^{Db}	11.492^{Ab}	9.681^{Cb}
Abomasum	8.352^{Ac}	7.062^{Cc}	8.381^{Ac}	7.641^{Bc}
Ileum	5.267^{Ad}	4.577^{Bd}	6.072^{Ad}	4.602^{Bd}
Feces	5.731^{Ad}	4.661^{Ad}	6.041^{Ad}	5.952^{Ad}

The standard error of diet equals 0.273.

The standard error of locations equals 0.305.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

FIG. 2.0 DIGESTIBILITY OF DRY MATTER MEASURED USING DYSPROSIUM AS AN INERT MARKER RELATIVE TO INTAKE

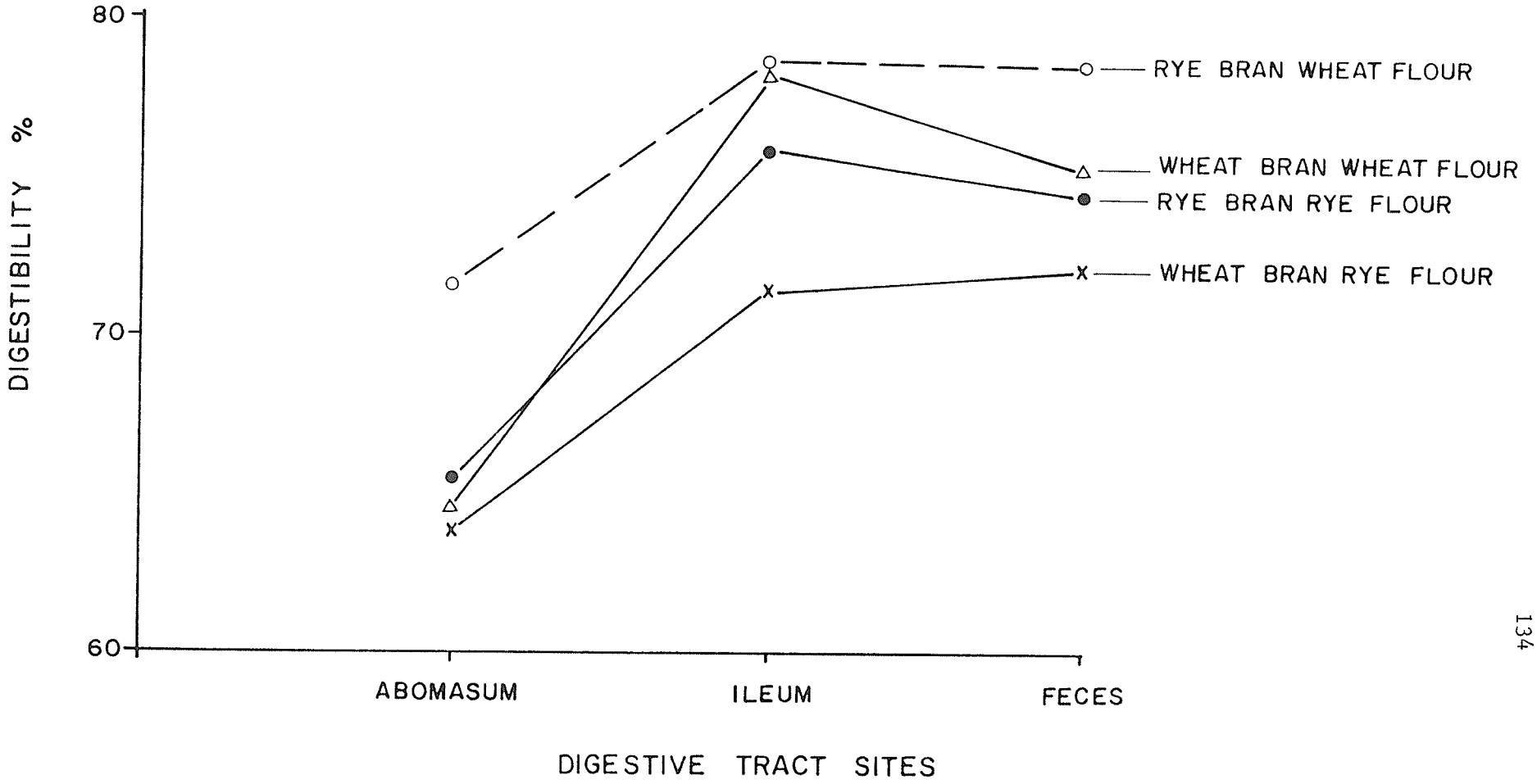


Table 3.5 Intake and flow of protein through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	423.80^{a}	677.79^{a}	502.40^{a}	664.94^{a}
Rumen	497.54^{Bb}	463.57^{Db}	534.57^{Ab}	486.11^{Cb}
Abomasum	358.34^{Ac}	350.20^{Bc}	362.55^{Ac}	320.57^{Cc}
Ileum	140.37^{Ad}	118.53^{Cd}	149.81^{Bd}	120.77^{Cd}
Feces	71.41^{Be}	81.25^{Ae}	70.91^{Be}	76.70^{ABe}

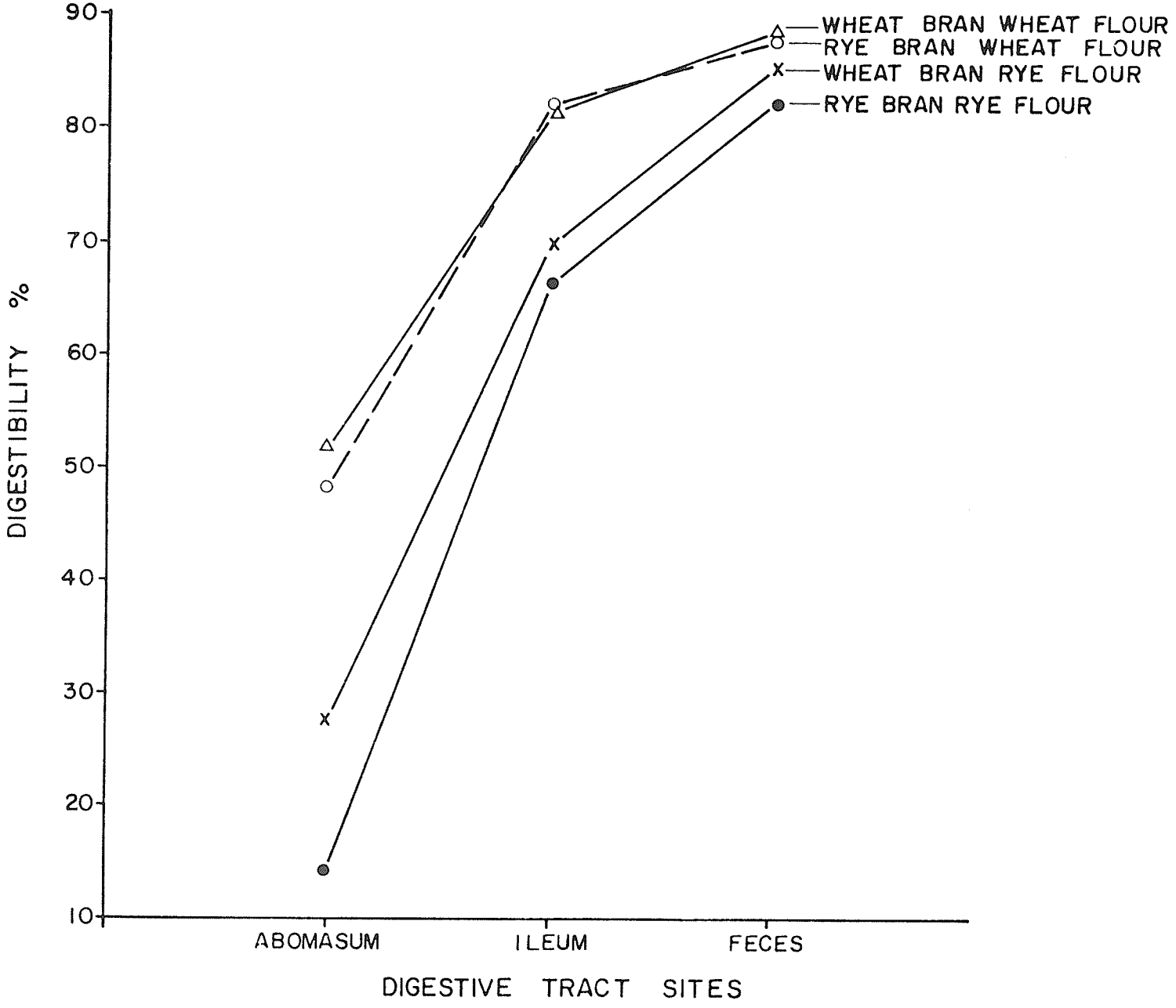
The standard error of diet equals 7.68.

The standard error of locations equals 8.59.

^{a,b,c,d,e}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

FIG. 3.0 DIGESTIBILITY OF CRUDE PROTEIN MEASURED AT THE ABOMASUM, ILEUM AND FECES USING DYSPROSIUM AS AN INERT MARKER RELATIVE TO INTAKE



fermentation as seen in poultry (Antoniou and Marquardt 1981a, Campbell et al. 1983a, Campbell et al. 1983, Ward 1982). The ileal and fecal digestibilities for diets containing RF tend to be lower relative to intake than diets containing WF (Fig. 2.0).

The total flor of energy through the gastrointestinal tract for the treatments RBRF, RBWF, WBRF and WBWF was 13.32, 14.33, 13.35 and 13.25 kcal/day, respectively with RBWF having the highest flow and differing significantly from the other treatments ($P<0.01$). Energy flow between digestive tract locations differed significantly with ruminal flow and abomasal flow differing significantly across all treatments ($P<0.01$) SEM 0.305, but, comparisons of ileal and fecal flow did not differ significantly across treatments ($P>0.01$) (Table 3.4). The fecal flow of energy across treatments was not significantly different ($P>0.01$) (Table 3.4).

Protein concentrations differed in the test diets (Table 3.5), resulting in RBWF and WBWF having higher intake levels of protein than RBRF or WBRF diets. The diets containing RBRF or WBRF had significantly higher ruminal flows of crude protein compared to intake ($P<0.01$). This increased ruminal protein flow was associated with reduced abomasal crude protein digestibility (Table 3.23 and Fig. 3.0) and higher ruminal bacterial nitrogen flow (Table 3.13) than the RBWF or WBWF diets. Buckley (1978) reported reduced nitrogen digestibility in rye compared to barley in an in vitro system. The reduced crude protein digestibility in the rumen or abomasum for diets containing rye flour (Fig. 3.0) would suggest that rye flour protein supplies more rumen escape protein than wheat flour. Higher amino acid flow can be substantiated by the

increased flow of lysine, arginine and histidine through the abomasum (Table 3.7, 3.11, 3.12) for cattle fed the diets containing rye flour (RF) compared to those containing WF. RBRF and WBRF showed no significant difference ($P>0.01$) with respect to fecal protein excretion (Table 3.5). RBRF showed the lowest apparent protein digestibility for ileal (Table 3.24) and for fecal digestibility (Table 3.25) differing significantly ($P<0.01$) from the other diets. WBRF showed a significantly lower ($P<0.01$) ileal protein digestibility (Table 3.24) and tended to be lower in fecal digestibility measurements than the diets containing wheat flour (WF). The flow of crude protein indicates (Table 3.5) that between the ileum and feces 49.12% and 52.66% of the remaining crude protein is assimilated for RBRF and WBRF respectively, while only 31.45% and 36.49% is assimilated for the RBWF and WBWF diets. This data would indicate that a larger proportion of the protein presented to the large bowel is fermented for diets containing rye flour (RF) than wheat flour (WF). Protein digestion throughout the whole gastrointestinal tract would indicate that diets containing rye flour (RF) are more resistant to protein degradation than diets containing wheat flour (WF) until they reach the ileal-caecal junction (Table 3.5). Once past the ileal-caecal junction the diets containing RBRF may cause a microbial growth phase with a concommitant increase in bacterial nitrogen flow (Table 3.13).

All treatments indicated significant differences in flow rates of ADF-N between the rumen and abomasum (Table 3.6). However, Table 3.23 indicates that abomasal digestibility of ADF-N was significantly lower

Table 3.6 Intake and flow of ADF-N through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	24.08^{a}	22.86^{a}	21.761^{a}	21.09^{a}
Rumen	21.59^{Ba}	18.57^{Ca}	25.18^{Aa}	21.03^{Ba}
Abomasum	14.19^{Bb}	11.29^{Db}	14.82^{Ab}	13.66^{Cb}
Ileum	6.27^{Bc}	4.38^{Cc}	9.07^{Ac}	6.41^{Bc}
Feces	8.24^{Ac}	6.63^{Bc}	8.69^{Ac}	8.80^{Ac}

The standard error of diet equals 0.51.

The standard error of locations equals 0.57.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

for WBRF ($P<0.01$) than any other treatment. All treatments showed significant reduction in flow rates between the abomasum and ileum indicating small intestinal assimilation of ADF-N (Table 3.6). The ileal digestibility of ADF-N (Table 3.24), indicates that WBRF shows the most digestibility resistance ($P<0.01$). There was no significant difference ($P>0.01$) in fecal digestibility of ADF-N across all treatments (Table 3.25).

The intake of lysine (Table 3.7) ranged from 15.53 g/day for RBWF to a high of 19.22 g/day for WBRF. The fecal excretion of lysine was not significantly different ($P>0.05$) across all treatments. The flow of lysine between digestive tract locations exhibited a significant increase ($P<0.01$) in the rumen and abomasum compared to intake across all treatments due to microbial synthesis (Bergen et al. 1968). The lysine disappearance between the rumen and abomasum (g/day), indicates that WBRF shows significantly higher lysine absorption than the other treatments ($P<0.01$) (Table 3.8). A significant loss of lysine in the digesta flow ($P<0.01$) appeared to occur between the abomasum and ileum. According to Armstrong and Hutton (1975) the ruminant possesses the same complement to proteases that assist protein hydrolysis within the small intestine as the non-ruminant. Therefore, the loss of lysine is likely due to absorption in the small intestine. The amount of lysine apparently absorbed in the small intestine between the abomasum and ileum is significantly higher for RBRF ($P<0.01$) than for RBWF or WBRF (Table 3.8). Lysine flow did increase however not significantly ($P>0.05$) from ileum to feces in all treatments except WBRF, again suggesting microbial synthesis in the lower intestine (Table 3.7).

Table 3.7 Intake and flow of lysine through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	17.26^{c}	15.53^{c}	19.22^{c}	17.75^{c}
Rumen	26.87^{Ba}	27.46^{Ba}	32.66^{Aa}	27.38^{Ba}
Abomasum	21.61^{Ab}	18.49^{Bb}	21.61^{Ab}	19.30^{Bb}
Ileum	7.84^{Bd}	6.18^{Cd}	9.36^{Ad}	6.42^{Cd}
Feces	8.67^{Ad}	7.98^{Ad}	8.60^{Ad}	9.05^{Ad}

The standard error of diet equals 0.50.

The standard error of locations equals 0.56.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.8 Lysine disappearance between rumen and abomasum and abomasum and ileum of cannulated Holstein steers g/day fed diets containing rye and wheat fractions

	Diets				
	RBRF	RBWF	WBRF	WBWF	SE
Rumen-abomasum	5.26^{C}	8.95^{B}	11.06^{A}	8.08^{B}	0.96
Abomasum-ileum	13.77^{A}	12.30^{B}	12.25^{B}	12.87^{AB}	0.40

^{A,B,C}Means within the same row having different letters are significantly different ($P<0.01$).

The flow of methionine showed significant interactive effects between digestive tract sites ($P<0.01$) (Table 3.9). In all cases when comparing flow of methionine through the rumen there was greater quantities available than indicated by intake from all treatments due to microbial synthesis (Armstrong and Hutton 1975), however, the differences for WBRF were not different ($P>0.01$). The RBRF diet shows an important interactive effect between intake and rumen with the lowest methionine intake and highest rumen content of methionine (Fig. 4.0). The ileum showed significantly less methionine flow ($P<0.01$) than from the rumen or abomasum in all treatments with all treatments showing interactive effects between these compartments because of small intestinal absorption. However, when measuring flow of methionine across all treatments (Table 3.9), the feces tended to exhibit greater flow than the ileum due to lower intestinal microbial synthesis. According to Table 3.10, the methionine disappearance between the rumen and abomasum was highest for RBRF and lowest for WBWF ($P<0.01$). The methionine absorbed between the abomasum and ileum was significantly higher for the WF diets than the RF diets (Table 3.10). The amount of lysine and methionine apparently absorbed (Table 3.8, 3.10) appears to be two times the amount that was calculated to be deposited in the gain according to data from Orskov (1982) and Satter (1980).

The flow of both arginine and histidine (Table 3.11, 3.12) showed significant interactive effects between diet and digestive tract location ($P<0.01$). When comparing flow of arginine and histidine (Table 3.11, 3.12), between location in the digestive tract both arginine and

Table 3.9 Intake and flow of methionine through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	8.66^{b}	12.11^{b}	10.84^{a}	11.55^{b}
Rumen	15.13^{Aa}	13.76^{Ba}	12.20^{Da}	13.18^{Ca}
Abomasum	7.54^{Db}	9.15^{Bc}	8.02^{Cb}	10.19^{Ab}
Ileum	2.70^{Bd}	2.39^{Ce}	2.94^{Ac}	2.13^{Dc}
Feces	5.51^{Ac}	4.48^{Bd}	3.26^{Cc}	3.15^{Cc}

The standard error of interaction equals 0.491.

The standard error of diets equals .098.

The standard error of locations equals .122.

^{a,b,c,d,e}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

FIG. 4.0 INTAKE AND FLOW OF METHIONINE THROUGH THE GASTROINTESTINAL TRACT OF CANNULATED HOLSTEIN STEERS (g / day)

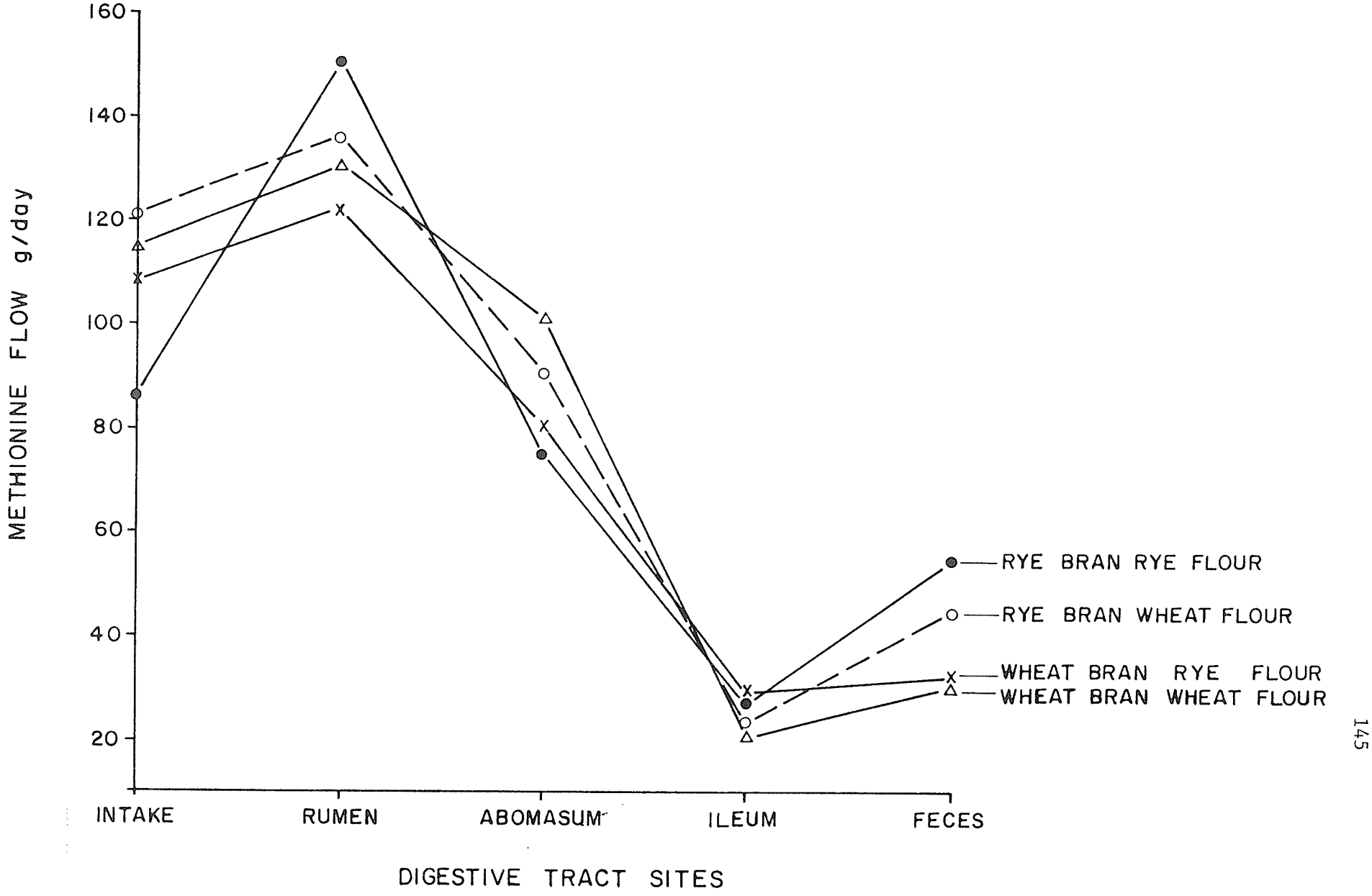


Table 3.10 Methionine disappearance between rumen and abomasum and ileum of cannulated Holstein steers g/day fed diets containing rye and wheat fractions

	Diets				
	RBRF	RBWF	WBRF	WBWF	SE
Rumen-abomasum	7.58^{A}	4.61^{B}	4.18^{B}	2.99^{C}	0.18
Abomasum-ileum	4.85^{C}	6.77^{B}	5.08^{C}	8.06^{A}	0.14

^{A,B,C}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.11 Intake and flow of arginine through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	24.50^{a}	25.97^{a}	29.75^{a}	35.30^{a}
Rumen	21.09^{Bb}	20.66^{Bb}	23.46^{Ab}	20.38^{Bb}
Abomasum	14.68^{Ac}	13.76^{Bc}	14.75^{Ac}	14.80^{Ac}
Ileum	4.12^{Bd}	5.34^{Ad}	4.22^{Bd}	3.46^{Bd}
Feces	5.60^{Ad}	4.29^{Ad}	4.70^{Ad}	5.21^{Ad}

The standard error of interaction equals 0.991.

The standard error of diets equals 0.198.

The standard error of location equals 0.248.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.12 Intake and flow of histidine through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	11.48^{a}	13.99^{a}	12.76^{a}	17.15^{a}
Rumen	11.40^{Aa}	10.10^{Cb}	10.98^{Bb}	10.13^{Cb}
Abomasum	7.21^{Ab}	5.85^{Dc}	7.00^{Bc}	6.28^{Cc}
Ileum	3.15^{Ac}	2.69^{Cd}	2.93^{Bd}	2.84^{Bd}
Feces	3.71^{Ac}	2.82^{Bd}	2.62^{Bd}	3.38^{Ad}

The standard error of interactions equals 0.541.

The standard error of diet equals 0.108.

The standard error of location equals 0.135.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.05$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.05$).

histidine show a proportionately large decrease in flow rate from the rumen relative to intake for WBWF compared to other diets. A significant difference ($P<0.01$) between ruminal and abomasal flow of arginine and histidine is indicated across all treatments with abomasal flow being consistently lower for both amino acids. The flow of both arginine and histidine is significantly lower ($P<0.01$) from the abomasum relative to intake partly because the rumen proteases may have converted these amino acids to carbon and ammonia (Satter and Roffler 1975), and because bacteria are disproportionately low in the amino acids arginine and histidine (Kaufman 1979). When comparing the flow of arginine and histidine between the abomasum and ileum, significant reduction of flow ($P<0.01$) is evident at the ileum compared to the abomasum for both amino acids. According to Armstrong and Hutton (1975) significant amino acid absorption occurs in the small intestine which would account for the reduction. The flow relative to intake through the abomasum for arginine and histidine (Table 3.11, 3.12), appears to be highest for RBRF and lowest for WBWF. This would suggest that rye bran and rye flour in combination tends to have more ruminal resistant protein than the wheat bran, wheat flour combination. When comparing the flow of arginine and histidine between ileum and feces neither amino acid exhibited any significant difference across all treatments ($P<0.01$). The fecal excretion in g/day was not different ($P>0.01$) among any treatments for arginine flow. The flow of fecal histidine was greater ($P<0.01$) for RBRF and WBWF compared to that of RBWF and WBRF.

The flow of bacterial nitrogen (Table 3.13), indicates a significant

Table 3.13 Flow of bacterial nitrogen through the gastrointestinal tract of cannulated Holstein steers g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Rumen	7.55^{Aa}	6.10^{Ba}	6.37^{Ba}	4.47^{Ca}
Abomasum	2.23^{Bb}	2.93^{Ab}	2.28^{Bb}	2.99^{Ab}
Ileum	2.79^{Ab}	2.07^{Bc}	2.06^{Bb}	1.99^{Bc}
Feces	1.94^{Ac}	1.37^{Bd}	1.78^{Ab}	1.65^{ABc}

The standard error of interaction 0.212.

The standard error of diet equals .043.

The standard error of location equals .053.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

interactive effect between diet and digestive tract location ($P<0.01$). When comparing bacterial nitrogen flow across treatments, the ruminal flow of bacterial nitrogen was significantly different ($P<0.01$) between RBRF and WBWF with 7.55 g/day compared to 4.47 g/day respectively. The flow of bacterial nitrogen through the rumen for treatments RBWF and WBRF was not significantly different at 6.10 and 6.37 g/day respectively. When comparing flow of bacterial nitrogen between locations in the digestive tract, RBRF and WBRF showed no significant difference ($P>0.01$) between abomasal and ileal flow. All other treatments showed less bacterial nitrogen flow at the ileum than at the abomasum indicating intestinal absorption of bacterial nitrogen. All experimental diets showed less bacterial nitrogen flow in the feces than in the ileum, however, RBRF and RBWF showed significantly different flows of bacterial nitrogen between ileum and feces ($P<0.01$) while WBRF and WBWF showed no significant difference in flow rates of bacterial nitrogen (Table 3.13). This would suggest very little lower intestinal microbial activity is taking place in the experimental animals. According to the data of Table 3.14, the yield of bacterial nitrogen/kg of rumen dry matter fermented, shows significantly higher ($P<0.01$) yields for the diets containing RF than the WF diets. This would suggest that the RF diets contain more rumen fermentable dry matter than the WF diets. The bacterial yield values are lower than reported values (Orskov 1982). This could be a result of protozoal scavenging of bacteria or dilution of diaminopimelic acid by excessive microbial slime coats. Cheng (1977) indicates that bacterial nitrogen may be diluted by slime and increased ash content.

Table 3.14 Yield of bacterial nitrogen per unit of rumen fermented dry matter, g/kg

	Diet				
	RBRF	RBWF	WBRF	WBWF	SE
Bact N/unit Rumen fermented Dry matter, (g/kg)	3.37^{A}	2.17^{C}	2.89^{B}	1.76^{C}	.107

^{A,B,C}Means within the same row having different letters are significantly different ($P<0.01$).

The flow of fat exhibited a significant interactive effect between diet and digestive tract location ($P<0.01$) (Table 3.15, Fig. 5.0). The intake of fat was significantly different between all treatments with WBRF having the highest intake of 107.48 g/day (Table 3.15). All rations exhibited significant differences between abomasal flow and intake with abomasal flow being significantly higher than intake ($P<0.01$). Increased lipid flow through the rumen has been observed by several workers (Bath and Hill 1967, Leat and Harrison 1969, Bines et al. 1978) who suggest the source of extra fat is from microbial synthesis.

All diets tended to show increased fecal fat flow compared to ileal fat flow (Table 3.15) with RF diets tending to show higher fecal excretion of fat. The RF diets showed significant interaction between the ileum and feces, while both RF and WF diets show interactive effects between the rumen and abomasum (Fig. 5.0). Ward et al. (1964) has suggested that increases in fecal fat compared to ileal fat could be related to microbial activity and synthesis in the large intestine. Differences across all treatments with respect to fecal flow were not significantly different ($P>0.01$).

There was a significant ($P<0.01$) interactive effect (Fig. 6.0) between diet and digestive tract location for ADF flow rates (Table 3.16). The intake of ADF was significantly different ($P<0.01$) among treatments with WBRF showing the highest intake at 569.34 g/day. The fecal output of ADF differed significantly across the treatments RBRF, RBWF and WBRF; with RBRF and WBWF showing no significant differences. The flow of ADF between digestive tract locations indicates no significant differences between rumen, abomasum and ileum across all

Table 3.15 Intake and flow of fat through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	80.99^{c}	62.22^{c}	107.48^{c}	69.03^{c}
Rumen	119.43^{Ab}	74.12^{Bb}	109.84^{Ab}	81.28^{Bb}
Abomasum	143.64^{Aa}	123.64^{Ca}	163.83^{Ba}	120.07^{Ca}
Ileum	20.27^{Ad}	11.68^{Ce}	25.33^{Bc}	11.45^{Cc}
Feces	37.35^{Ad}	27.94^{Ad}	33.33^{Ac}	26.27^{Ac}

The standard error of diet x location equals 6.13.

The standard error of diet equals 1.23.

The standard error of location equals 1.53.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.16 Intake and flow of ADF through the gastrointestinal tract of Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	423.28^{a}	378.64^{a}	569.34^{a}	492.17^{a}
Rumen	294.69^{Ab}	279.14^{Bb}	276.40^{Bb}	224.12^{Cb}
Abomasum	281.00^{Ab}	271.19^{Bb}	260.42^{Cb}	211.88^{Db}
Ileum	273.37^{Ab}	265.68^{Bb}	256.22^{Cb}	208.36^{Db}
Feces	165.66^{Cc}	170.43^{Bc}	203.19^{Ac}	163.38^{Cc}

The standard error of diet x location interaction equals 12.726.

The standard error of diet equals 2.55.

The standard error of location equals 3.19

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

FIG. 5.0 INTAKE AND FLOW OF FAT THROUGH THE GASTROINTESTINAL TRACT OF CANNULATED HOLSTEIN STEERS (g / day)

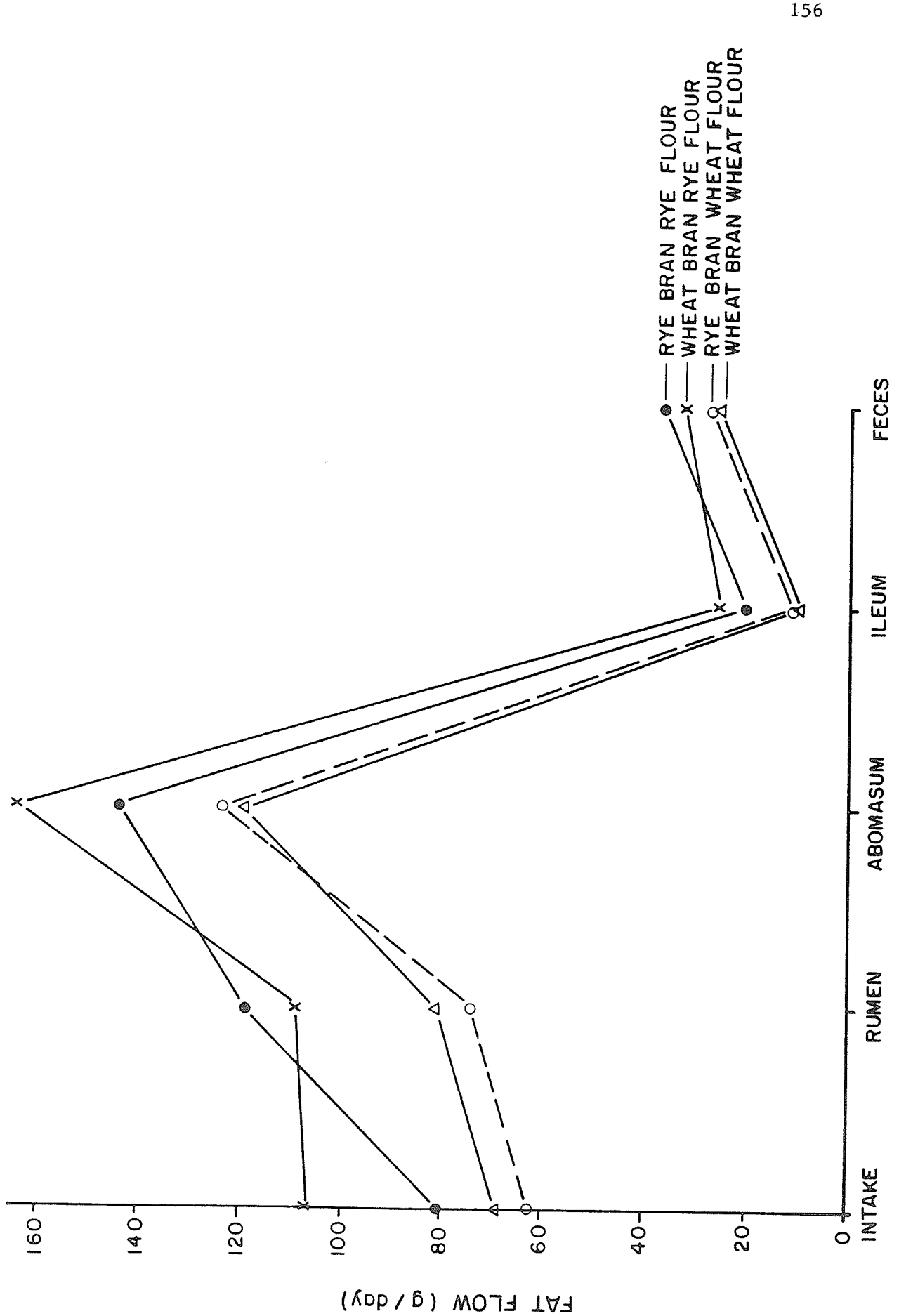
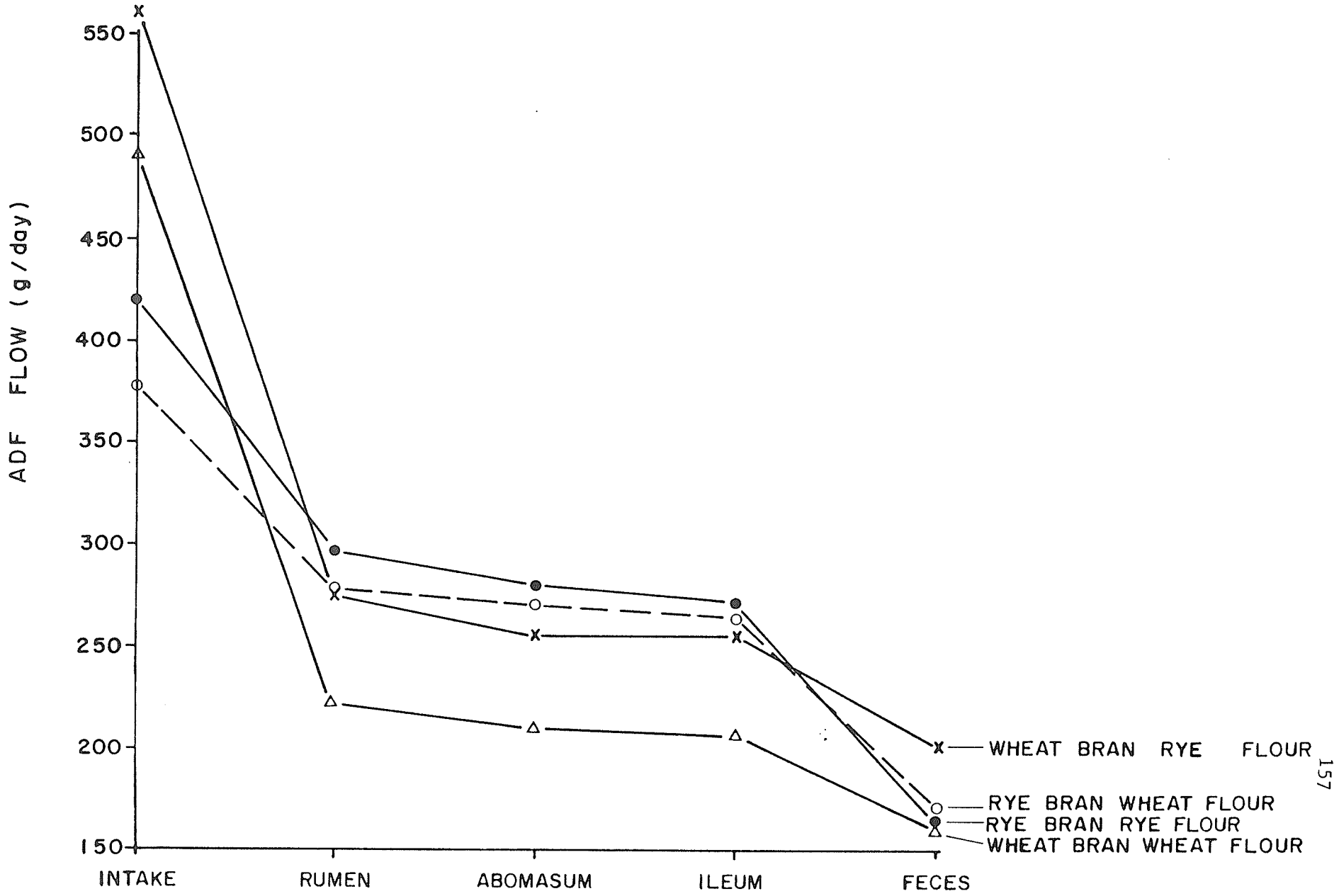


FIG. 6.0 INTAKE AND FLOW OF ADF THROUGH THE GASTROINTESTINAL TRACT OF CANNULATED HOLSTEIN STEERS (g/day)



treatments ($P<0.01$), however significant interaction exists between the ileum and the feces for diets WBRF, RBWF and RBRF. A significant reduction of flow of ADF ($P<0.01$) (Table 3.16), is evident across all treatments at the abomasum compared to intake. This would indicate significant ruminal digestion. Abomasal digestibility (Table 3.23), for ADF is significantly lower ($P<0.01$) for the diets RBRF and RBWF compared to WBRF and WBWF. This data would indicate that the ADF of RB is more resistant to ruminal degradation than the ADF of WB. Very little difference ($P>0.01$) in ADF flow exists across all treatments between the abomasum and ileum (Table 3.16). Since cellulolytic activity is virtually non-existent in the small intestine of ruminants, no digestibility would be expected to take place between the compartments. However, because of the lower intestinal microbial cellulolytic activity, a significant reduction in fecal flow of ADF ($P<0.01$) is evident across all treatments compared to ileal flow (Fig. 6). The apparent fecal digestibility of ADF (Table 3.25) was significantly different between each treatment. The two diets containing RB showed lower fecal digestibilities compared to intake than the two WB diets however disappearance from the ileum to feces was greater ($P<0.01$) for diets containing RB (Table 3.16).

The flow of the pentosan sugar xylose (Table 3.17) through the gastrointestinal tract did not show any significant diet by location interaction. The flow of xylose was significantly different ($P<0.01$) between each location across all treatments. The fecal flow of xylose was not significantly different between RBRF and WBWF ($P>0.01$), however,

Table 3.17 Intake and flow of xylose through the gastrointestinal tract of cannulated Holstein steers g/day, fed diets containing rye and wheat fractions

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	295.71^{Aa}	278.20^{Ba}	312.3^{Ca}	293.94^{Aa}
Rumen	97.76^{Ab}	64.03^{Bb}	116.47^{Cb}	70.68^{Db}
Abomasum	63.37^{Ac}	43.48^{Bc}	74.22^{Cc}	47.05^{Dc}
Ileum	33.46^{Ad}	26.98^{Bd}	43.86^{Cd}	27.28^{Bd}
Feces	0.115^{Ae}	0.049^{Be}	0.136^{Ce}	0.114^{Ae}

The standard error of treatments equals 3.55.

The standard error of location equals 3.97.

^{a,b,c,d,e}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

RBWF and WBRF showed significant differences in fecal excretion excretint 49.0 mg/day and 136.2 mg/day respectively. The digestibility of xylose in the abomasum was significantly lower ($P<0.01$) for the diets containing rye flour (RF) than those containing wheat flour (WF) (Table 3.23). Data from Table 3.24 indicates that the diets containing rye flour (RF) had lower ileal digestibilities of xylose than the diets containing wheat flour (WF). Fecal digestibilities would indicate that virtually 100% of the xylose was digested in all treatments (Table 3.25). Data from Table 3.17, shows a significant decline ($P<0.01$) in flow of xylose as digesta travels through the large intestine, indicating lower gut fermentation of the remaining feed xylose. The least amount of xylose is excreted from cattle receiving the RBWF diets at only 49 mg/day with the other diets resulting in excretion of more than double this amount (Table 3.17).

The flow of arabinose showed a significant ($P<0.01$) diet by location interactive effect (Table 3.18) between intake and rumen for WBWF. The WBWF diet shows no differences in rumen flow compared to RBRF even though the intake was significantly higher for the WBWF diet. The digestibility of arabinose in the abomasum (Table 3.23) is significantly lower digestibility for the diets containing rye flour (RF) than wheat flour (WF). However arabinose digestibility for all diets in the abomasum exceeded 80%. All diets tended to show reduced flow of arabinose (Table 3.18) at the ileum compared to abomasum which indicates small intestinal carbohydrate absorption or microbial fermentation (Dehority 1973). There was a significant ($P<0.01$) reduction of arabinose flow in the

Table 3.18 Intake and flow of arabinose through the gastrointestinal tract of cannulated steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	143.73^{a}	142.25^{a}	207.41^{a}	186.91^{a}
Rumen	37.18^{Bb}	23.92^{Cb}	61.12^{Ab}	35.96^{Bb}
Abomasum	23.41^{Bc}	16.24^{Cb}	38.10^{Ac}	24.18^{Bbc}
Ileum	13.66^{Bc}	11.35^{Cb}	22.10^{Ad}	13.94^{Bc}
Feces	0.11^{Ad}	0.04^{Bc}	0.12^{Ae}	0.12^{Ad}

The standard error of diet x location equals 4.92.

The standard error of diet equals 0.98.

The standard error of location equals 1.23.

^{a,b,c,d,e}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

large intestine as measured by fecal output and ileal flow for all the treatments (Table 3.18). This data suggests large bowel fermentation which results in almost 100% digestibility of arabinose in all diets. The RBWF diet showed minimum fecal excretion of arabinose 36.0 mg/day, and maximum digestibility of 99.97%. Howard (1955) studied the in vitro fermentation of water soluble wheat flour pentosans using rumen bacteria. Stripping off of the arabinose side chains appeared to proceed first followed by fragmentation of the remaining xylan chain increasing the X/A ratio. However, no microbial pentosanase activity could be detected. Approximately 90% of the substrate pentosans had disappeared within 4 hours in an in vitro system. Apparently hydrolysis proceeded, much more rapidly than the fermentation so that considerable amounts of arabinose, xylobiose, xylotriose and very little free xylose was detected. Morrison (1975), Morrison (1979) and Heald (1955) suggest that the microbial hemicellulases degrade the pentosans and hemicellulose to fragments of arabinose xylobiose and xylotriose which are small enough to be transported across the bacterial membrane for further metabolism. Gaillard and Richards (1975) and Leatherwood (1973) indicate that exogenous microbial pentosanases are not capable of hydrolyzing hemicellulose present in intact or delignified cell walls. Preece and Hobrick (1955) and Preece and McDougall (1958) determined that the arabinose was hydrolyzed first followed by fragmentation of the xylan chains. These workers also determined that as arabinose side chains were hydrolyzed off, the remaining polymers were less soluble. The endogenous pentosanase activity of rye plus the hemicellases of

microbial origin are likely the most important sources of ruminal pentosan digestion (Antoniou 1980).

The xylose:arabinose ratio (Table 3.19) indicates a (X/A ratio) ranging from 1.50 for WBRF to 2.05 for the RBRF diet relative to intake. Following the X/A ratio through the rumen (Table 3.26) and the abomasum (Table 3.27), the X/A ratio increased relative to intake which indicates that arabinose is being hydrolyzed and fermented before xylose similar to studies by Preece and Hobrick (1955) and Howard (1955). As digesta dry matter enters the large intestine the X/A ratio tends to be highest for the diets containing the rye bran (RB) and lower for the diets containing wheat bran (WB) (Table 3.28). Antoniou and Marquardt (1981) indicate the main effect of rye and the associated pentosan in poultry is the low X/A ratio. In this study the RBRF diet contained the lowest X/A ratio in the centrifuged ileal fluid (Table 3.36, 3.37) which contributes to the very high ileal viscosity values (Table 3.22) for RBRF. Cheng et al. (1977) states that the production of an microbial extracellular slime coat is proportional to the soluble carbohydrate available in the diet, and the slime may be over produced when soluble carbohydrates are available in high concentration leading to significant increases in viscosity of fluids. Overabundance of bacteria however, is not likely the cause of the high ileal viscosity because the flow of bacterial nitrogen does not appear to be disproportionately high (Table 3.13) for RBRF.

The flow of sodium (Table 3.20), indicates a significant ($P<0.01$) diet by digestive tract location interaction between intake and rumen

Table 3.19 Dietary parameters measured on dry matter of feed allocated to cannulated Holstein steers fed diets containing rye and wheat fractions

Treatments	RBRF	WBWF	WBRF	WBWF
Energy Mcal/kg	3.852	3.84	3.92	3.905
Fat %	1.622	1.205	2.160	1.392
ADF-N %	0.493	0.462	0.447	0.428
ADF %	8.57	7.532	11.547	9.98
Crude protein %	8.80	13.57	10.18	13.52
Arginine %	0.492	0.522	0.60	0.710
Histidine %	0.230	0.280	0.260	0.342
Methionine %	0.172	0.242	0.22	0.235
Lysine %	0.349	0.314	0.390	0.361
Xylose g/100 g	5.97	5.62	6.322	5.97
Arabinose g/100 g	2.90	2.87	4.20	3.80
X/A ratio	2.05	1.95	1.50	1.57
Bacterial N mg/100 g DM	0.00	0.00	0.00	0.00
Sodium %	0.510	0.43	0.535	0.565
Potassium %	0.87	0.93	0.76	0.77
Dyprosium mg/day	55.75	59.98	59.42	54.51

Table 3.20 Intake and flow of sodium through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	25.26^{a}	21.27^{a}	25.65^{b}	27.74^{a}
Rumen	25.77^{Aa}	17.64^{Bb}	28.83^{Aa}	27.33^{Aa}
Abomasum	3.49^{Bb}	3.22^{Bc}	6.41^{Ac}	6.73^{Ab}
Ileum	6.82^{Bb}	5.75^{Cc}	7.49^{Bc}	8.62^{Ab}
Feces	4.20^{Bb}	3.25^{Cc}	5.62^{Ac}	2.55^{Dc}

The standard error diet x location interaction equals 0.092.

The standard error of diet equals .018.

The standard error of location equals .023.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

and ileum and feces for WBWF (Fig. 7.0). Sodium appears to be secreted in the rumen for WBWF and RBRF diets and shows a higher sodium absorption between the ileum and feces than the other treatments. The comparison of sodium flow between intestinal tract location showed that all treatments exhibited a significant loss of sodium between rumen and abomasum while all treatments showed a non-significant increase ($P>0.01$) between abomasum and ileum due to intestinal secretion. There was no significant differences between the ileal flow and fecal flow of sodium on treatments RBRF, RBWF and WBRF, however a significant difference was shown between ileal flow and fecal flow of sodium on the WBWF diet. The fecal excretion of sodium on diet WBWF was significantly less ($P<0.01$) than the other experimental diets at 2.55 g/day.

A significant ($P<0.01$) diet by digestive tract location interaction exists between all sites (Fig. 8.0) for the flow of potassium (Table 3.21). The flow between digestive tract locations was significantly different between rumen and abomasum ($P<0.01$) for all treatments with the abomasum showing much less flow than the rumen indicating ruminal absorption. All experimental treatments showed an increased flow of potassium through the ileum relative to the abomasum but only RBRF and WBRF exhibited significant ($P<0.01$) increases of potassium between the two locations. There was a significant decrease in fecal potassium flow relative to ileal potassium flow for the RBRF and WBRF treatments. The treatments RBWF and WBWF did not exhibit significant differences in potassium flow between the ileum and feces.

FIG. 7.0 INTAKE AND FLOW OF SODIUM THROUGH THE GASTROINTESTINAL TRACT OF CANNULATED HOLSTEIN STEERS (g/day)

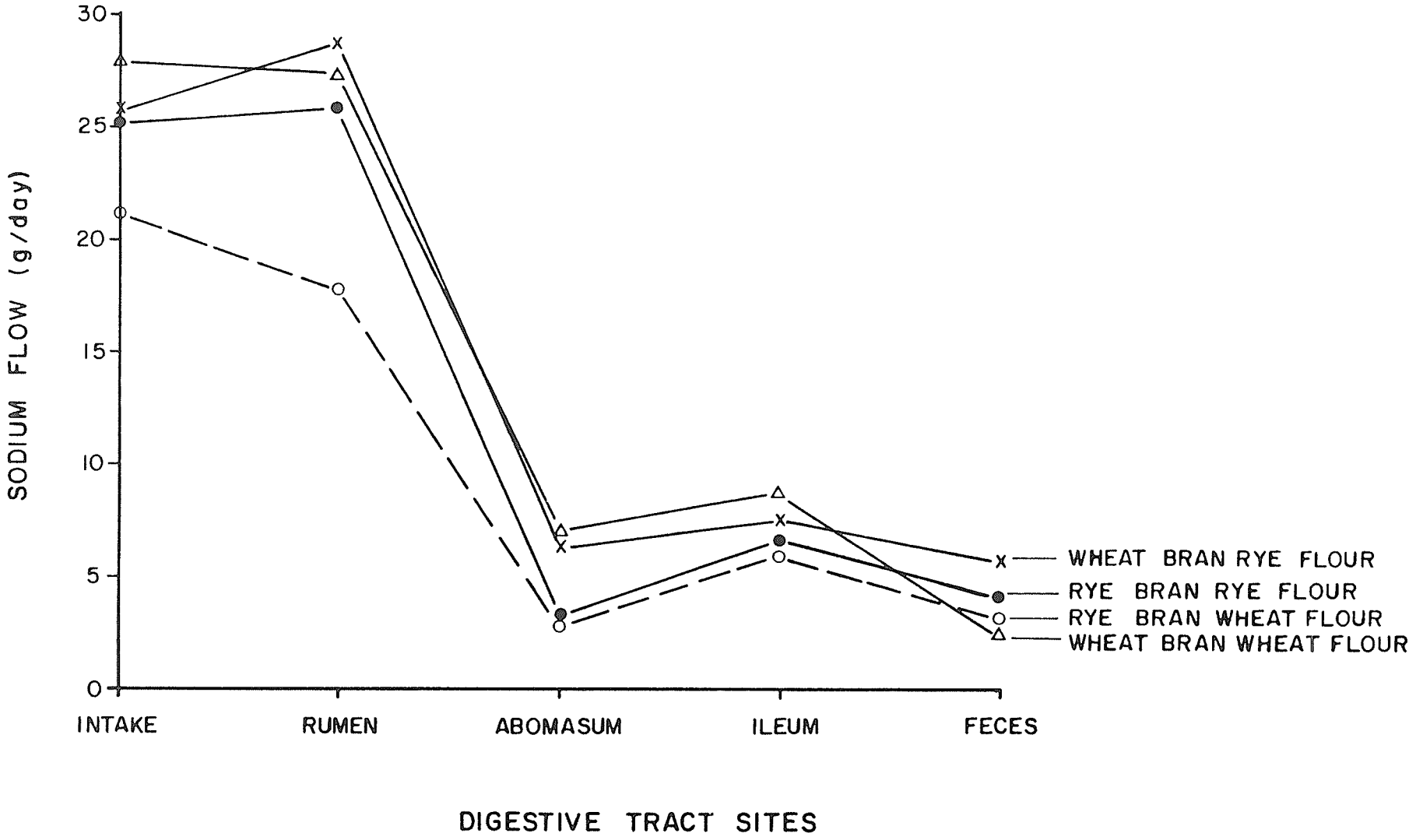


FIG. 8.0 INTAKE AND FLOW OF POTASSIUM THROUGH THE GASTROINTESTINAL TRACT OF CANNULATED HOLSTEIN STEERS (g/day)

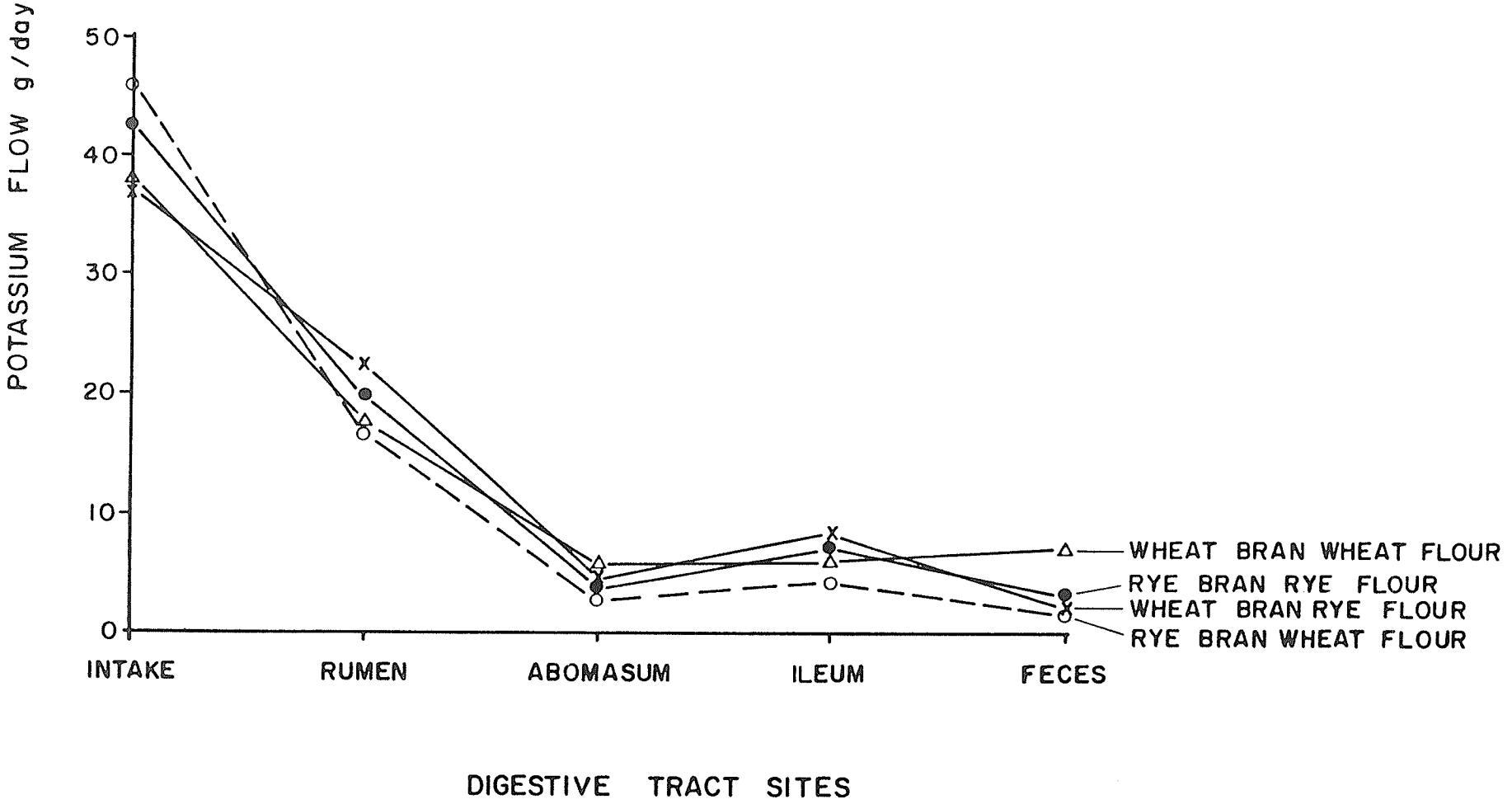


Table 3.21 Intake and flow of potassium through the gastrointestinal tract of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
Location	RBRF	RBWF	WBRF	WBWF
Intake	43.04^{a}	46.01^{a}	37.52^{a}	37.86^{a}
Rumen	19.99^{Bb}	17.07^{Cb}	22.56^{Ab}	17.15^{Cb}
Abomasum	3.70^{Cd}	3.35^{Cc}	4.80^{Bd}	5.33^{Ac}
Ileum	7.53^{Bc}	4.65^{Dc}	8.69^{Ac}	6.50^{Cc}
Feces	3.05^{Bd}	2.51^{Bc}	2.59^{Bd}	7.13^{Ac}

The standard error of diet x location interaction equals 1.30.

The standard error of diet equals .26.

The standard error of location equals .325.

^{a,b,c,d}Means within the same columns having different letters are significantly different ($P<0.01$).

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Antoniou (1980), Ward (1982) and Drews (1970) have shown that the nutritional value of rye can be improved by extracting in dilute acid pH 2.0. They postulate that the pentosans could be hydrolyzed or partially hydrolyzed and the subsequent removal of arabinose will decrease solubility and allow the pentosan to precipitate.

The viscosity of rumen fluid is significantly higher ($P<0.01$) for the diets containing rye flour than those containing wheat flour (Table 3.22). Misir and Marquardt (1978c) found that in studies with poultry the greatest growth depressing fraction was associated with rye flour. As digesta moves from the rumen with a slightly acidic pH of 6.0 (Table 3.38), to the abomasum with a lower average pH value of 3.0 the viscosity of the fluid declined significantly for all treatments ($P<0.01$). However, when the fluid viscosity was measured in the alkaline pH of the ileum (average pH 7.44) the values increased significantly ($P<0.01$). As pointed out by McNeil et al. (1975), Holas et al. (1971), Antoniou (1980) and Golenkov and Traubenberg (1966), sodium hydroxide treatment or dilute alkali will aid in the extraction of the highly viscous insoluble pentosan thereby increasing the total viscosity of the aqueous solutions. The most probable cause of the increase in viscosity from the abomasum to the ileum is the transition from acidic to alkaline conditions which increase the extractability of the remaining undigested insoluble pentosans. These undigested insoluble pentosans enter the large intestine and result in fermentation within the large bowel.

The lowest fecal pH of 6.30 (Table 3.38) resulted from the diet RBRF which also exhibited the highest ileal viscosity (Table 3.22).

Table 3.22 Viscosity of gastrointestinal fluids from cannulated Holstein steers fed diets containing rye and wheat fractions (seconds)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen	598.5^{Bb}	276.00^{Cb}	662.00^{Ab}	230.00^{Db}
Abomasum	121.5^{Cc}	154.25^{Bc}	161.25^{Ac}	110.75^{Dc}
Ileum	2639.75^{Aa}	642.00^{Da}	810.25^{Ca}	904.5^{Ba}

Standard error of diet x location equals 3.65.

Standard error of diet equals -0.73.

Standard error of location equals -0.912.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the same column having different letters are significantly different ($P<0.01$).

Fecal material from rye fed birds tends to contain increased concentration of volatile moncarboxylic acids especially acetic acid and butyric acids which have a tendency to lower the fecal pH (Misir and Marquardt 1978a). According to several workers (Wagner and Thomas 1977a, Banes et al. 1972, Untawale and McGinnis 1979, Scott 1976) chicks fed rye based diets tended to have significantly higher levels of fecal butyric acid compared to birds fed rye free diets. These authors claim the anaerobic clostridium spore formers proliferate in the intestine of rye fed birds. Cattle fed the diet containing WBRF showed the highest mMole/100 ml rumen fluid content of acetate than any other treatment (Table 3.30). The diets containing WBWF showed significantly ($P<0.01$) less concentration of acetate in rumen fluid than the other diets.

The ileal fluid contained no butyric acid for any treatment. The total acetate concentration for ileal fluid (Table 3.32) showed significantly higher levels ($P<0.01$) for the rye flour diets than the wheat flour diets. The measurement of lactic acid concentration (Table 3.34) indicates that the diet containing the RBRF contained the highest ruminal and ileal lactic acid concentrations in the fluids ($P<0.01$). A tendency toward lower ileal pH and fecal pH (Table 3.38) for RBRF plus the higher lactic acid concentration could indicate that there is some lower gut fermentation taking place, however not sufficient to cause any adverse physiological conditions such as diarrhea in the experimental cattle since none was observed throughout the trial.

The concentration of ammonia in digestive fluids given in Table 3.35, indicates that the diets containing WF produced more ruminal, abomasal and ileal fluid ammonia than diets containing RF. This suggests that the protein of WF is more readily deaminated than the protein of RF diets.

No significant differences ($P>0.01$) were shown with respect to rumen volume measured by manual emptying (Table 3.33). According to Table 3.36 and Table 3.37 the concentrations of arabinose and xylose are significantly higher in the rumen and abomasum fluids of the steer fed the rye flour rations than the wheat flour rations. The ileal fluids from the rye flour fed steers contain significantly more ($P<0.01$) arabinose and xylose than the wheat flour fed steers. All diets show significantly ($P<0.01$) lower concentrations of arabinose and xylose in the ileal fluid compared to the abomasal fluid.

According to Table 3.39 the lowest fractional rumen turnover was associated with the RBWF (0.46 rumens/day).

The average daily weight gains were not significantly different ($P>0.01$) for cattle fed RBRF and WBRF at 453.0 g/day and 469.0 g/day respectively (Table 3.40). However, cattle fed RBWF and WBWF diets showed significantly higher average daily gains at 544.0 g/day and 608.0 g/day respectively (Table 3.40). Although RF diets resulted in lower gains these data must be used with caution because of the relatively short periods and very limited numbers.

Table 3.23 Abomasal digestibility of nutrients measured using dysprosium as an inert marker relative to intake of diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Dry matter	65.51	71.64	63.98	64.54	1.87
Energy %	56.04^{C}	62.83^{A}	56.79^{C}	60.22^{B}	0.41
ADF %	33.26^{B}	28.33^{C}	57.66^{A}	56.23^{A}	0.78
ADF-N %	40.73^{A}	49.74^{A}	29.01^{B}	34.75^{A}	3.70
Fat %	-82.29	-100.33	-64.57	-76.39	8.77
Arabinose %	83.17^{C}	88.48^{A}	81.72^{D}	86.85^{B}	0.31
Xylose %	78.51^{B}	84.37^{A}	76.23^{C}	83.99^{A}	0.18
Potassium %	91.76^{B}	93.39^{A}	87.28^{C}	85.46^{D}	0.18
Sodium %	85.95^{A}	84.86^{A}	74.99^{B}	75.29^{B}	1.12
Crude protein %	14.67^{C}	48.33^{A}	27.84^{B}	51.79^{A}	1.77
Lysine %	-25.54^{A}	-19.07^{AB}	-11.98^{B}	-8.76^{B}	3.11
Methionine %	12.43^{B}	24.42^{A}	25.79^{A}	11.83^{B}	1.63

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.24 Ileal digestibility of nutrients using dysprosium as an inert marker relative to intake of diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Dry matter %	75.94^{C}	78.72^{A}	71.57^{D}	78.24^{B}	0.06
Energy kcal/kg	72.47^{B}	75.90^{A}	68.16^{C}	76.02^{A}	0.10
Fat %	74.25^{C}	79.76^{B}	75.79^{C}	82.69^{A}	0.64
ADF-N %	73.82^{B}	80.57^{A}	56.61^{C}	69.46^{B}	0.33
ADF %	35.06^{B}	29.79^{C}	54.37^{A}	57.01^{A}	0.86
Crude protein %	66.66^{C}	82.51^{A}	70.17^{B}	81.88^{A}	0.64
Arabinose %	90.72^{B}	91.88^{A}	89.41^{C}	92.34^{A}	0.20
Xylose %	88.68^{C}	90.30^{B}	85.96^{D}	90.72^{A}	0.05
Methionine %	68.81^{C}	80.24^{A}	72.86^{B}	81.57^{A}	0.56
Lysine %	54.43^{B}	60.26^{A}	51.37^{B}	63.73^{A}	1.16
Potassium %	82.54^{B}	89.88^{A}	76.85^{C}	82.86^{B}	0.30
Sodium %	73.01^{A}	74.84^{A}	70.94^{AB}	68.89^{B}	0.94

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.25 Fecal digestibility of nutrients using dysprosium as an inert marker relative to intake of diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Dry matter %	74.57^{B}	78.52^{A}	72.25^{C}	75.06^{B}	0.18
Energy kcal/kg	69.93^{B}	75.46^{AB}	68.83^{B}	68.68^{B}	1.86
Fat %	53.06^{C}	54.83^{C}	69.24^{A}	61.00^{B}	3.57
ADF-N %	65.59	78.31	57.06	56.44	3.57
ADF %	60.63^{C}	54.95^{D}	63.80^{B}	66.19^{A}	0.53
Crude protein %	82.63^{B}	88.00^{A}	85.72^{A}	88.35^{A}	0.71
Methionine %	36.35^{C}	63.01^{B}	69.86^{A}	72.50^{A}	1.79
Lysine %	49.78	48.59	55.35	48.49	3.25
Xylose %	99.96^{B}	99.98^{A}	99.95^{B}	99.96^{B}	0.21
Arabinose %	99.92^{C}	99.97^{A}	99.94^{B}	99.93^{B}	0.11
Sodium %	83.13^{B}	84.74^{B}	78.18^{C}	90.75^{A}	0.50
Potassium %	92.86^{A}	94.52^{A}	93.08^{A}	80.99^{B}	1.28

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.26 Rumen parameters measured on digesta dry matter from cannulated Holstein steers fed diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Energy Mcal/kg	4.55	4.59	4.58	4.57	0.01
Fat %	5.20^{A}	3.99^{B}	4.36^{B}	3.84^{B}	0.12
ADF-N %	0.94	1.00	1.00	0.99	0.03
ADF %	12.96^{B}	15.04^{A}	11.18^{C}	10.69^{C}	0.15
Crude protein %	21.68^{C}	24.98^{A}	21.33	22.97^{B}	0.02
Arginine %	0.91^{B}	1.10^{A}	0.93^{B}	0.92^{B}	0.004
Histidine %	0.49^{B}	0.54^{A}	0.43^{D}	0.47^{C}	0.002
Methionine %	0.65^{B}	0.74^{A}	0.48^{D}	0.62^{C}	0.002
Lysine %	1.25^{C}	1.48^{A}	1.30^{B}	1.29^{B}	0.005
Xylose g/100 g	4.26^{B}	3.45^{C}	4.64^{A}	3.34^{D}	0.02
Arabinose g/100 g	1.62^{C}	1.29^{D}	2.38^{A}	1.70^{B}	0.01
X/A ratio	2.63	2.67	1.95	1.96	
Bacterial N mg/100 g DM	12.30^{A}	12.30^{A}	9.50^{B}	7.90^{C}	0.10
Sodium %	1.14^{B}	0.95^{C}	1.23^{A}	1.29^{A}	0.02
Potassium %	0.87^{B}	0.92^{A}	0.90^{A}	0.81^{C}	0.008

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.27 Abomasal parameters measured on digesta dry matter from cannulated Holstein steers fed diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Energy Mcal/kg	4.99^{A}	5.04^{A}	4.71^{B}	4.87^{B}	0.003
Fat %	8.58^{C}	8.83^{B}	9.21^{A}	7.66^{D}	0.006
ADF-N %	0.84^{B}	0.80^{D}	0.83^{C}	0.87^{A}	0.001
ADF %	16.77^{B}	19.38^{A}	14.86^{C}	13.65^{D}	0.135
Crude protein %	21.39^{B}	25.01^{A}	20.38^{C}	20.45^{C}	0.089
Arginine %	0.87^{C}	0.98^{A}	0.83^{D}	0.94^{B}	0.006
Histidine %	0.41^{A}	0.41^{A}	0.39^{B}	0.40^{B}	0.003
Methionine %	0.45^{B}	0.65^{A}	0.45^{B}	0.64^{A}	0.001
Lysine %	1.29	1.32	1.21	1.23	0.024
Xylose g/100 g	3.78^{B}	3.10^{C}	4.17^{A}	3.00^{D}	0.001
Arabinose g/100 g	1.40^{C}	1.12	2.14^{A}	1.54^{B}	0.014
X/A ratio	2.70	2.67	1.95	1.95	
Bacterial N mg/100 g DM	5.00^{C}	7.85^{A}	4.80^{C}	7.15^{B}	0.058
Sodium %	0.21^{C}	0.23^{C}	0.36^{B}	0.43^{A}	0.013
Potassium %	0.22^{B}	0.24^{B}	0.27^{B}	0.34^{A}	0.012

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.28 Ileal parameters measured on digesta dry matter from cannulated Holstein steers fed diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Energy Mcal/kg	4.40	4.36	4.34	4.32	0.024
Fat %	1.70^{B}	1.11^{C}	1.82^{A}	1.09^{C}	0.017
ADF-N %	0.52^{C}	0.41^{D}	0.64^{A}	0.61	0.007
ADF %	23.08^{B}	25.32^{A}	18.58^{D}	19.74^{C}	0.273
Crude protein %	11.75^{A}	11.29^{A}	10.70^{B}	11.30^{A}	0.164
Arginine %	0.34^{A}	0.31^{C}	0.30^{D}	0.32^{B}	0.002
Histidine %	0.26^{A}	0.25^{B}	0.20^{C}	0.26^{A}	0.002
Methionine %	0.22^{A}	0.22^{A}	0.20^{B}	0.20^{C}	0.001
Lysine %	0.68^{A}	0.59^{B}	0.67^{A}	0.62^{B}	0.010
Xylose g/100 g	2.80^{B}	2.57^{C}	3.13^{A}	2.56^{C}	0.013
Arabinose g/100 g	1.14^{C}	1.08^{D}	1.64^{A}	1.31^{B}	0.014
X/A ratio	2.45	2.38	1.91	1.95	
Bacterial N mg/100 g DM	8.75^{A}	7.40^{B}	5.50^{D}	7.00^{C}	0.462
Sodium %	0.57^{B}	0.51^{B}	0.53^{B}	0.81^{A}	0.092
Potassium	0.63^{A}	0.44^{B}	0.62^{A}	0.61^{A}	0.014

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.29 Fecal parameters measured on digesta dry matter from grab samples of feces from cannulated Holstein steers fed diets containing rye and wheat fractions

Treatments	RBRF	RBWF	WBRF	WBWF	SE
Energy Mcal/kg	4.52^{A}	4.44^{B}	4.42^{B}	4.33^{C}	0.006
Fat %	2.94^{A}	2.67^{AB}	2.41^{B}	1.92^{C}	0.093
ADF-N %	0.65	0.63	0.64	0.64	0.019
ADF %	13.20^{AB}	16.28^{A}	15.12^{AB}	12.24^{B}	0.744
Crude protein %	12.79^{C}	13.49^{B}	12.01^{D}	13.70^{A}	0.043
Arginine %	0.44^{A}	0.41^{B}	0.34^{D}	0.38^{C}	0.004
Histidine %	0.29	0.27	0.18	0.24	0.003
Methionine %	0.43^{A}	0.42^{B}	0.23^{C}	0.23^{D}	0.001
Lysine %	0.68^{B}	0.76^{A}	0.63^{D}	0.66^{C}	0.004
Xylose mg/100 g	9.06^{A}	4.68^{D}	10.00^{C}	8.13^{B}	0.105
Arabinose mg/100 g	8.40^{C}	3.40^{D}	8.98^{B}	9.06^{A}	0.072
X/A ratio	1.08	1.37	1.11	0.89	
Bacterial N mg/100 g DM	1.14^{A}	0.98^{B}	0.98^{B}	0.9^{C}	0.011
Sodium %	0.33^{B}	0.31^{B}	0.41^{A}	0.19^{C}	0.010
Potassium %	0.28^{B}	0.24^{C}	0.19^{D}	0.52^{A}	0.007
Dysprosium mg/day	52.98	52.78	51.49	49.16	2.987
% Dy recovery	91.96	92.05	93.46	92.42	2.170

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.30 mMole concentration of rumen volatile fatty acids found in centrifuged digesta fluids measured on cannulated Holstein steers fed diets containing rye and wheat fractions

	Rumen fluid concentration (mMole/100 ml)				
	RBRF	RBWF	WBRF	WBWF	SE
Propionic acid	3.32^{B}	3.81^{A}	3.21^{B}	2.75^{C}	0.052
Acetic acid	5.37^{C}	5.93^{B}	6.64^{A}	4.90^{D}	0.036
Butyric acid	2.37^{B}	2.87^{A}	2.47^{B}	2.72^{A}	0.068
Total VFA	11.89^{C}	13.51^{A}	13.19^{B}	11.27^{D}	0.050
A/P ratio	1.62	1.55	2.06	1.78	

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.31 mMole concentration of abomasal volatile fatty acids found in centrifuged abomasal fluids measured on cannulated Holstein steers fed diets containing rye and wheat fractions

	Abomasal fluid concentration (mMole/100 ml)				
	RBRF	RBWF	WBRF	WBWF	SE
Propionic acid	0.31^{A}	0.14^{B}	0.12^{B}	0.17^{B}	0.012
Acetic acid	0.44^{B}	0.46^{B}	0.52^{C}	0.70^{A}	0.013
Butyric acid	0.02^{B}	0.02^{A}	0.02^{B}	0.02^{B}	0.001
Total VFA	0.85^{B}	0.63^{C}	0.66^{C}	0.94^{A}	0.011
A/P ratio	1.41	3.28	4.33	4.10	

^{A,B,C,D} Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.32 mMole concentration of ileal volatile fatty acids found in centrifuged ileal fluids measured on cannulated Holstein steers fed diets containing rye and wheat fractions

	Ileal fluid concentration (mMole/100 ml)				
	RBRF	RBWF	WBRF	WBWF	SE
Propionic acid	0.98^{B}	1.29^{A}	0.91^{B}	0.50^{C}	0.021
Acetic acid	0.85^{B}	0.55^{C}	0.93^{A}	0.82^{B}	0.013
Butyric acid	0	0	0	0	0
Total VFA	2.10^{A}	2.26^{A}	2.12^{A}	1.46^{B}	0.060
A/P ratio	0.86	0.42	1.02	1.64	

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.33 Average rumen volume measured on cannulated Holstein steers fed diets containing rye and wheat fractions (litres)

Diets				
RBRF	RBWF	WBRF	WBWF	SE
18.00	18.75	18.25	17.50	0.500

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.34 Lactic acid concentration of centrifuged digesta fluids measured on cannulated Holstein steers fed diets containing rye and wheat fractions (mMole/100 ml)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen fluid	1.005^{Ab}	0.727^{Bb}	0.565^{Cb}	0.620^{Cb}
Abomasum fluid	0.355^{Bc}	0.455^{Ac}	0.472^{Ab}	0.325^{Cc}
Ileal fluid	3.027^{Aa}	1.692^{Ba}	1.447^{Ba}	1.50^{Ba}

Standard error of diet x location interaction equals 0.047.

Standard error of diet equals .016.

Standard error of location equals .012.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the column having different letters are significantly different ($P<0.01$).

Table 3.35 Ammonia concentration of centrifuged digesta fluids measured on cannulated Holstein steers fed diets containing rye and wheat fractions (mg/100 ml)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen fluid	19.251^{Ca}	27.822^{Ba}	19.001^{Ca}	33.087^{Aa}
Abomasal fluid	8.737^{Bc}	9.532^{Bc}	7.262^{Cb}	14.137^{Ab}
Ileal fluid	10.951^{Bb}	13.153^{Ab}	7.071^{Cb}	13.142^{Ac}

Standard error of diet x location interaction equals 0.214.

Standard error of diets equals -0.071.

Standard error of location equals -0.054.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the same column having different letters are significantly different ($P<0.01$).

Table 3.36 Concentration of arabinose measured in centrifuged digesta fluids from cannulated Holstein steers fed diets containing rye and wheat fractions (mg/100 ml)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen	34.37^{Aa}	13.00^{Ca}	25.78^{Ba}	7.03^{Da}
Abomasum	30.21^{Aa}	12.84^{Ca}	23.01^{Ba}	7.00^{Da}
Ileal	3.90^{Ab}	0.00^{b}	1.56^{Bb}	0.00^{b}

Standard error of diet x location interaction equals 2.42.

Standard error of diet equals 0.806.

Standard error of location equals 0.605.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the same column having different letters are significantly different ($P<0.01$).

Table 3.37 Concentration of xylose measured in centrifuged digesta fluids from cannulated Holstein steers fed diets containing rye and wheat fractions (mg/100 ml)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen	35.92^{Aa}	17.34^{Ca}	29.68^{Ba}	4.69^{Da}
Abomasum	35.70^{Aa}	16.34^{Ca}	27.58^{Ba}	4.65^{Da}
Ileum	4.68^{Bb}	2.34^{Cb}	5.46^{Ab}	2.31^{Db}

Standard error of diet x location interaction equals 2.21.

Standard error of diet equals 0.73.

Standard error of location equals 0.55.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the same column having different letters are significantly different ($P<0.01$).

Table 3.38 pH of gastrointestinal fluids from cannulated Holstein steers fed diets containing rye and wheat fractions

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen	5.87^{c}	6.17^{b}	6.20^{b}	6.30^{c}
Abomasum	3.15^{d}	2.90^{c}	2.95^{c}	3.00^{d}
Ileum	7.27^{a}	7.50^{a}	7.50^{a}	7.50^{a}
Feces	6.30^{Cb}	7.22^{Aa}	7.17^{Aa}	6.67^{Bb}

Standard error 0.38.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

^{a,b,c,d}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.39 Rumen turnover measured in cannulated Holstein steers fed diets containing rye and wheat fractions (rumens/day)

	Diets			
	RBRF	RBWF	WBRF	WBWF
Rumen fraction/day	0.64^{AB}	0.46^{C}	0.60^{B}	0.66^{A}

Standard error 0.042.

^{A,B,C,D}Means within the same row having different letters are significantly different ($P<0.01$).

Table 3.40 Average daily weight gain of cannulated Holstein steers fed diets containing rye and wheat fractions, g/day

	Diets			
	RBRF	RBWF	WBRF	WBWF
Average daily gain	453.0^{C}	544.0^{B}	469.0^{C}	608.0^{A}

Standard error 9.62 g/day.

^{A,B,C}Means within the same row having different letters are significantly different ($P<0.01$).

GENERAL DISCUSSION

Studies conducted by Winter (1973) and Winter (1975) concluded that ergot free rye can be included up to 80% in the ruminant ration with no significant reduction in intake. Sharma et al. (1983) concluded that alkali treated rye increased the consumption of rye non-significantly by 13% compared to untreated rye when fed to lactating dairy cows. Sharma et al. (1981) found that the dry matter intake was reduced ($P<0.05$) when lactating dairy cows were fed 25, 50 or 75% rye in their grain mixture compared to barley. However, no significant differences were determined on production parameters of rye fed dairy cows. Sharma et al. (1981) measured the weight gain and feed consumption of weaned calves from 7-18 weeks of age fed either 0, 30, 60, 80% dry rolled or 80% roasted rye. The dry matter intake and ADG were different ($P<0.05$) among the five dietary treatments. Calves receiving the 60% rye diet consumed less ($P<0.05$) feed and had less weight gain compared with those fed the barley control (0% rye) or 80% roasted rye diets and similar amounts to those receiving the 30 and 80% rye diets. Sharma et al. (1981) shows regression analysis of average daily gain on rye content in calf diets and indicates a reduction in average daily gain with increasing rye in the diet which was negatively correlated ($r = 0.911$).

Factors which could influence appetite and growth rate in young animals include the soluble nonstarch polysaccharides especially the pentosans (Baker 1931), pectins (Wagner and Thomas 1977) or pectin like compounds (Misir and Marquardt 1978b). Misir and Marquardt (1978c) have indicated that rye contains at least two detrimental factors, an

appetite-depressing factor located in the bran and a growth depressing factor in the bran, flour and middlings. Data from Table 2.3, shows a significant difference ($P<0.01$) in dry matter intake for dairy cattle receiving the rye based experimental rations. The data from Table 2.4, shows a significant reduction in acid detergent fibre digestibilities for the rye fed cattle ($P<0.05$), while the digestibilities of dry matter, crude protein and energy tended to be lower compared to the barley control ration. Sharma et al. (1981) showed no differences in digestibilities of dry matter, protein, acid detergent fibre, fat and energy for rye fed calves, however, calves fed 60% and 80% rye ration tended to show lower digestibilities of nutrients.

Part of the reason for variability in rye experiments could be because of variety and environmental conditions. Data presented by Drews and Seibel (1976) have shown that the level of the soluble pentosans of rye can increase above 2.5% while their viscosity decreases. Drews and Seibel (1976) also report that in very dry years the levels of soluble pentosans can be as low as 1.5% but they are much more viscous in nature. Therefore a large variation of total and soluble pentosans can exist and depends on environmental conditions.

Other reasons for variability could be due to microbial hemicellulases (Leatherwood 1973) and endogenous plant pentosanases (Drews 1970). Data from Drews (1970) show that as the pH of an aqueous solution approaches 4.9 the pentosan solubility is reduced and pentosanase activity is enhanced especially as the temperature approaches 40 degrees celsius. Reduced acid detergent fibre digestibility could be due to the

fact that rumen pH normally ranges around 6.5, thereby maintaining a very viscous fluid, and the endogenous rye pentosanases are not functioning at maximum potential because of the high pH.

The tendency for reduced digestibilities of rye grains could be due to the fact that pentosans have an ability to adsorb large quantities of water and swell forming a gel (Antoniou 1980, Rees 1971). Polysaccharide gels are essentially carboxylic cation (weak acid) exchangers (Mod 1981). The monovalent ions such as potassium and sodium are more strongly held than the divalent ions such as calcium and magnesium (Mod 1981). When pentosans of rye enter the small intestine of the ruminant they are exposed to increasing pH values, which will increase the viscosity as seen in Experiment 3, Table 3.22. The polysaccharide gels formed at the ileal-cecal junction could be responsible for increased viscosity in this gastrointestinal compartment which bind nutrients such as monovalent and divalent minerals as well as protein through tyrosine-ferulic acid binding (Neukom 1976) so that their excretion is increased and digestibility slightly reduced. Painter and Neukom (1968) have shown that wheat flour pentosans will undergo a gelation reaction but because of the high ash content will cause spontaneous breakdown of the gel. Perhaps feeding a slightly higher mineral content in diets of ruminants would result in reduced viscosity of pentosans when ingested.

Several workers (Antoniou 1980, McNeill et al. 1975, Holas et al. 1971, Golenkov and Traubenberg 1966, Ward 1982), have shown that the nutritional value of rye can be improved by extracting with dilute acid at pH 2.0. They postulate that the extract contains hydrolyzed or

partially hydrolyzed soluble pentosan. These extracts showed lower viscosity values than NaOH treated extracts. The cannulated steer from which the rumen fluid was taken for the viscosity Chapter 1 had an average rumen pH value of 6.5. After incubation in vitro for 1 hour the pH value was decreased to pH 2.5, to simulate the pH and viscosity change as feed passes through the abomasum. All treatments showed a decreased in viscosity except for rye bran and whole rye which showed an increase in the abomasum. The most probable reason for this increase in viscosity in rye bran and whole rye is due to the acidic conditions hydrolyzing the fibrous fractions and releasing the highly viscous insoluble pentosans associated with these fractions. A general trend of all treatments as the pH was raised from 2.5 to 7.5 using NaOH was for the viscosity to increase. As pointed out by McNeil et al. (1975), Holas et al. (1971), Antoniou (1980) and Golenkov and Traubenberg (1966), sodium hydroxide or dilute alkali will aid in the extraction of the highly viscous insoluble pentosans thereby increasing the total viscosity of the aqueous solution. Therefore from the in vitro analysis when whole rye or whole wheat enter the rumen the viscosity of the solutions will be similar, however when the digesta enters the abomasum, the viscosity of whole rye will be more viscous than whole wheat, and as digesta passes from the abomasum to the ileum where a basic pH occurs physiologically, the whole rye will be more viscous than whole wheat. Antoniou (1980) has reported that pentosan can absorb large quantities of water. The adsorption of large quantities of water and the formation of a carbohydrate gel could result in lower intestinal fermentation, increased volatile fatty acid formation and

reduced net energy available to the ruminant.

Cattle fed diets containing RF showed significantly less average daily gain than cattle fed WF diets. This coincides with the data of Misir and Marquardt (1978c) who found that RF possessed a growth depressing effect in poultry. Chapter 3 indicates there is significantly more dry matter entering the ileum of cattle fed diets containing rye flour ($P<0.01$) while there is no significant differences in fecal dry matter excretion. Diets containing rye flour had the highest ruminal flow of crude protein, highest bacterial nitrogen flow through the rumen and ileum and the highest ruminal flow of lysine, arginine and histidine. Buckley (1978) has reported reduced nitrogen digestibility in rye compared to barley in vitro. The amount of lysine apparently absorbed between the abomasum and ileum (g/day), indicates that there was little difference among diets except the RBRF resulted in about 1.5 g more ($P<0.01$) absorption than RBWF or WBRF diets.

The methionine apparently absorbed between the abomasum and ileum was significantly higher ($P<0.01$) for the WF diets. Therefore, significantly less methionine ($P<0.01$) is available from RF diets for lower intestinal absorption than WF diets. This could explain some of the variable responses seen in rye experiments. Perhaps if rye is fed in combination with other feed sources high in bypass methionine less experimental variability would result.

The flow of xylose was significantly different ($P<0.01$) between each location across all treatments. The fecal flow of xylose was not significantly different between RBRF and WBWF ($P<0.01$), however, RBWF and

WBRF showed significant differences in fecal excretion excreting 49.0 mg/day and 136.2 mg/day respectively. The digestibility of xylose in the abomasum tended to be significantly lower for the diets containing rye flour (RF) than those containing wheat flour (WF). Diets containing rye flour (RF) had lower ileal digestibilities of xylose than the diets containing wheat flour. However, the data would indicate that virtually 100% of the xylose was digested in the total tract for all treatments. The data shows a significant decline ($P<0.01$) in flow of xylose as digesta travels through the large intestine, indicating lower gut fermentation of the remaining feed xylose. The RBWF diet indicates that the least amount of xylose is excreted from cattle at 49 mg/day with the other diets excreting more than double this amount.

The digestibility of arabinose in the abomasum shows significantly lower digestibility for the diets containing rye flour (RF) than wheat flour (WF). However arabinose digestibility for all diets in the abomasum exceeded 80%. All diets tended to show reduced flow of arabinose measured at the ileum compared to abomasum which indicates small intestinal carbohydrate absorption or microbial fermentation (Dehority 1973). A significant ($P<0.01$) loss of arabinose flow in the large intestine and feces compared to the ileal flow for all treatments was indicated. This data suggest significant large intestinal fermentation resulting in almost 100% digestibility of arabinose in all diets. The RBWF diet showed minimum fecal excretion of arabinose 36.0 mg/day and maximum digestibility of 99.9%. Howard (1955) studied the in vitro fermentation of water soluble wheat flour pentosans using rumen bacteria.

Stripping off of the arabinose side chains appeared to proceed first followed by fragmentation of the remaining xylan chain increasing the X/A ratio. However, no microbial pentosanase activity could be detected. Approximately 90% of the substrate pentosans had disappeared within 4 hours. Apparently hydrolysis proceeded much more rapidly than the fermentation so that considerable amounts of arabinose, xylobiose, xylotriose and very little free xylose was detected. Data from Morrison (1975), Morrison (1979) and Heald (1955) suggest that the microbial hemicellulases degrade the pentosans and hemicellulose to fragments of arabinose, xylobiose and xylotriose which are small enough to be transported across the bacterial membrane for further metabolism. Other workers (Gaillard and Richards 1975, Leatherwood 1973) indicate the exogenous microbial pentosanases may not be capable of hydrolyzing hemicellulose present in intact or delignified cell walls.

The presence of endogenous pentosanases in rye and wheat was first shown by Preece and Hobrick (1955) who extracted and used them for digestion of the rye arabinoxylan. Data from Preece and Hobrick (1955) and Preece and McDougall (1958) determined that the arabinose was hydrolyzed first followed by fragmentation of the xylan chains. These workers also discovered that as arabinose side chains were hydrolyzed off, the remaining polymers were less soluble. The endogenous pentosanase activity or rye plus the hemicellases of microbial origin are likely the most important sources of ruminal pentosan digestion (Antoniou 1980).

The data indicates that the xylose:arabinose ratio (X/A ratio) ranges from 1.50 for WBRF to 2.05 for the RBRF diet relative to intake. Following the X/A ratio through the rumen and abomasum the X/A ratio is increasing which indicates that arabinose is being hydrolyzed and fermented before xylose similar to studies by Preece and Hobrick (1955) and Howard (1955). The ileal parameters suggest that as digesta dry matter enters the large intestine the X/A ratio tends to be highest for the diets containing the rye bran (RB) and lower for the diets containing wheat bran (WB). According to Antoniou and Marquardt (1981) the main effect of rye and the associated pentosans in poultry is the low X/A ratio. Under the conditions of this study the RBRF diet contained the lowest X/A ratio in the centrifuged ileal fluid which contributes to the very high ileal viscosity values for RBRF. Cheng et al. (1977) states that the production of a microbial extracellular slime coat is proportional to the soluble carbohydrate available in the diet, and the slime may be over produced when soluble carbohydrates are available in high concentration leading to significant increases in viscosity of fluids. Over abundance of bacteria, however, is not likely the cause of the high ileal viscosity of RBRF because the flow of bacterial nitrogen did not appear to be disproportionately high.

The intake of sodium differed significantly ($P<0.01$) across treatments RBRF, RBWF and WBWF while RBRF and WBRF showed no significant sodium intake differences ($P>0.01$). The comparison of sodium flow between intestinal tract location showed that all treatments exhibited a significant loss of sodium between rumen and abomasum while all treatments

showed a non-significant increase ($P>0.01$) between abomasum and ileum due to intestinal secretion. There was no significant difference between the ileal flow and fecal flow of sodium on treatments RBRF, RBWF and WBRF, however a significant difference was shown between ileal flow of sodium on the WBWF diet. The fecal excretion of sodium on diet WBWF was significantly less ($P<0.01$) than the other experimental diets at 2.55 g/day.

The flow between digestive tract locations was significantly different between rumen and abomasum ($P<0.01$) for all treatments with the abomasum showing much less flow than the rumen indicating ruminal absorption. All experimental treatments showed an increase flow of potassium through the ileum relative to the abomasum with RBRF and WBRF exhibiting significant differences between the two locations. There was a significant decrease in fecal potassium flow relative to ileal potassium flow for the diets containing rye flour (RF). The treatments RBWF and WBWF did not exhibit significant differences in potassium flow between the ileum and feces.

Data from several workers (Antoniou 1980, Ward 1982, Drews 1970) has shown that the nutritional value of rye can be improved by extracting in dilute acid pH 2.0. They postulate that the pentosans could be hydrolyzed or paritally hydrolyzed and the subsequent removal of arabinose will decrease solubility and allow the pentosan to precipitate. The viscosity of rumen fluid is significantly higher ($P<0.01$) for the diets containing rye flour than those containing wheat flour. Misir and Marquardt (1978c) found that in studies with poultry the greatest growth

depressing fraction was associated with rye flour. As digesta moves from the rumen with a slightly acidic pH 6.0 to the abomasum with a lower average pH value of 3.0 the viscosity of the fluid declined significantly for all treatments ($P<0.01$). However, when the fluid viscosity was measured in the alkaline pH of the ileum (average pH 7.44) the values increased significantly ($P<0.01$). As pointed out by several workers (McNeil et al. 1975, Holas et al. 1971, Antoniou 1980, Golenkov and Traubenberg 1966), sodium hydroxide treatment of dilute alkali will aid in the extraction of the highly viscous insoluble pentosan thereby increasing the total viscosity of the aqueous solutions. The most probable cause of the increase in viscosity from the abomasum to the ileum is the transition from acidic to alkaline conditions which increase the extractibility of the remaining undigested insoluble pentosans. These undigested insoluble pentosans enter the large intestine and result in fermentation within the large bowel.

The lowest fecal pH of 6.30 resulted from the diet RBRF which also exhibited the highest ileal viscosity. Fecal material from rye fed birds tends to contain an increased concentration of volatile monocarboxylic acids especially acetic acid and butyric acids which tend to lower the fecal pH (Misir and Marquardt 1978a). According to several workers (Wagner and Thomas 1978, Banes et al. 1972, Untawale and McGinnis 1979, Scott 1976) chicks fed rye based diets tended to have significantly higher levels of fecal butyric acid compared to birds fed rye free diets. These authors claim the anaerobic clostridium spore formers proliferate in the intestine of rye fed birds. Cattle fed the diets containing

rye flour (RF) contained 45-50% of the total volatile fatty acids in the rumen as acetate. The diet containing WBWF showed significantly less acetate than the other diets.

The ileal fluid contained no butyric acid for any treatment. The total acetate for ileal fluid show significantly higher levels ($P<0.01$) for the rye flour diets than the wheat flour diets. The lactic acid levels indicate that the diet containing the RBRF contained the highest ruminal and ileal lactic acid concentrations in the fluids ($P<0.01$). A tendency toward lower ileal pH and fecal pH for RBRF plus the higher lactic acid concentration could indicate that there is some lower gut fermentation taking place, however not sufficient to cause any adverse physiological conditions such as diarrhea in the experimental cattle since none was observed throughout the trial.

The ADF of rye bran appears to be more resistant to ruminal, abomasal and ileal degradation than wheat bran. Sharma et al. (1981) showed that ADF digestibility although not significantly different tended to be lower for cattle fed rye diets.

Diets containing rye flour showed significantly higher flow of fat through the rumen and ileum than wheat flour diets. The increase of fat could be associated with increased microbial synthesis as shown by higher bacterial nitrogen content in these compartments. Bath and Hill (1967) and Leat and Harrison (1969) suggest that a source of extra fat in the rumen and feces, is from microbial synthesis. Campbell et al. (1983b) has indicated that the increased flow of fat or steatorrhea in the feces of birds is due to increased lower gut microbial activity and associated deconjugation of bile salts.

CONCLUSIONS

1) The digestibility of ADF was significantly lower for cattle fed processed rye or compared to dry rolled barley.

2) In vitro viscosity studies indicate that whole rye or rye bran or rye flour exhibited higher viscosity values than whole wheat or wheat bran or wheat flour at pH 2.5 and 7.5. The rye flour exhibited the highest viscosity value at pH 7.5 while whole rye and rye bran showed the highest viscosity values at pH 2.5 and 7.5.

3) Diets containing rye flour had a higher ruminal level of crude protein, ruminal bacterial nitrogen level, and level of lysine, arginine and histidine compared to diets containing wheat flour.

4) Diets containing rye flour had a lower apparent methionine disappearance in the small intestine than wheat flour diets.

5) Diets containing rye flour had equivalent apparent lysine absorption values compared to wheat flour diets in the small intestine.

6) Protein digestion throughout the whole gastrointestinal tract would indicate that diets containing rye flour are more resistant to protein degradation in the ruminant.

7) Flow of xylose was significantly higher ($P<0.01$) in the ileum and feces for cattle fed diets containing rye flour. Cattle fed

rye flour diets, especially WBRF had the highest ileal flow for arabinose and fecal excretion of arabinose.

8) Cattle fed rye flour diets had significantly higher ileal acetate levels and the RBRF diet showed the highest lactic acid content in the rumen and ileum compared to wheat flour.

9) RBRF diet showed the lowest ileal and fecal pH values and the rye flour diets showed the highest ruminal and ileal viscosities.

10) ADF digestibilities in the abomasum, ileum and feces were lower for diets containing rye bran than those with wheat bran.

11) Rye flour diets showed significantly higher ($P<0.01$) flow of fat through the abomasum and ileum compared to wheat flour. Fecal fat excretion tended to be higher for the rye flour diets. The lowest apparent fecal fat digestibility measured between the ileum and feces was associated with the rye bran diets.

12) The digestibility of dry matter tends to be lower for diets containing rye flour.

13) Diets containing rye flour showed significantly lower ($P<0.01$) energy digestibility throughout the abomasum, ileum and feces than wheat flour diets.

LITERATURE CITED

Akin, D.E. 1976. Ultrastructure of rumen bacterial attachment to forage cell walls. Appl. Environ. Microbial J. 31:562.

Akin, D.E. 1979. Microscopic evaluation of forage digestion by rumen microorganisms. J. of Anim. Sci. 48:701.

Akin, D.E. and Barton, F.E. II. 1983. Rumen microbial attachment and degradation of plant cell walls. Fed. Proc. 42:114.

Allison, M.J., Robinson, I.M., Dougherty, R.W. and Bucklin, J.A. 1975. Grain overload in cattle and sheep: Changes in microbial populations in the cecum and rumen. Am. J. Vet. Res. 36:181.

Antoniou, T. 1980. Identification, isolation, modification and partial characterization of an antinutritional factor in rye grain. Ph.D. Thesis, Dept. of Anim. Sci., University of Manitoba, Winnipeg, Canada.

Antoniou, T., Marquardt, R.R. and Misir, R. 1980. The utilization of rye by growing chicks as influenced by calcium, vitamin D3, and fat type and level. Poultry Sci. 59:758.

Antoniou, T. and Marquardt, R.R. 1981a. Influence of rye pentosans on the growth of chicks. Poultry Sci. 60:1898.

Antoniou, T., Marquardt, R.R. and Cansfield, P.E. 1981b. Isolation, partial characterization and antinutritional activity of a factor (pentosans) in rye grain. J. Agr. Food 29:1240.

Antoniou, T. and Marquardt, R.R. 1982. Utilization of rye diet by chicks as affected by lipid type and level and penicillin supplementation. Poultry Sci. 61:107.

Armstrong, D.G. 1974. In cereal suppl. and utilization. P. 21. Tech. Publ. U.S. Feed Grains Council, London, England.

Armstrong, D.G. and Beever, D.E. 1969. Post-abomasal digestion of carbohydrates in the adult ruminant. Proc. Nut. Soc. 28:121.

Armstrong, D.G. and Hutton, K. 1975. Fate of nitrogenous compounds entering the small intestine. Digestion and metabolism in the ruminant. MacDonald, I.W. and Warner, A.C.I. The University of New England Publishers. New York.

Aspinall, G.O. and Greenwood, C.T. 1962. Aspects of the chemistry of cereal polysaccharides. J. Inst. Brew. 68:167.

Aspinall, G.O. and Ross, K.M. 1963. The degradation of two periodate oxidized arabinoxylans. J. Chem. Soc. pp. 1681.

Aspinall, G.O. and Sturgeon, R.J. 1957. Cereal Germs. Part II. The constitution of an arabinoxylan from rye flour. J. Chem. Soc. 4469.

Association of Official Analytical Chemists. 1970. Official Methods of Analysis, 11th ed., Washington, D.C., Association of Official Analytical Chemists.

Baker, M.L. 1931. Corn, wheat and rye for fattening lambs. Nebraska Exp. Sta. Bull. 256:1.

Balch, C.C., Balch, D.A., Bartlett, S., Cox, C.P. and Rowland, S.J. 1952. Studies of the secretion of milk of low fat content by cows on diets low in hay and high in concentrates. I. The effect of variations in the amount of hay. J. Dairy Res. 19:39.

Balch, C.C., Balch, D.A., Bartlett, S., Hosking, Z.D., Johnson, V.W., Rowland, S.J. and Turner, J. 1955. Studies of the secretion of milk of low fat content by cows on diets low in hay and high in concentrates. V. The importance of the type of starch in the concentrates. J. Dairy Res. 22:10.

Baldwin, R.L. and Allison, M.J. 1983. Rumen metabolism. J. Anim. Sci. 57: Supple. 2.

Baldwin, R.L. 1965. Second International Symposium on the physiology of digestion in the ruminant. R.W. Dougherty ed. Butterworth Inc. pp. 379.

Baldwin, R.L. and Milligan, L.P. 1964. Electron transportation. Peptostreptococcus elsdenii. Biochim. Biophys. Acta 92:421.

Baldwin, R.L., Wood, W.A. and Emergy, R.S. 1963. Conversion of glucose -C14 tp propionate by the rumen microbiota. J. Bacteriology 85:1346.

Ballard, D.J., Hanson, R.W. and Kronfeld, D.S. 1969. Gluconeogenesis and lipogenesis in tissue from ruminant and non-ruminant anaimals. Fed. Proc. 28:218.

Balwani, T.C., Johnson, R.R. and Dehority, J. 1969. Comparison of cellulose and pentosan digestibilities in roughage feeds. J. Dairy Sci. 52:1290.

Barnes, E.M., Mead, G.C., Barnum, D.A. and Harry, E.G. 1972. The intestinal flora of the chicken in the period 2 to 6 weeks of age, with particular reference to the anaerobic bacteria. Br. Poultry Sci. 13:311.

Bath, I.H. and Hill, K.J. 1967. The lipolysis and hydrogenation of lipids in the digestive tract of sheep. J. Agric. Sci. 68:139.

Bauchop, T. 1979. Rumen anaerobic fungi of cattle and sheep. Appl. Environ. Microbiol. 38:148.

Bauman, D.E., Davis, C.L., Frobish, R.A. and Sachan, D.S. 1971. Evaluation of polyethylene glycol method in determining rumen fluid volume in dairy cows fed different diets. J. Dairy Sci. 54:928.

Bell, C.F. 1977. Principles and applications of metal chelation. Clarendon Press, Oxford, pp. 140.

Bell, J.M. and Owen, B.D. 1973. Swine production - feeding. Agric. Canada Publication 1442 (Sec. 2) pp. 29.

Bergen, W.G., Purser, D.B. and Cline, J.H. 1968. Effect of ration on the nutritive quality of rumen microbial protein. J. Anim. Sci. 27:1497.

Beever, D.E., Coelkoda Silva, J.F., Prescott, J.H.D. and Armstrong, D.E. 1972. The effect in sheep of physical form and stage of growth on the sites of digestion of a dried grass. I. Sites of digestion of organic matter, energy and carbohydrate. Brit. J. Nutr. 28:347.

Beever, D.E., Thomson, D.J., Pfeffer, E. and Armstrong, D.G. 1971. The effect of drying and ensiling grass on its digestion in sheep: Sites of energy and carbohydrate digestion. Brit. J. Nutr. 26:123.

Beever, D.E., Coelkoda de Silva, J.F. and Armstrong, D.G. 1970. (Part of: Abstracts of Communications 218th Meeting). The effect of processing maize on its digestion in sheep. (Abstract). Proc. Nut. Soc. 29:43A.

Bines, J.A., Brumby, P.E., Storry, J.E., Fulford, R.J. and Braithwaite, G.D. 1978. The effect of protected lipids on nutrient intake, blood and rumen metabolites and milk secretion in dairy cows during early lactation. J. Agric. Sci. 91:135.

Binnerts, W.T., van't Klooster, A.Th. and Frens, A.M. 1968. Soluble chromium indicator measured by atomic absorption in digestion experiments. Vet. Record 82:470.

Bird, S.H. and Lang, R.A. 1978. The effects of defaunation of the rumen on the growth of cattle on low-protein high-energy diets. Br. J. Nutr. 40:163.

Blake, J.D. and Richards, G.N. 1971. Evidence for molecular aggregation in hemicelluloses. Carbohyd. Res. 18:11.

Brown, W.H., Sullivan, L.M., Cheatham, L.F., Halback, K.J. and Stull, J.W. 1970. Steam processing versus pelleting of two ratios of milo and barley for lactating cows. J. Dairy Sci. 53:1448.

Bryant, M.P. 1979. Microbial methane production theoretical aspects. J. Anim. Sci. 48:193.

Bryant, M.P. 1978. (Symposium on the Role of Dietary Fiber in Health) Cellulose Digesting bacteria from human feces. Am. J. Clin. Nutr. 31:9113.

Bryant, M.P. 1977. Microbiology of the rumen: In M.J. Swenson (ed.) Duke's Physiology of Domestic Animals, 9th Ed. Cornell Univ. Press, Ithaca, N.Y.

Bryant, M.P. and Wolin, M.J. 1975. Rumen bacteria and their metabolic interactions in: Proc. First Intersect. Congr. Internat. Assoc. Microbial Soc. Development Microbiol, Ecology 2:297. T. Hasegawa (ed.) Science Council, Tokyo.

Bryant, M.P. 1974. Nutritional features and ecology of predominant anaerobic bacteria of the intestinal tract. Am. J. of Clin. Nutr. 27:1313.

Bryant, M.P. 1973. Nutritional requirements of the predominant rumen cellulolytic bacteria. Fed. Proc. 32:1809.

Bryant, M.P., Tzeng, S.F., Robinson, I.M. and Joyner, A.E. 1971. Nutrient requirements of methanogenic bacteria. P. 23. In F.G. Pohland (ed.) Anaerobic Biological Treatment Processes. Advances in Chemistry Series 105, Amer. Chem. Soc. Washington, D.C.

Bryant, M.P. 1962. Some nutritional characteristics of predominant culturable rumen bacteria. J. Bact. 84:605.

Bryant, M.P. and Robinson, I.M. 1961. An improved nonselective culture medium for ruminal bacteria and its use in determining the diurnal variation in members of bacteria. J. Dairy Sci. 44:1446.

Bryant, M.P. 1959. Bacterial species of the rumen. Bacteriol. Rev. 23:125.

Buckley, K.E. 1978. In vitro rumen digestion of processed feed grains and faba bean cultivars. M.Sc. Thesis, Dept. of Anim. Sci., University of Manitoba.

Burfening, P.J. 1973. Ergotism. J. Amer. Vet. Med. Assoc. 163:1288.

Bushuk, W. 1976. Rye Production, Chemistry & Technology. AACC St. Paul, MN.

Caldwell, D.R. and Bryant, M.P. 1966. Medium without rumen fluid for non-selective enumeration and isolation of rumen bacteria. Appl. Microbial 14:794.

Campbell, G.L., Campbell, L.D. and Classen, H.L. 1983a. Utilization of rye by chickens: Effect of microbial status supplementation. Br. Poultry Sci. 24:191.

Campbell, G.L., Classen, H.L., Reicher, R.D. and Campbell, L.D. 1983b. Improvement of the nutritive value of rye for broiler chickens by gamma irradiation induced viscosity reduction. Br. Poultry Sci. 24:205.

Casier, J.P.J. and Soenen, M. 1967. Die wasserunloslichen pentosane aus roggen und weizen und ihr einflub auf die backwerte. Getreide Hehl. 17:46.

Cave, N.A. 1978. The effect of whole wheat and whole rye plus wheat as grower rations and the growth and performance of broiler breeders. Poultry Sci. 57:1609.

Chen, C.H. and Bushuk, W. 1970. Nature of proteins in triticale and its parental species. I. Solubility characteristics and amino acid composition of endosperm protein. Can. J. Plant Sci. 50:9.

Cheng, K.J., Akin, D.E. and Costerton, J.W. 1977. Rumen bacteria: Interaction with particulate dietary components and response to dietary variation. Fed. Proc. 36:193.

Chittenden, L.W., Mitchell, G.E. Jr., Tucker, R.E. and Schelling, G.T. 1974. Abstract 84. Amylase response to duodenally infused carbohydrate in sheep. J. Anim. Sci. 38:232.

Clark, J.L., Hembry, F.G., Thompson, G.B. and Preston, R.L. 1972. Ration effect on polyethylene glycol as a rumen marker. J. Dairy Sci. 55:1160.

Coates, M.E., Cole, C.B., Fuller, R., Houghton, S.B. and Yokota, H. 1981. The gut microflora and uptake of glucose from the small intestine of the chick. British Poultry Science 22:289.

Conrad, H.R. 1966. Symposium on factors influencing the voluntary intake of herbage by ruminants: physiological and physical factors limiting feed intake. J. Anim. Sci. 25:227.

Coleman, G.S. 1979. The role of protozoa in the metabolism of ruminants given tropical feeds. Trop. Anim. Prod. 4:199.

Coombe, N.B. and Siddons, R.C. 1973. Carbohydrases of the bovine small intestine. Br. J. Nutr. 30:269.

Corbett, J.L., Greenhalgh, J.F.D. and Florence, G. 1959. Distribution of chromium sesquioxide and PEG in the rumen reticulum of cattle. Br. J. Nutr. 13:337.

Corbett, J.L., Greenhalgh, J.F.D., Gwynn, P.E. and Walker, D. 1958. Excretion of chromium sesquioxide and polyethylene glycol by dairy cows. Br. J. Nutr. 12:266.

Crampton, E.W. and Harris, L.E. 1968. Applied Animal Nutrition. (2nd Edition) W.H. Freeman & Co., San Francisco. p. 753.

Crampton, E.W. 1933. The comparative feeding value for livestock of barley, oats, wheat, rye and corn. N.R.C. report No. 28. In: Haeberle, B.G. 1974. M.Sc. Thesis, University of Manitoba, p. 7.

Crooker, B.A., Clarke, J.H. and Sharko, R.D. 1982. Rare earth elements as markers for rate of passage measurement of individual feedstuffs through the digestive tract of ruminants. J. Anim. Sci. 53:1353.

D'Appolonia, B.L. 1973. Structure and composition of cereal non-starchy polysaccharides as related to their potential industrial utilization. In: Industrial uses of Cereals, American Association of Cereal Chemists, Inc. St. Paul, Minnesota.

D'Appolonia, B.L., Gilles, K.A., Osman, E.M. and Pomeranz, Y. 1971. In: Y. Pomeranz (ed.) Wheat Chemistry and Technology. American Association of Cereal Chemists, Inc., St. Paul, Minnesota.

Dea, I.C.M. and Morrison, A. 1975. Chemistry and interaction of seed galactomannans. In: R.S. Tipson and D. Horton (eds.) Adv. Carbohydrate Chemistry. Biochem. Vol. 31. Academic Press, New York.

Dea, I.C.M. and Rees, A. 1973. Aggregation with change and conformation in solutions of hemicellulose xylans. Carbohydr. Res. 29:363.

Dehority, B.A. 1973. Hemicellulose degradation by rumen bacteria. Fed. Proc. 32:1819.

Dehority, B.A. 1967. Rate of isolated hemicellulose degradation and utilization by pure cultures of rumen bacteria. Appl. Microbiol. 15:987.

Dehority, B.A. and Scott, H.W. 1967. Extent of cellulose and hemicellulose digestion in various forages by pure culture of rumen bacteria. J. Dairy Sci. 50:1136.

Dehority, B.A. 1965. Degradation and utilization of isolated hemicellulose by pure cultures of cellulolytic rumen bacteria. J. Bacteriol. 89:1515.

Dehority, B.A. 1963. Isolation and characterization of several cellulolytic bacteria from in vitro rumen fermentations. J. Dairy Sci. 56:217.

Deodikar, G.B. 1963. Rye Secale cereale Linn Indian Council Agr. - Res: New Delhi.

Dinnusson, W.E., Haugse, C.N. and Knutson, R.D. 1971. Ergot in rations for fattening cattle. North Dakota Farm Res. 29:20.

Downs, A.M. and McDonald, I.W. 1964. The chromium-51 complex of ethylenediamine tetraacetic acid as a soluble rumen marker. Br. J. Nutr. 18:153.

Drews, E. and Seibel, W. 1976. Bread making and other uses around the world. In: W. Bushuk (ed.) Rye Production Chemistry and Technology. American Association of Cereal Chemists, Inc. St. Paul, Minnesota.

Drews, E. 1970. Beschaffenheitsmerkmale der Pentosane des Roggenmehles. Brot. Beback 24:41.

Eastwood, M.A. 1973. Vegetable fibre. Its physical properties. Proc. Nutr. Soc. 32:138.

Eggum, B.O. 1973. Biological availability of amino acid constituents in grain protein found in nuclear techniques for seed protein improvement. Inter. Atomic Energy Agency. Vienna.

el Shazley, K. and Hungate, R.E. 1966. Method for measuring diaminopemelic acid in total rumen contents and its application to the estimation of bacterial growth. Appl. Microbiol 14:27.

Ellis, W.C. 1968. Dysprosium as an indigestible marker and its determination by radioactive analysis. J. Agric. Ed. Chem. 16:220.

Elyssen, G. and De Somer, P. 1967. Effects of Streptococcus faecalis and a filterable agent on growth and nutrient absorption in Gnotobiotic chicks. Poultry Sci. 46:323.

Erwin, E.S., Marco, G.J. and Emery, E.M. 1961. Volatile fatty acid analysis of blood and rumen fluid by gas chromatography. J. Dairy Sci. 44:1768.

Evans, L.E., Dedio, W. and Hill, R.D. 1973. Variability of alkyl-resorcinol content of rye grain. Can. J. Plant Sci. 53:485.

Faichney, G.J. and Griffiths, D.A. 1978. Behavior of solute and particle markers in the stomach of sheep given a concentrate diet. Br. J. Nutr. 40:71.

Faichney, G.J. 1975. The use of markers to partition digestion within the gastrointestinal tract of ruminant. In: Digestion and Metabolism in the Ruminant, I.W. McDonald and A.C.I. Warner, ed., University of the New England Publishing Unit, Australia, p. 277.

Faichney, G.J. 1969. Production of volatile fatty acids in the sheep caecum. Aust. J. of Ag. Res. 20:491.

Fernandez, R., Kim, S.M., Buenrostro, J.L. and McGinnis, J. 1973. Triticale and rye as main ingredients in diets for laying hens. Poultry Sci. 52:2244.

Fernandez, R., Lucas, E. and McGinnis, J. 1973b. Fractionation of a chick growth depressing factor from rye. Poultry Sci. 52:2252.

Food and Agricultural Organization. 1972. Production Yearbook 26:43.

Forsberg, C.W., Beveridge, T.J. and Hilstrom, A. 1981. Cellulase and xylanase release from bacteriodes succinogenes and its importance in the rumen environment. Appl. Environ. Microbiol. 42:886.

Francis, G.L., Gawthorne, J.M. and Storer, G.B. 1978. Factors affecting the activity of cellulases isolated from the rumen digesta of sheep. Appl. Environ. Microbiol. 36:643.

Friend, D.W. 1970. Comparison of some milling products of barley and rye when fed to rats. Can. J. Anim. Sci. 50:345.

Friend, D.W. and MacIntyre, T.M. 1969. Digestibility of rye and its value in pelleted rations for pigs. Can. J. Anim. Sci. 49:375.

Gaillard, B.D.E. and Richards, G.N. 1975. Presence of soluble lignin-carbohydrate complexes in the bovine rumen. Carbohydrate Res. 42:135.

Gawthorne, J.M. 1979. Extracellular carbohydrase complex from rumen contents. Anm. Rech. Vet. 10:249.

Goering, H.K. and Van Soest, P.J. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). U.S. Dept. of Agric. Handbook #379, pp. 8.

Goings, R.L., Braund, D.G., Dolge, K.L. and Steele, R.L. 1976. Acceptability of dairy grain mixes containing rye or feed flavors. Final report of the dairy research Co-Op research farm Fabius, New York (unpublished).

Goldsmith, H. and Perlin, A.S. 1963. Interbranch sequences in the wheat arabinoxylan. Selective enzymolysis studies. Can J. Chem. 41:2272.

Golenkov, V.F. and Traubenberg. 1966. Study of swelling and water soluble carbohydrates of winter rye. Prikladnaya Biokhim. Mikrobiol. 2:27.

Goodall, E.D. and Kay, R.N.B. 1973. The use of the chromium complex of ethylenediaminetetraacetic acid for studies of digestion in sheep. Proc. Nutr. Soc. 32:22A.

Gorleau, D. and Forsberg, C.W. 1981. Cellulolytic activity of the rumen bacterium Bacteriodes succinogenes. Can. J. Microbiol. 27:517.

Graber, G., Thomas, M.C., Lucas, E.W. and Norvell, M.J. 1976. Influence of grain type on the magnitude of the antibiotic response. Poultry Sci. 53:1929 (Abstract).

Gradel, C.M. and Dehority, B.A. 1972. Fermentation of isolated pectin and pectin from intact forages by pure cultures of rumen bacteria. Appl. Microbiol. 23:332.

Grovum, W.L. and Hecker, J.F. 1973. 1. Rate of passage of digesta in sheep. 2. The effect of level of feed intake on digesta retention times and on water and electrolyte absorption in the large intestine. Br. J. Nutr. 30:221.

Haeberle, B.C. 1974. Mode of inheritance and nutritional significance of the 5-n-alkylresorcinols of rye (Secale cereale L.) M.Sc. Thesis, University of Manitoba.

Haley, T.J. 1965. Pharmacology and toxicology of the rare earth elements. J. Pharm. Sciences 54:663.

Hartnell, G.F. and Satter, L.D. 1979a. Extent of particulate marker (Samarium, Lanthanium, Cerium) movement from one digesta particle to another. J. Anim. Sci. 48:375.

Hartnell, G.F. and Satter, L.D. 1979b. Determination of rumen fill, retention time and ruminal turnover rates of ingesta at different states of lactation in dairy cows. J. Dairy Sci. 48:381.

Heald, P.J. 1953. The fermentation of xylans in the rumen of sheep. Br. J. of Nutr. 7:124.

Heald, P.J. 1951. The fermentation of pentoses and uronic acids by bacteria from the rumen contents of sheep. J. Biochem. 50:503.

Hembry, F.G., Bell, M.C. and Hall, R.F. 1967. Intestinal carbohydrase activity and carbohydrate utilization in mature sheep. J. Nutr. 93:175.

Ho, T.L. 1977. Hard and soft acids and bases principles in organic chemistry. Academic Press, N.Y.

Hobson, P.N. and Wallace, R.J. 1982. Microbial ecology and activities in the rumen. Part I and Part II. Critical reviews in Microbiol Apr. (pp. 165-225) and May (253-320).

Hogan, J.P. 1964. The digestion of food by the grazing sheep. 1. The rate of flow of digesta. Aust. J. Agric. Res. 26:199.

Holas, J. and Hampl. J. 1973. Study of pentosans during rye bread production. Scientific Papers of the Institute of Chemical Technology (Food) Prague E38, pp. 53.

Holas, J., Hampl, J. and Picmanova, B. 1972. Uber die hemizellulosen des roggenborns. Getreide Hehl Brot. 26:144.

Holas, J., Hampl, J. and Karlova, S. 1971. Bietrag zur strukturforschung der Roggenpentosane. Scientific Papers of the Institute of Chemical Technology (Food), Prague E35, pp. 279.

Holdeman, L.V., Good, I.J. and Moore, W.E.C. 1976. Appl. Environ. Microbiol. 31:359.

Holloway, W.D., Tasman-Jones, C. and Bell, E. 1980. The hemicellulose component of dietary fiber. Am. J. Clin. Nutr. 33:260.

Holmes, J.H.G., Drennan, M.J. and Garret, W.N. 1970. Digestion of steam processed milo by ruminants. J. Anim. Sci. 31:409.

Howard, B.H. 1967. In: Symbiosis 2:317. Academic Press, New York.

Howard, B.H. 1955. Ruminal fermentation of pentosan. J. Biochem. 60:i.

Huhtanen, C.N. and Pensack, J. 1965. The role of Streptococcus faecalis in the antibiotic growth effect in chickens. Poultry Sci. 44:830.

Hulse, J.H. and Laing, E.M. 1974. Nutritive value of triticale protein. Int. Develop. Res. Cent: Ottawa, Canada.

Hungate, R.E. 1966. The rumen and its microbes. Academic Press. New York, N.Y.

Hungate, R.E. 1950. The anaerobic mesophilic cellulolytic bacteria. Bacteriol. Rev. 14:1.

Hutcheon, W.L. and Paul, E.A. 1966. Control of protein content of Thatcher wheat by nitrogen fertilizer and moisture stress. Can. J. of Soil. Sci. 46:101.

Hutton, K. and Annison, E.F. 1972. Control of nitrogen metabolism in the ruminant. Proc. Nutr. Soc. 31:151.

Hyden, S. 1961. The use of reference substances and the measurement of flow in the alimentary tract. In: Digestive Physiology and Nutrition of the Ruminant. D. Lewis (ed.) Butterworths, pp. 35.

Hyden, S. 1955. A turbidimetric method for determination of higher polyethylene glycols in biological materials. Ann. Roy. Agr. Coll. Sweden. 22:139.

Ibrahim, E.A. and Ingalls, J.R. 1972. Microbial protein biosynthesis in the rumen. J. Dairy Sci. 55:971.

Ingalls, J.R. and Phillips, G.D. 1971. Effect of triticale ergot on calf growth. Can. J. Anim. Sci. 51:819.

Joyner, A.E. and Baldwin, R.L. 1966. Enzymatic studies of pure cultures of rumen microorganisms. J. Bacteriol. 93:1321.

Karr, A.L. and Albersheim, P. 1970. Polysaccharide degrading enzymes are unable to attach plant cell walls without prior action by a wall-modifying enzyme. Plant Physiol. 46:69.

Karr, M.R., Little, C.O. and Mitchell, G.E. 1966. Starch disappearance from different segments of the digestive tract of steers. J. Anim. Sci. 25:652.

Kaufman, W. 1979. In: Feeding strategy for the high yielding dairy cow. W.H. Broster and H. Swan (ed.) Granada Publishing Ltd., Frogmore, England, p. 90.

Kearns, D.R., Wolfson, J.M. and Jones, C.R. 1978. Rare earth ion probes of metal binding sites on yeast tRNAphe. In: The Rare Earths in Modern Science and Technology, ed. by Gregory, J. McCarthy and J.J. Rhyne, Plenum Press, N.Y.

Kennelly, J.J., Turner, B.V. and Apps, M.J. 1982. Determination of non radioactive liquid phase markers CO-EDTA and CR-EDTA, by neutron activation analysis. J. Sci. Food Agr. 33:1235.

Kennelly, J.J., Apps, M.J., Turner, B.V. and Aherne, F.X. 1980. Dyprosium, Cerium and Chromium marker determination by Instrumental Neutron Activation Analysis. Can. J. Anim. Sci. 60:749.

Kern, D.L., Slyter, L.L., Weaver, J.M. and Oltjen, R.R. 1974. Ponies vs. steers: Microbial and chemical characteristics of intestinal ingesta. J. Anim. Sci. 38:559.

Kern, D.L., Slyter, L.L., Weaver, J.M., Leffel, E.C. and Samuelson, G. 1973. Pony cecum vs. steer rumen: The effect of oats and hay on the microbial ecosystem. J. Anim. Sci. 37:463.

Keys, J.E. Jr., Van Soest, P.J. and Young, E.P. 1969. Comparative study of the digestibility of forage cellulose and hemicellulose in ruminants and nonruminants. J. Anim. Sci. 29:11.

Kihlberg and Erickson. 1964. Amino acid composition of rye flour and the influence of amino acid supplementation of rye flour and bread on growth, nitrogen efficiency ratio and liver fat on the growing rat. J. Nutr. 82:385.

Kim, S.K. and D'Applonia, B.L. 1976. Note on a simplified procedure for the purification of wheat flour pentosans. Cereal Chem. 53:871.

Kim, Y.S., Spritz, N., Blum, M., Terz, J. and Sherlock, P. 1966. The role of altered bile acid metabolism in the steatorrhea of experimental blind loop. J. of Clin. Invest. 45:956.

King, K.W. 1961. Enzymes of the cellulose complex. Adv. Chem. Ser. 95:7.

Kistner, A. 1965. Physiology of digestion in the ruminant. Washington, D.C. Butterworths In. PT 419.

Knipfel, T. 1979. Comparative protein quality of triticale, wheat and rye. Cereal Chem. 46:313.

Kotb, A.R. and Luckey, T.D. 1972. Markers in nutrition. Nutr. Abstr. Rev. 42:813.

Kyker, G.C. 1962. Rare earths. In Mineral Metabolism. C.L. Comar and F. Bronner, eds., Chap. 36, Vol. 2, part B, Academic Press, New York.

Ladd, J.N. 1959. The fermentation of lactic acid by a gram negative coccus. Bio. Chem. J. 71:16.

Latham, M.J., Brooker, B.E., Pettipher, G.L. and Harris, P.J. 1978a. Ruminococcus flavefaciens cell coat and adhesion to cotton cellulose and to cell walls in leaves of perennial rye grass. Appl. Environ. Microbiol. 35:

Latham, M.J., Brooker, B.E., Pettipher, G.L. and Harris, P.J. 1978b. Adhesion of Bacteriodes succinogenes in pure culture and in the presence of Ruminococcus flavefaciens to cell walls in leaves of perennial rye grass. Appl. Environ. Microbiol. 35:1166.

Lascano, C. and Ellis, W.C. 1979. An evaluation of lanthanides as particulate markers. (Abs.) 71st Annual meeting of Am. Soc. of Anim. Sci.

Lazar, V.A. and Monson, W.G. 1965. X-ray spectrographic determination of chromic oxide in steer feces. J. Agric. Fd. Chem. 13:161.

Leat, W.M.F. and Harrison, F.A. 1969. Lipid digestion in the sheep. Effect of bile and pancreatic juice on the lipids of intestinal contents. Quar. J. Exp. Physiol. 59:131.

Leatherwood, J.M. 1973. Cellulose degradation of Ruminococcus. Fed. Proc. 32:1814.

Leatherwood, J.M. 1969. In: Cellulases and their application. Advan. Chem. 95:53. E.T. Reese and G. Hajny, eds. Amer. Chem. Soc. Washington, D.C.

Leng, R.A. 1969. Formation and production of volatile fatty acids in the rumen. In: Physiology of Digestion and Metabolism in the Ruminant. Ed. A.T. Phillipson, Oriel Press, pp. 636.

Lindas, C. and D/Applonia, B.L. 1972. Note on the effect of purification treatment on water soluble pentosans. Cereal Chem. 49:731.

Lindsay, J.R. and Hogan, J.P. 1972. Digestion of two legumes and rumen bacterial growth in defaunated sheep. Aust. J. Agr. Res. 23:321.

Luckey, T.D., Venugopal, B. and Hutcheson, W. 1975. Heavy metal toxicity and safety. Environ. Qual. Saf. Suppl. 1.

MacAuliffe, T., Zaviezo, D. and McGinnis, J. 1979. Effect of gamma irradiation, fractionation, and penicillin supplementation on the rachitogenic activity of rye for chicks. Poultry Sci. 58:329.

MacAuliffe, T. and McGinnis, J. 1971. Effects of antibiotic supplements to diets containing rye on chick growth. Poultry Sci. 50:1130.

MacRae, J.C. 1974. The use of intestinal markers to measure digestive function in ruminants. Proc. Nutr. Soc. 33:147.

MacRae, J.C. and Armstrong, D.G. 1969. Studies on intestinal digestion in the sheep. 2. Digestion of some carbohydrate constituents in hay, cereal and hay-cereal rations. Br. J. Nutr. 23:377.

Mann, S.O. and Orskov, E.R. 1973. The effect of rumen and post-rumen feeding of carbohydrates on the caecal microflora of sheep. J. of Appl. Bacteriol. 36:475.

Mares, D.J. and Stone, B.A. 1973a. Studies on wheat endosperm. I. Chemical composition and ultrastructure of cell walls. Aust. J. Biol. Sci. 26:793.

Marquardt, R.R., Ward, A.T. and Misir, R. 1979. The retention of nutrients by chicks fed rye diets supplemented with amino acids and penicillin. Poultry Sci. 58:631.

Martnell, A.E. 1974. Organic ligands. In: Stability constants of metal ion complexes. (Sillen, L.G., Martnell, A.E.; eds). Special Publ. No. 25. The Chemical Society, London, 1974.

Marusich, W.L., Ogrinz, E.F., Camerlengo, N. and Mitrovic, M. 1978. Use of a rye-soybean ration to evaluate growth promotants in chickens. Poultry Sci. 57:1297.

Mayes, R.W. and Orskov, E.F. 1974. The utilization of gelled maize starch in the small intestine of sheep. Br. J. Nutr. 32:143.

McDonald, B.E., Zillman, P. and Larter, E.N. 1974. Assessment of triticale for factors affecting feed intake and growth of mice. Paper No. 103. Triticale Symposium, 34th Annual Meeting of Food Technologists. New Orleans. May 12-15, 1974.

McGinnis, J. 1972. Biological evaluation of cereal grains for nutritional value, triticale, rye wheat, Rep. submitted to Rockfeller Foundation on CIMMYT - Dept. of Anim. Sci., Washington State University, Pullman, Wash. 99163. In: Hulse, J.H. and Laing, E.M. 1974. Pg. 100.

McKeon, F.W. and Eagan, D.A. 1971. Lameness in cattle fed ergotized silage. Irish Vet. J. 25:67.

McNeal, F.H., Berg, M.A., McGuire, C.F., Steward, V.R. and Baldridge, D.E. 1972. Grain and plant nitrogen relationships in eight spring wheat caryopses. Crop Sci. 12:599.

McNeil, M., Albersheim, P., Taiz, L. and Jones, R.L. 1975. The structure of plant cell walls. Plant Physiol. 55:64.

McNeill, J.W., Tucker, R.E., Schelling, G.T. and Mitchell, G.E. Jr. 1974. Abstract 83. Ovine maltase response to level of carbohydrate intake. J. Anim. Sci. 38:232. (Abstract).

McNeill, J.W., Potter, G.D. and Riggs, J.K. 1971. Ruminal and postruminal carbohydrate utilization in steers fed processed sorghum grain. J. Anim. Sci. 33:1371.

Medcalfe, D.G., D'Appolonia, B.L. and Gilles, K.A. 1968. Comparison of chemical composition and properties between hard red spring and durum wheat endosperm pentosan. Cereal Chem. 48:539.

Metzler, D.E. 1977. Fermentations based on the Embden Meyerhof pathway. In: Biochemistry and chemical reactions of living cells. Academic Press, San Francisco, p. 547.

Miller, D.F. 1958. Composition of cereal grains and forages. Publication 585, National Academy of Science N.R.C., Washington, D.C.

Miller, T.L. and Jenesel, S.E. 1979. Enzymology of butyrate formation by Butyrivibrio fibrisolvens. J. Bact. 138:98.

Minato, H., Endo, A., Highuchi, M., Ootamo, Y. and Uemura, T. 1966. Ecological treatise on the rumen fermentation. I. The fractionation of bacteria attached to the digesta solids. J. Gen. Appl. Microbiol. 12:39.

Mink, R.W. and Hespell, R.B. 1978. Starvation and survival of Selenomonas ruminatium. Pg. 86 in Abstr. Ann. Mtg. An. Soc. Microbiol.

Misir, R. and Marquardt, R.R. 1978. Factors affecting rye utilization in growing chicks. III. The influence of milling fractions. Can. J. Anim. Sci. 58:717.

Misir, R. and Marquardt, R.R. 1978a. Factors affecting rye (Secale cereale L.) utilization in growing chicks. I. The influence of rye level, ergot and penicillin supplementation. Can. J. Anim. Sci. 58:691-701.

Misir, R. and Marquardt, R.R. 1978b. Factors affecting rye (Secale cereale L.) utilization in growing chicks. II. The influence of protein type, protein level and penicillin. Can. J. Anim. Sci. 58:703.

Misir, R. and Marquardt, R.R. 1978c. Factors affecting rye (Secale cereale L.) utilization in growing chicks. IV. The influence of autoclave treatment, pelleting, water extraction and penicillin supplementation. Can. J. Anim. Sci. 58:731.

Mod, R.R., Ory, R.L., Morris, N.M. and Normand, F.L. 1981. Chemical properties and interactions of rice hemicellulose with trace minerals in vitro. J. Agric. Food Chem. 29:449.

Monod, J. 1949. The growth of bacterial cultures. Ann. Rev. Microbiol. 25:71.

Montgomery and Baumgardt. 1965a. Regulation of food intake in ruminants. 1. Pelleted rations varying in energy concentration. J. Dairy Sci. 48:569.

Montgomery and Baumgardt. 1965b. Regulation of food intake in ruminants. 2. Rations varying in energy concentration and physical form. J. Dairy Sci. 48:1623.

Montgomery, R. and Smith, F. 1956. A review of carbohydrates of wheat and other cereal grain. Agr. Food Chem. 8:716.

Moore, H.I. 1966. Grass and grasslands, New Naturalist, Vol. 48, Collins, London.

Moran, E.T. Jr., Lall, S.P. and Summers, J.D. 1970. Altering the proportion of rye to maize in the grain fraction of practical broiler rations: Effect on live performance, litter moisture, dressing yield and carcass quality. Brit. Poultry Sci. 11:147.

Moran, E.T. Jr., Lall, S.P. and Summers, J.D. 1969. The feeding value of rye for the growing chick: Effect of enzyme supplements, antibiotics, autoclaving and geographical area of production. Poultry Sci. 48:939.

Morgan, C.A. and Campling, R.C. 1978. Digestibility of whole barley and oat grains by cattle of different ages. Anim. Prod. 27:323.

Morrill, J.L., Abe, R.K., Dayton, A.D. and Deyoe, C.W. 1970. Feeding young calves processed starch combined with an amylolytic enzyme. J. Dairy Sci. 53:566.

Morrison, F.B. 1957. Feeds and Feeding. The Morrison Publishing Co. Ithaca, N.Y.

Morrison, I.M. 1979. Carbohydrate metabolism in the ruminant. (Symposium) Proc. Nutr. Soc. 38:269.

Munck, L. 1972. Improvement of nutritional value in cereals. Heriditas 72:1.

Munck, L. 1964. The variation of nutritive value in barley. Heriditas 52:1.

Murphy, M.R., Baldwin, R.L. and Koony, L.J. 1982. Estimation of stoichiometric parameters for rumen fermentation of roughage and concentrates diets. J. Anim. Sci. 55:411.

National Academy of Sciences. 1971. Atlas of Nutritional Data on United States and Canadian Feeds. Washington, D.C. pp. 772.

Neilson, M.J. and Richards, G.N. 1978. The fate of the soluble lignin carbohydrate complex produced in the bovine rumen. J. Sci. Food Agr. 29:513.

Nelson, K.J. and Potter, N.N. 1980. Iron availability from wheat gluten, soy isolate, and casein complexes. J. Food Sci. 45:52.

Neudoerffer, T.S., McLaughlin, D.R., Slinger, S.J. and Horney, F.D. 1973. Difficulties associated with the use of tritiated polyethylene glycol as a water-soluble digestion marker in ruminants. J. Anim. Sci. 36:749.

Neukom, H. and Markwalder, H.U. 1978. Oxidative gelation of wheat flour pentosans: A new way of cross-linking polymers. Cereal Foods World 23:374.

Neukom, H. 1976. Chemistry and properties of the non-starchy polysaccharides (NSP) of wheat flour. Review article - Lebensm - Wiss. & Technol. 9:143.

Neukom, H., Providole, L., Gremli, H. and Hui, P.A. 1967. Recent investigations on wheat flour pentosans. Cereal Sci. 44:238.

Nicholson, J.W.G. and Sutton, J.D. 1969. The effect of diet composition and level of feeding on digestion in the stomach and intestine of sheep. Br. J. Nutr. 23:585.

Norman, A.G. 1937. The biochemistry of cellulose. Clarendon Press, Oxford.

Oklahoma Feed Manufacturers Assoc. 1964. Fifteenth annual Oklahoma feed industry conference and workshop, March 6-7, 1964. Oklahoma State University, Stillwater, p. 18.

Orskov, E.R. 1982. Protein Nutrition in Ruminants. Academic Press Inc. (London) Ltd., p. 108.

Orskov, E.R., Soleman, H.S. and MacDearmid, A. 1978. Intake of hay by cattle given supplements of barley subjected to various forms of physical treatment or treated with alkali. J. Agric. Sci. Camb. 90:611.

Orskov, E.R. and Greenhalgh, J.F.D. 1977. Alkali treatment as a method of processing whole grain for cattle. J. Agric. Sci. Camb. 89:253.

Orskov, E.R. 1976. The effect of processing on digestion and utilization of cereals by ruminants. Proc. Nutr. Soc. 35:245.

Orskov, E.R. 1973. The capacity for digestion of carbohydrates in different segments of the gut of ruminants. In: Production diseases in farm animals: Whitefriar Press Ltd., London, England.

Orskov, E.R., Mayes, R.W. and Mann, S.O. 1972. Postruminal digestion of sucrose in sheep. Br. J. of Nutr. 28:425.

Orskov, E.R., Fraser, C. and McDonald, I. 1971. (B) Br. J. of digestion of concentrates in sheep. 3. Effects of rumen fermentation of barley and maize diets on protein digestion. Br. J. of Nutr. 26:477.

Orskov, E.R., Mayes, R.W. and Penn, A. 1971. (Part of: Abstracts of Communications 224th Scientific Meeting). The capacity for the removal of glucose from the small intestine by mature sheep. (Abstract). Proc. Nutr. Soc. 30:43A.

Orskov, E.R., Fraser, C., Mason, V.C. and Mann, S.D. 1970. Influence of starch digestion in the large intestine of sheep on caecal fermentation, caecal microflora and faecal nitrogen excretion. Br. J. Nutr. 24:671.

Orskov, E.R. and Foot, M.H. 1969. (Part of: Abstracts of Communications 203rd meeting). The influence of caecal starch infusion in sheep on faecal output of nitrogen, starch and dry matter. (Abstract). Proc. Nutr. Soc. 28:31A.

Orskov, E.R., Flatt, W.P., Moe, P.W., Munson, A., Hemken, R.W. and Klatz, I. 1969. The influence of ruminal infusion of volatile fatty acids on milk yield and composition and on energy utilization by lactating cows. Br. J. Nutr. 23:443.

Packett, L.V., Myers, L.L. and Jackson, H.D. 1966. Gastrointestinal content and mucosal oxidation of volatile fatty acids in sheep. J. Anim. Sci. 25:402.

Painter, T.J. and Neukom, H. 1968. The mechanism of oxidative gelation of a glycoprotein from wheat flour. Evidence from a Model System Based Upon Caffeic Acid. Biochimica et Biophysica Acta 158:363.

Papasolomontos, S.A. 1977. Digestion of heat processed cereal by an adult sheep. Ph.D. Thesis. University of Newcastle Upon Tyne.

Parra, R. 1978. In: The Ecology of Arboreal Folivores. G.G. Montgomery, ed. Smithsonian Institution Press, Washington, D.C. Pg. 205.

Patel, M.B., Jami, M.S. and McGinnis, J. 1980. Effect of gamma irradiation, penicillin and/or pectic enzyme on chick growth depression and fecal stickiness caused by rye, citrus pectin and guar gum. Poultry Sci. 59:2105.

Perlin, A.S. and Reese, E.T. 1963. Dimensions of the substrate site involved in the enzymolysis of a polysaccharide. Can. J. Biochem. Physiol. 41:1842.

Perlin, A.S. 1951a. Structure of the soluble pentosans of wheat flours. Cereal Chem. 28:382.

Perlin, A.S. 1951b. Isolation and composition of the soluble pentosans of wheat flours. Cereal Chem. 27:370.

Perry, T.W., Hammond, L.M., Peterson, R.C. and Beeson, W.M. 1970. Value of roasting corn and of injectable vitamin E or selenium for finishing heifers. Ind. Cattle Feeders Day Rep. Mar. 26, 1970, pp. 29-32. Purdue Univ. Agric. Exp. Stn.

Pettipher, G.L. and Latham, M.J. 1979a. Characteristics of enzymes produced by Ruminococcus flavefaciens which degrade plant cell walls. J. Gen. Microbiol. 110:21.

Pettipher, G.L. and Latham, M.J. 1979b. Production of enzymes degrading plant cell walls and fermentation of cellobiose by Ruminococcus flavefaciens in batch and continuous culture. J. Gen. Microbiol. 110:29.

Podrazky, V. and Fantik, J. 1964. Increase of the viscosity values of gums during storage of rye flour. Cereal Chem. 42:107.

Poppi, D.P. 1980. Voluntary intake of leaf and stem fractions of tropical forage offered to cattle and sheep. Ph.D. Thesis, Univ. of Queensland.

Preece, I.A. and MacDougall, M. 1958. Enzymic degradation of cereal hemicellulose. II. Pattern of pentosan degradation. J. Inst. Brew. 64:489.

Preece, I.A. and Hobrick, R. 1955. Non-starchy polysaccharides of cereal grains. VII. Preliminary study of pentosan enzymolysis. J. Inst. Brew. 61:393.

Preece, I.A. and Hobrick, R. 1953. Non-starchy polysaccharides of cereal grains. (Higher molecular gums of common cereals). J. Inst. Brew. 59:385.

Preece, I.A. and MacKenzie, K.G. 1952. Non-starchy polysaccharides of cereal grains. (Distribution of water-soluble gum-like materials in cereals). J. Inst. Brew. 58:457.

Prins, R.A. 1977. Biochemical activities of the gut microorganisms. In: R.J. Clarke and T. Bauchop (ed.). Microbial ecology of the gut. Academic Press Inc., London, England.

Purser, D.B. and Buechler, M.S. 1966. Amino acid composition of rumen organisms. J. Dairy Sci. 49:81.

Rees, D.A. and Scott, W.E. 1971. Polysaccharide conformation. Part VI. Computer model-building for linear and branched pyranoglycans. Correlations with biological function. Preliminary assessment of inter-residue forces in aqueous solution. Further interpretation of optical rotation in terms of chain conformation. J. Chem. Soc. B:469.

Rees, D.A. 1967. The shapes of polysaccharides: carbohydrate polymers. Oliver and Boyd Ltd. London.

Reid, R.L. 1950. Studies on the carbohydrate metabolism of sheep. 1. The range of blood-sugar values under several conditions. Aust. J. of Agr. Res. 1:182.

Russell, J.B. and Hespell, R.B. 1981. Microbial rumen fermentation. J. Dairy Sci. 69:1153.

Russell, J.B. and Baldwin, R.L. 1979. Comparison of substrate affinities among several rumen bacteria. A possible determinant of rumen bacterial competition. Appl. Environ. Microbiol 37:537.

Russell, J.B. and Baldwin, R.L. 1978. Substrate preferences in rumen bacteria. Evidence of catabolite regulatory mechanisms. Appl. Environ. Microbiol 36:319.

Russell, J.R., Young, A.W. and Jorgensen, N.A. 1981. Effect of dietary corn starch intake on ruminal small intestinal and large intestine starch digestion in cattle. J. Anim. Sci. 52:1170.

Satter, L.D. 1980. Protein requirement for cattle. Oklahoma State University. Proceedings of an International Symposium at Oklahoma State University. November 19-21, p. 282.

Satter, L.D. and Roffler, R.E. 1975. Nitrogen requirement and utilization in dairy cattle. J. Dairy Sci. 58:1237.

Schuh, J.D., Lima, O.A., Hale, W.H. and Theurer, B. 1970. Steam-processed flaked grains versus steam-rolled grains for dairy calves. J. Dairy Sci. 53:475.

Schneider, V.W. and Lantzsch, H.J. 1971. Die Verdaulechkeit verschiedener Roggenschrote nach Versuchen met Hammelun und Schweinen. Landwirtsch, Forsch 24:217.

Scott, M.L., Nesheim, M.C. and Young, R.J. 1976. Nutrition of the chicken. M.L. Scott and Associates, Ithaca, New York.

Shane, B.S., Gouws, L. and Kistner, A. 1969. Cellulolytic bacteria occurring in the rumen of sheep conditioned to low protein Teff hay. J. Gen. Microbiol. 55:445.

Sharma, H.R., Ingalls, J.R. and McKirdy, J.A. 1983. Feeding value of alkali treated whole rye (Secale cereale L.) grain for lactating cows and its digestibility for sheep. Anim. Feed Sci. Technol. 10:77.

Sharma, H.R., Ingalls, J.R., McKirdy, J.A. and Sanford, L.M. 1981. Evaluation of rye grain in the diets of young Holstein calves and lactating dairy cows. J. Dairy Sci. 69:441.

Sheppard, A.J., Forbes, R.M. and Johnson, C.B. 1959. Rate of acetic acid formation in the rumen determined by isotope dilution. Proc. Soc. Expt. Biol. Med. 101:715.

Siddons, R.C. 1968. Carbohydrase activities in the bovine digestive tract. Biochem. J. 108:839.

Sikka, K., Duggal, S.K., Singh, R., Gupta, D.P. and Joshi, M.G. 1978. Comparative nutritive value and amino acid content of triticale, wheat and rye. J. Ag. Food Chem. 26:788.

Sinha, K.N., Martz, F.A., Johnson, H.D. and Hahn, L. 1970. Use of polyethylene glycol in estimating volume and weight of rumen contents and digestion in cattle. J. Anim. Sci. 30:467.

Smith, P.H., Sweeney, J., Rooney, K., King, W. and Moore, W.E. 1956. Stratifications and kinetic changes in the ingesta of the bovine rumen. J. Dairy Sci. 39:598.

Smith, R.E. and MacIntyre, T.M. 1960. The feeding value of rye to growing chickens. Can. J. Anim. Sci. 40:107.

Snedecor, G.W. and Cochran, W.G. 1967. Statistical Methods (6th ed.). The Iowa State University Press, Ames, Iowa, U.S.A.

Southgate, D.A.T. 1973. Fibre and the other unavailable carbohydrates and their effects on the energy value of the diet. Proc. Nutr. Soc. 32:131.

Sperber, I., Hyden, S. and Ekman, J. 1953. The use of polyethylene glycol as a reference substance in the study of ruminant digestion. Ann. Roy. Agr. Coll. Sweden, 30:337.

Stevens, C.E. 1978. Physiological implications of microbial digestion in the large intestine of mammals: Relation to dietary factors. Am. J. Clin. Nutr. 31:S161.

Storry, J.E. and Rook, J.A.F. 1965. The effects of a diet low in hay and high in flaked maize on milk-fat secretion of certain constituents in the blood plasma of the cow. Br. J. Nutr. 19:101.

Tacu, A. 1972. Lucraride Stuntifice ale Institutului de Cercetari pentru Nutritie Animala Nut. Abstr. and Rev. 44:520. Abstr. 4609.

Takeda, H. and Kritchevsky, D. 1976. Correlation between the physical properties of dietary fibers and their protective activity against amaranth toxicity in rats. J. Nutr. 109:388.

Teeter, R.G. and Owens, F.N. 1983. Characteristics of water soluble markers for measuring rumen liquid volume and dilution rate. J. Anim. Sci. 56:717.

Thompson, D.J., Beever, D.E., Coelha de Silva, J.F. and Armstrong, D.G. 1972. Br. J. Nutr. 28:347.

Till, A.R. and Downes, A.M. 1965. The preparation of tritium-labelled polyethylene glycol and its use as a soluble rumen marker. Br. J. Nutr. 19:435.

Tkachuk and Irvin. 1969. Amino acid compositions of cereals and oil-seed meals. Cereal Chem. 46:206.

Topps, J.H., Kay, R.N.B. and Goodall, E.E. 1968. The fate of carbohydrates in the small intestine of the ruminant. Br. J. of Nutr. 22:261.

Uden, P., Colucci, P.E. and Van Soest, P.J. 1980. Investigation of chromium, cerium and cobalt as markers in digesta and rate of passage studies. J. Sci. Food Agric. 31:625.

Ulyatt, M.J., Waghorn, G.C., John, A., Reid, C.W.S. and Munroe, J. 1983. Effect of intake and feeding frequency on feeding behavior and quantitative aspects of digestion in sheep fed chaffed lucerne hay. (Unpublished).

Ulyatt, M.J., Dellow, D.W., Reid, C.S.W. and Bauchop, T. 1975. Structure and function of the large intestine. In: Digestion and metabolism in the ruminant (ed.) McDonald, I.W. and Wrner, A.C.I. The University of New England Publishing Unit. Armidale, W.S.W. 2351 Australia.

Ulyatt, M.J. and MacRae, J.C. 1974. Quantitative digestion of digestion of fresh herbage by sheep. 1. The sites of digestion of organic matter, energy, readily fermentable carbohydrate, structural carbohydrate and lipid. J. Agric. Sci. (Camb.) 82:295.

Ulyatt, M.J. 1964. The use of polyethylene glycol as a marker for measuring rumen water volume and the rate of flow of water from the rumen of grazing sheep. J. Agric. Res. 7:713.

Underwood, E.J. 1977. Trace elements in human and animal nutrition. Academic Press, New York.

Untawale, G.G. and McGinnis, J. 1979. Effect of rye and levels of raw and autoclaved beans (Phaseolus vulgaris) on adhesion of microflora to the intestinal mucosa. Poultry Sci. 58:928.

Van Soest, P.J. 1980. Rumen function conference. Oklahoma Agr. Exp. Sta. Misc. Publication.

Venugopal, B. and Luckey, T.D. 1975. Toxicology of nonradioactive heavy metals and their salts. Environ. Qual. Saf. Suppl. 1:4.

Verdeal, K. and Lorenz, K. 1977. Alkylresorcinols in wheat, rye and triticale. Cereal Chem. 54:475.

Vogels, G.D., Hoppe, W.F. and Strumm, C.K. 1980. Association of methanogenic bacteria with rumen ciliates. Appl. Environ. Microbiol. 40:608.

Wagner, D.D. and Thomas, O.P. 1978. Influence of diets containing rye or pectin on the intestinal flora of chicks. Poultry Sci. 57:971.

Wagner, D.D. and Thomas, O.P. 1977a. Pectin, the probable major growth depressing factor in rye. In: Proc. Maryland Nutr. Conf. for Feed Manuf. pp. 92.

Wagner, D.D. and Thomas, O.P. 1977b. A rye type growth depression of chicks fed pectin. Poultry Sci. 56:615.

Walker, D.M. 1959. The development of the digestive system of the young animal. 1. Carbohydrase enzyme development in the young lamb. J. Agric. Sci. (Camb.) 53:374.

Walker, D.J. 1965. In: Second International Symposium on the Physiology of digestion in the ruminant, pp. 296. R.W. Dougherty, ed. Butterworth Inc.

Wallnofer, P. and Baldwin, R.L. 1967. Pathway of propionate formation in Bacteriodes ruminicola. J. Bacteriol. 93:504.

Wallnofer, P., Baldwin, R.L. and Stagno, E. 1966. Conversion of C14 labelled substrates to volatile fatty acids by the rumen. Appl. Microbiol. 14:1004.

Walker, D.J., Eagan, A.R., Nader, C.J., Ulyatt, M.J. and Storer, G.B. 1975. Rumen microbial protein synthesis and non microbial nitrogen flowing to the intestine of sheep. Aust. J. Agric. Res. 26:699.

Ward, A.T. 1982. The effect of fat type and various treatments on the antinutritional properties of rye (Secale cereale L.) and the partial isolation of rye fractions containing the antinutritional compounds (pentosans). Ph.D. Thesis. Dept. of Anim. Sci., University of Manitoba.

Ward, A.T. and Marquardt, R.R. 1981. Effect of rye grain and its fractionation products on nutrient retention of growing chickens. Poultry Sci. 60:1751.

Ward, P.F.V., Scott, T.W. and Dawson, R.M.C. 1964. The hydrogenation of unsaturated fatty acids in the ovine digestive system. Biochem. J. 92:60.

Warner, A.C.I. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutr. Abstr. and Review 51:789.

Warner, A.C.I. 1969. Binding of the 51 Cr complex of ethylenediamine tetraacetic acid to particulate matter in the rumen. Vet. Record 84:441.

Warner, A.C.I. and Stacy, B.D. 1968. The fate of water in the rumen. 1. A critical appraisal of the use of soluble markers. Br. J. Nutr. 22:369.

Weiringa, G.W. 1967. On the occurrence of growth inhibiting substances in rye. Institute for storage and processing of agricultural produce. Publ. 156, Wageningen, Netherlands.

Welch, J.G. and Smith, A.M. 1978. Particle sizes passed from rumen. J. Anim. Sci. 46:309.

Wellers, R.A., Pilgrim, A.F. 1974. Passage of protozoa and volatile fatty acids from the rumen of the sheep and from a continuous in vitro fermentation system. Br. J. Nutr. 32:341.

Wellers, R.A., Pilgrim, A.F. and Gray, F.V. 1962. Digestion of foodstuffs in the rumen of the sheep and the passage of digesta through its compartments. 3. The progress of nitrogen digestion. Br. J. Nutr. 16:83.

Wenckert, E., Leosere, M., Mahapatra, S.N., Wilson, E.M. and Schenker, F. 1964. Wheat bran phenols. J. Org. Chem. 29:435.

Weston, R.H. and Hogan, J.P. 1967. The digestion of chopped and ground roughages by sheep. I. The movement of digesta through the stomach. Aust. J. Agric. Res. 18:789.

Wheeler, W.W. and Nollen, L.H. 1977. Gastrointestinal tract pH and starch in feces of ruminants. J. Anim. Sci. 44:131.

White, R.G., Williams, V.J. and Morris, R.J.H. 1971. Acute in vivo studies on glucose absorption from the small intestine of lambs, sheep and rats. Br. J. Nutr. 25:57.

Wilkie, K.C.B. 1979. The hemicelloses of grasses and cereals. In: R.S. Tipson and D. Horton (eds.) Advances in carbohydrate chemistry and biochemistry. Vol. 36:215. Academic Press, N.Y.

Williams, C.H., David, D.J. and Iismeaa, O. 1962. The determination of chromic oxide in feces samples by atomic absorption spectrophotometry. J. Agric. Sci. 59:381.

Williams, P.C. 1966. Reasons underlying variations in the protein content of Australian wheat. Cereal Sci. Today. 11:332.

Williams, V.J. 1965. Microbial metabolism in the forestomachs and the large intestine of sheep. Aust. J. of Ag. Res. 16:77.

Winter, K.A. 1975. Rye for growing steers. Canadex Livestock #42060.

Winter, K.A. 1973. Rye grain in high energy steer rations. Canadex Livestock #42060.

Wolever, T.M.S., Jenkins, D.J.A., Leeds, A.R., Gassull, M.A., Dilawari, J.B., Goff, D.V., Metz, G.L. and Alberti, K.G.M.M. 1978. Dietary fibre and glucose tolerance importance of viscosity. Proc. Nutr. Soc. 37:47 (Abstr.).

Wolin, M.J. 1976. Interaction between H2 producing and methane-producing species. In: H.G. Schlegel, G. Gottschalk and N. Pfenning (ed.). Microbial formation and utilization of gases (H2, CH4, CO). Gotlze, K.G., Gottingen, p. 141.

Young, M.C., Husken, F.E., Wacks, M.E., Theurer, B. and Ogden, P.R. 1975. Neutron activation analysis of Dysprosium (A potential inert marker) in hay and feces. J. Anim. Sci. 41:178.

Young, M.C., Theurer, B., Ogden, P.R., Nelson, G.W. and Hale, W.H. 1976. Dysprosium as an inert indicator in cattle digestion trials. J. Anim. Sci. 43:1270.

APPENDIX

1. ESTIMATION OF MISSING VALUES

$Y_{ijk} = \mu + A_i + B_j + T_k + e_{ijk}$

A_i = effect of the ith row $\quad i = 1, 2, \ldots nt$

B_j = effect of the jth column $\quad j = 1, 2, \ldots t$

T_k = effect of the kth treatment $\quad k = 1, 2, \ldots t$

Let t = number of treatments = number of columns.

Let n = number of observations per treatment cycle.

n is some multiple of t and nt = number of observations per column.

$N = nt^2$ = total number of observations.

The missing value is Y'_{ijk} $\quad$ Let $Y'_{ijk} = X$

$$\text{SS Total} = \sum_{ijk} (\bar{Y}_{ijk} - \bar{Y}_{...})^2$$

$$\text{SS Treatment} = nt\Sigma (\bar{Y}_{..k} - \bar{Y}_{...})^2$$

$$\text{SS Animals} = t\Sigma (\bar{Y}_{i..} - \bar{Y}_{...})^2$$

$$\text{SS Periods} = nt\Sigma (\bar{Y}_{.j.} - \bar{Y}_{...})^2$$

Residual = Total - Treatment - row - column sum squares.

$$\text{Residual} = Y_{ijk} - \bar{Y}_{...} - \{(\bar{Y}_{..k} - \bar{Y}_{...}) + (\bar{Y}_{i...} - \bar{Y}_{...}) + (\bar{Y}_{.j.} - \bar{Y}_{...})\}$$

$$= Y_{ijk} - \bar{Y}_{i..} - \bar{Y}_{.j.} - \bar{Y}_{..k} + 2\bar{Y}_{...}$$

Let Q(X) = SSE where Y_{ijk} is replaced by X.

$$\text{Where SSE} = \sum_{i=1}^{nt} \sum_{j=1}^{t} \sum_{k-1}^{t} (Y_{ijk} - \bar{Y}_{i..} - \bar{Y}_{.j.} - \bar{Y}_{..k} + 2\bar{Y})^2$$

$$= \sum_{i=1}^{nt} \sum_{j=1}^{t} \sum_{k=1}^{t} (Y_{ijk}^2 - \frac{\Sigma Y_{i..}^2}{t} - \frac{\Sigma Y_{.j.}^2}{nt} - \frac{\Sigma Y_{..k}^2}{nt} + \frac{2Y_{...}^2}{nt^2}$$

$$= x^2 - \frac{1}{t}(Y'_{i..} + X)^2 - \frac{1}{nt}(Y'_{.j.} + X)^2 - \frac{1}{nt}(Y'_{..k} + X)^2 + \frac{2}{nt^2}(Y'_{...} + X)^2$$

$$\frac{DQ(X)}{D(X)} = 2X - \frac{2}{t}(Y'_{i..} + X) - \frac{2}{nt}(Y'_{.j.} + X) - \frac{2}{nt}(Y'_{..k} + X) + \frac{4}{nt^2}(Y'_{...} + X) = 0$$

$$\therefore\ 2X = \frac{2}{t}(Y'_{i..} + X) + \frac{2}{nt}(Y'_{.j.} + X) + \frac{2}{nt}(Y'_{..k} + X) - \frac{4}{nt^2}(Y'_{...} + X)$$

Multiply by nt and simplify.

$$2ntX = 2n(Y'_{i..} + X) + 2(Y'_{.j.} + X) + 2(Y'_{..k} + X) - \frac{4}{t}(Y'_{...} + X)$$

$$= (2nY'_{i..} + 2Y'_{.j.} + 2Y'_{..k} - \frac{4Y'_{...}}{t}) + 2nX + 2X + 2X - \frac{4X}{t}$$

$$\therefore\ 2ntX - 2nX - 4X + \frac{4X}{t} = 2(nY'_{i..} + Y'_{.j.} + Y'_{..,k} - \frac{2Y'_{...}}{t})$$

$$\therefore\ X(nt - n - 2 \pm \frac{2}{t}) = nY'_{i..} + Y'_{.j.} + Y'_{..k} - \frac{2Y'_{...}}{t}$$

$$X = \frac{nY'_{i..} + Y'_{.j.} + Y'_{..k} - \frac{2Y'_{...}}{t}}{nt - n - 2 + \frac{2}{t}}$$

Multiply top and bottom of RHS by t

$$X = \frac{ntY'_{i..} + tY'_{.j.} + tY'_{..k} = 2Y'_{...}}{nt^2 - nt - 2t + 2}$$

$$= \frac{ntY'_{i..} + tY'_{.j.} + tY'_{..k} - 2Y'_{...}}{(t - 1)(nt - 2)}$$

$$= \frac{t(nY'_{i..} + Y'_{.j.} + Y'_{..k}) - 2Y'_{...}}{(t - 1)(nt - 2)}$$

Where X is the estimate of the missing value from the ith row in the jth column on the kth treatment.

2. CALCULATION OF THE CORRECTED F STATISTIC

Let $Q = SSE$ $\quad Y'_{ijk}$ is missing

$$Q = \sum_{i}^{nt} \sum_{j}^{t} \sum_{k}^{t} (Y_{ijk} - \mu - \alpha_i - B_j - T_k)^2 \qquad \text{Where Ho:} T_k = 0$$

$$\text{Ha:} T_k \neq 0$$

$$\frac{DQ}{D\mu} = -2 \sum_{i}^{nt} \sum_{j}^{t} \sum_{k}^{t} (Y_{ijk} - \mu - \alpha_i - B_j - T_k) = 0$$

α'_i, B'_j, and T'_k indicates animal, period and treatment containing the missing value.

Adding over ijk

$$1)\ Y_{...} - (nt^2 - 1)\hat{\mu} - t \sum_{i}^{nt} \hat{\alpha}_i - (t-1)\hat{\alpha}'_i - nt \sum_{j}^{t} \hat{B}_j - (nt-1)\hat{B}'_j$$

$$- nt \sum_{k}^{T} \hat{T}'_k - (nt-1)\hat{T}'_k = 0$$

$$\hat{\mu} = \bar{Y}_{...} + \frac{1}{nt^2 - 1}(\hat{\alpha}'_i + \hat{B}'_j + \hat{T}'_k)$$

$$\frac{DQ}{D\alpha_i} = -2 \sum_{j}^{t} \sum_{k}^{t} (Y_{ijk} - \hat{\mu} - \hat{\alpha}_i - \hat{B}_j - T_k) = 0$$

$$2)\ Y_{i..} - t\hat{\mu} - t\hat{\alpha}_i = 0$$

$$\hat{\alpha}_i = \bar{Y}_{i..} - \hat{\mu} \quad \text{for all } i = nt \text{ except for } i \text{ with missing value.}$$

For i = missing value

$$\frac{DQ}{D\hat{\alpha}'_i} = -2 \sum_{j}^{} \sum_{k}^{} (Y'_{ijk} - \hat{\mu} - \hat{\alpha}'_i - \hat{B}'_j - \hat{T}'_k) = 0$$

3) $Y'_{i..} - (t-1)\hat{\mu} - (t-1)\alpha'_i - \Sigma\hat{B}_j - \Sigma\hat{T}_k = 0$

$\bar{Y}'_{i..} = \hat{\mu} + \hat{\alpha}'_i - \frac{\hat{B}'_j}{t-1} - \frac{\hat{T}'_k}{t-1}$ Note: $\bar{Y}_{i..} = \frac{1}{t-1} Y'_{i..}$

For j ≠ to period with missing value

$$\frac{DQ}{DB_j} = -2 \sum_{i}^{nt} \sum_{k}^{t} (Y_{ijk} - \hat{\mu} - \hat{\alpha}_i - \hat{B}_j - \hat{T}_k) = 0$$

4) $\hat{B}_j = \bar{Y}_{.j.} - \hat{\mu}$

For j = period with missing value = j'

$$\frac{DQ}{D\hat{B}_j} = -2 \sum_{i}^{nt} \sum_{k}^{t} (Y_{ijk} - \hat{\mu} - \hat{\alpha}_i - B'_j - T'_k) = 0$$

$Y_{.j.} - (nt-1)\hat{\mu} - \Sigma\alpha_i - (nt-1)B'_j - 2\Sigma\hat{T}_k - T'_k = 0$

5) $B'_j = \bar{Y}'_{.j.} - \hat{\mu} + \frac{1}{nt-1}(\alpha'_i + T'_k)$ Note: $\bar{Y}'_{.j.} = \frac{1}{nt-1} Y'_{.j.}$

For k ≠ to treatment with missing value

$$\frac{DQ}{DT_k} = -2 \sum_{i}^{nt} \sum_{j}^{t} (Y_{ijk} - \hat{\mu} - \hat{\alpha} - \hat{B}_j - \hat{T}_k) = 0$$

6) $\hat{T}_k = \bar{Y}_{..k} - \hat{\mu}$

For k = treatment with missing value

$$\frac{DQ'}{DT_k} = -2 \sum_{i}^{nt} \sum_{j}^{t} (Y'_{ijk} - \hat{\mu} - \hat{\alpha}_i - \hat{B}_j - \hat{T}'_k) = 0$$

$$Y'_{..k} - (nt - 1)\hat{\mu} + \hat{\alpha}'_i + B'_j - (nt - 1)\hat{T}'_k = 0$$

7) $T'_k = \bar{Y}'_{..k} - \hat{\mu} + \frac{1}{nt-1}(\hat{\alpha}'_i + \hat{B}'_j)$ Note: $\bar{Y}'_{..k} = \frac{1}{nt-1} Y'_{..k}$

Use equation 1, 3, 5, 7 to solve for $\hat{\mu}$, $\hat{\alpha}'_i$, $\hat{B}'_j$, $\hat{T}'_k$

1. $\hat{\mu} = \bar{Y}_{...} + \frac{1}{nt^2-1}(\hat{\alpha}'_i + \hat{B}'_j + \hat{T}'_k)$

$(nt^2 - 1)\hat{\mu} = Y_{...} + \hat{\alpha}'_i + \hat{B}'_j + \hat{T}'_k$

3. $\hat{\mu} = \bar{Y}'_{i..} - \hat{T}'_k + \frac{1}{t-1}(\hat{B}'_j + \hat{T}'_k)$

$(t - 1)\hat{\mu} = Y'_{...} - (t - 1)\alpha'_i + B'_j + T'_k$

5. $\hat{\mu} = \bar{Y}'_{.j.} - \hat{B}'_j + \frac{1}{nt-1}(\alpha'_i + T'_k)$

$(nt - 1)\hat{\mu} = Y'_{.j.} - (nt - 1)B'_j + \hat{\alpha}'_i + \hat{T}'_k$

7. $\hat{\mu} = \bar{Y}'_{..k} - T'_k + \frac{1}{nt-1}(\hat{\alpha}'_i + \hat{B}'_j)$

$(nt - 1)\hat{\mu} = Y'_{..k} - (nt - 1)\hat{T}'_k + \hat{\alpha}'_i + \hat{B}'_j$

Now to find min Q we consider $Q' = \sum_{i}^{nt} \sum_{j}^{t} \sum_{k}^{t} (Y_{ijk} - \mu - \alpha_i - B_j)^2$

When minimizing Q' calculations proceed as above except no T_k terms are included.

Thus: 1) $\hat{\mu} = \bar{Y}_{...} + \frac{1}{nt^2-1}(\hat{\alpha}'_i + \hat{B}'_j)$ or $Y_{...} = (nt^2-1)\hat{\mu} - \hat{\alpha}'_i - \hat{B}'_j$

2) $\hat{\alpha}'_i = \bar{Y}_{i..} - \hat{\mu}$

3) $\alpha'_i = Y'_{i..} - \hat{\mu} + \frac{\hat{B}'_j}{t-1}$ or $Y'_{i..} = (t - 1)\alpha'_i + (t - 1)\hat{\mu} - \hat{B}'_j$

4) $B_j = \bar{Y}_{.j.} - \hat{\mu}$

5) $B'_j = Y'_{.j.} - \hat{\mu} + \frac{\alpha'_i}{nt-1}$ or $Y'_{.j.} = (nt - 1)\hat{\mu} + (nt - 1)\hat{B}'_j - \alpha'_i$

Use equation 1, 3, and 5 to find $\hat{\mu}$, $\hat{\alpha}'_i$, $\hat{B}'_j$

(1-3) $Y'_{...} - Y'_{i..} = (nt^2-1)\hat{\mu} - \hat{\alpha}'_i - B'_j - (t - 1)\hat{\alpha}'_i - (t - 1)\hat{\mu} + B'_j$

$= (nt^2-t)\hat{\mu} - t\alpha'_i - 0$

(1-5) $Y'_{...} - Y'_{.j.} = (nt^2-1)\hat{\mu} - \hat{\alpha}'_i - B'_j - (nt-1)\hat{\mu} - (nt-1)B'_j + \hat{\alpha}'_i$

$= (nt^2-nt)\hat{\mu} - 0 - ntB'_j$

1) $Y'_{...} = (nt^2-1)\hat{\mu} - \hat{\alpha}'_i - \hat{B}'_j$

Thus to solve $\hat{\mu}$, $\hat{\alpha}'_i$ and B'_j the matrix formation

$$\begin{pmatrix} nt^2-1 & -1 & -1 \\ nt^2-nt & -t & 0 \\ nt^2-nt & 0 & -nt \end{pmatrix} \begin{pmatrix} \hat{\mu} \\ \hat{\alpha}_i \\ \hat{B}'_j \end{pmatrix} = \begin{pmatrix} Y'_{...} \\ Y'_{...} - Y'_{i..} \\ Y'_{...} - Y'_{.j.} \end{pmatrix}$$

Where $Y'_{...}$ Total without missing value

$Y'_{i..}$ Total α_i without missing value

$Y'_{.j.}$ Total B_j without missing value

$Y'_{..k}$ Total T_k without missing value

Solve for $\hat{\mu}$, α'_i and B'_j

Then solve other $\hat{\alpha}'_i$ and $\hat{B}'_j$

Then calculate $Q' = \sum_i^{nt} \sum_j^t \sum_k^t (Y_{ijk} - \hat{\mu} - \hat{\alpha}_i - \hat{B}_j)^2$

Do not include missing value when calculating Q'

Test Stat $F(t-1)\,(nt^2-nt-2\,(t-1)) - 1 = \dfrac{\dfrac{Q' - Q}{t-1}}{\dfrac{Q}{nt^2-nt-2(t-1)-1}}$

For Q 1) Calculate missing value

2) Then calculate crossover design as normal

3) Remove one degree of freedom from error and total to account for missing value

4) Q = SSE

APPENDIX 2

Analysis of variance table for (Experiment 1), "to measure the effect of rye and wheat fractions in fluids at various pH values on viscosity using an in vitro rumen fluid system", using a completely randomized block design and using orthogonal comparisons on the treatments.

Anova Table (EXPERIMENT 1)

VISCOSITY OF RUMEN FLUID AT VARIOUS pH VALUES

SOURCE	DF	SS	MS	F	SIG
RB*WB VS RF*WF	1	611.740	611.740	174.73	SIG
RB VS WB	1	3104.720	3104.720	886.81	SIG
RF VS WF	1	7779.210	7779.210	2221.89	SIG
WR VS WW	1	4913.710	4913.710	1403.51	SIG
TREATMENT	5	16622.310	3324.460	949.57	SIG
pH	2	3329.370	1664.685	475.42	SIG
TREATMENT x pH	10	4687.821	468.780	133.88	SIG
ERROR	36	126.053	3.501		

($P<0.01$)

LEGEND

WR	WHOLE RYE	WW	WHOLE WHEAT
RB	RYE BRAN	WB	WHEAT BRAN
RF	RYE FLOUR	WF	WHEAT FLOUR

Selected analysis of variance tables from (Experiment 2), "Feeding of processed rye grain to lactating dairy cattle", using a Latin square statistical design.

Anova Tables (EXPERIMENT 2)

FAT CORRECTED MILK

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	375.08	125.03	2.18	NS
COWS	7	1210.92	172.98	3.02	NS
TREATMENTS	3	293.75	97.91	1.71	NS
ERROR	17	973.16	57.24		
TOTAL	30	2852.91			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

AVERAGE DAILY MILK PRODUCTION

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	309.02	103.0	1.36	NS
COWS	7	2409.80	344.25	4.55	SIG
TREATMENTS	3	237.05	79.02	1.04	NS
ERROR	17	1285.56	75.62		
TOTAL	30	4241.40			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

AVERAGE DAILY MILK PROTEIN %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	0.126	0.042	1.67	NS
COWS	7	1.797	0.25	10.26	SIG
TREATMENTS	3	0.054	0.018	0.72	NS
ERROR	17	0.425	0.025		
TOTAL	30	2.401			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

APPARENT DIGESTIBILITY OF DRY MATTER %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	4.060	1.354	2.77	NS
COWS	3	11.677	3.893	7.98	SIG
TREATMENTS	3	2.398	0.799	1.64	NS
ERROR	5	2.440	0.488		
TOTAL	14	20.576			

(P<0.05)

Anova Tables (EXPERIMENT 2)

APPARENT ADF DIGESTIBILITY %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	2.322	0.774	0.71	NS
COWS	3	94.631	31.543	28.79	SIG
TREATMENTS	3	41.634	13.877	12.66	SIG
ERROR	5	5.477	1.095		
TOTAL	14	146.465			

(P<0.05)

Anova Tables (EXPERIMENT 2)

APPARENT DIGESTIBILITY OF ENERGY %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	2.361	0.787	2.37	NS
COWS	3	8.621	2.873	8.66	SIG
TREATMENTS	3	3.738	1.246	3.75	NS
ERROR	5	1.659	0.332		
TOTAL	14	16.378			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

APPARENT PROTEIN DIGESTIBILITY %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	4.487	1.490	0.47	NS
COWS	3	0.113	0.375	0.01	NS
TREATMENTS	3	31.890	10.630	3.37	NS
ERROR	5	15.730	3.146		
TOTAL	14	52.220			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

APPARENT DIGESTIBILITY FAT %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	30.805	10.268	3.32	NS
COWS	3	2.190	0.730	0.24	NS
TREATMENTS	3	15.116	5.139	1.63	NS
ERROR	5	15.453	3.091		
TOTAL	14	63.564			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

APPARENT DIGESTIBILITY ADF-N %

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	29.158	9.719	3.38	NS
COWS	3	62.841	20.947	7.30	SIG
TREATMENTS	3	32.731	10.910	3.80	NS
ERROR	5	14.345	2.869		
TOTAL	14	139.075			

($P<0.05$)

Anova Tables (EXPERIMENT 2)

INTAKE OF DRY MATTER/DAY (kg)

SOURCE	DF	SS	MS	F	SIG
PERIODS	3	3.274	1.091	0.90	NS
COWS	7	63.100	9.014	7.48	SIG
TREATMENTS	3	42.708	14.236	11.81	SIG
ERROR	17	20.499	1.206		
TOTAL	30	129.580			

($P<0.05$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Intake of Fat (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	2135.155	711.718	24.54	SIG
PERIODS	3	1036.835	345.612	11.92	SIG
TREATMENTS	3	4770.914	1590.305	54.83	SIG
ERROR	6	174.014	29.002		

($P<0.01$)

Ruminal Flow of Fat (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	1393.338	464.44	8.86	SIG
PERIODS	3	830.386	276.795	5.27	SIG
TREATMENTS	3	5742.276	1914.092	36.50	SIG
ERROR	6	314.64	52.44		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Abomasal Flow of Fat (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	1536.662	512.221	39.38	SIG
PERIODS	3	1040.914	346.971	26.67	SIG
TREATMENTS	3	4906.453	1635.484	125.75	SIG
ERROR	6	78.033	13.005		

(P<0.01)

Ileal Flow of Fat (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	4.780	1.593	2.54	NS
PERIODS	3	20.239	6.746	10.76	SIG
TREATMENTS	3	556.609	185.537	295.98	SIG
ERROR	6	3.76	0.627		

(P<0.01)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Fecal Flow of Fat (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	178.832	59.611	2.43	NS
PERIODS	3	124.568	41.522	1.69	NS
TREATMENTS	3	309.021	103.007	4.21	NS
ERROR	6	146.734	24.455		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Intake of Energy (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	32.770	10.923	800.23	SIG
PERIODS	3	20.652	6.884	504.30	SIG
TREATMENTS	3	0.379	0.126	9.26	SIG
ERROR	6	0.082	0.013		

($P<0.01$)

Ruminal Flow of Energy (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	9.456	3.152	225.32	SIG
PERIODS	3	6.340	2.113	151.08	SIG
TREATMENTS	3	18.779	6.259	447.45	SIG
ERROR	6	0.084	0.014		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Abomasal Flow of Energy (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	4.885	1.628	95.56	SIG
PERIODS	3	3.332	1.111	65.17	SIG
TREATMENTS	3	4.805	1.601	94.00	SIG
ERROR	6	0.102	0.017		

($P<0.01$)

Ileal Flow of Energy (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	2.246	0.748	74.55	SIG
PERIODS	3	1.785	0.595	59.26	SIG
TREATMENTS	3	5.962	1.987	197.94	SIG
ERROR	6	0.063	0.010		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Fecal Flow of Energy (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	3.044	1.014	2.17	NS
PERIODS	3	1.607	0.535	1.15	NS
TREATMENTS	3	4.874	1.625	3.49	NS
ERROR	6	2.797	0.466		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Intake of Arabinose (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	2160.027	720.009	29.84	SIG
PERIODS	3	3056.951	1018.983	42.23	SIG
TREATMENTS	3	12579.186	4193.062	173.78	SIG
ERROR	6	144.764	24.127		

($P<0.01$)

Ruminal Flow of Arabinose (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	105.351	35.117	23.73	SIG
PERIODS	3	109.611	36.537	24.69	SIG
TREATMENTS	3	2912.519	970.839	656.14	SIG
ERROR	6	8.877	1.479		

($P<0.01$)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Abomasal Flow of Arabinose (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	59.607	19.869	8.88	NS
PERIODS	3	69.514	23.171	10.35	SIG
TREATMENTS	3	1002.739	344.246	149.41	SIG
ERROR	6	13.422	2.237		

(P<0.01)

Ileal Flow of Arabinose (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	20.100	6.700	9.70	SIG
PERIODS	3	31.194	10.398	15.05	SIG
TREATMENTS	3	316.825	105.608	152.94	SIG
ERROR	6	4.143	0.691		

(P<0.01)

Selected analysis of variance tables for (Experiment 3), on various flow parameters using a Latin square statistical design.

Anova Tables

Fecal Flow of Arabinose (g/day)

SOURCE	DF	SS	MS	F	SIG
COWS	3	6.237	2.079	0.98	NS
PERIODS	3	11.667	3.889	1.82	NS
TREATMENTS	3	210.115	70.038	32.87	SIG
ERROR	6	12.781	2.130		

($P<0.01$)

Analysis of variance tables in (Experiment 3), using a completely randomized block design with interaction to measure the differences in flow rates of selected nutrients within each treatment between the intake, rumen, abomasum, ileum and feces (gut locations).

Anova Tables

Flow of Fat Between Gut Locations (g/day)

SOURCE	DF	SS	MS	F	SIG
MAIN EFFECTS	7	165836.784	23690.969	157.610	SIG
TREATMENT	3	11541.703	3847.234	25.595	SIG
LOCATION	4	154295.081	38573.770	256.621	SIG
INTERACTIONS					
TRT X LOC	12	4743.574	395.298	2.630	SIG
ERROR	60	9018.840	150.314		
TOTAL	79	179599.198	2273.408		

($P<0.01$)

Analysis of variance tables in (Experiment 3), using a completely randomized block design with interaction to measure the differences in flow rates of selected nutrients within each treatment between the intake, rumen, abomasum, ileum and feces (gut locations).

Anova Tables

Flow of Energy Between Gut Locations (Kcal/day)

SOURCE	DF	SS	MS	F	SIG
MAIN EFFECTS	7	2114.785	302.112	203.115	SIG
TREATMENT	3	24.235	8.078	5.431	SIG
LOCATION	4	2090.551	522.638	351.378	SIG
INTERACTIONS					
TRT X LOC	12	10.566	0.881	0.592	NS
ERROR	60	89.244	1.487		
TOTAL	79	2214.595	28.033		

($P<0.01$)

Analysis of variance tables in (Experiment 3), using a completely randomized block design with interaction to measure the differences in flow rates of selected nutrients within each treatment between the intake, rumen, abomasum, ileum and feces (gut locations).

Anova Tables

Flow of Arabinose Between Gut Locations (g/day)

SOURCE	DF	SS	MS	F	SIG
MAIN EFFECTS	7	296157.230	42308.176	436.598	SIG
TREATMENT	3	9438.734	3146.245	32.468	SIG
LOCATION	4	286718.496	71679.624	739.696	SIG
INTERACTIONS					
TRT X LOC	12	7258.653	631.888	6.521	SIG
ERROR	60	5814.254	96.904		
TOTAL	79	309554.136	3918.407		

($P<0.01$)