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Rumen passage rates and fiber digestibilities for wheat straw, alfalfa hay and flaked sorghum grain in mixed diets for steers

Poore, Matthew Henry, M.S.

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RUMEN PASSAGE RATES AND FIBER DIGESTIBILITIES FOR WHEAT STRAW, ALFALFA HAY AND FLAKED SORGHUM GRAIN IN MIXED DIETS FOR STEERS

by

Matthew Henry Poore

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This thesis has been approved on the date shown below:

R. Spencer Swingle   May 1, 1987

R. Spencer Swingle
Associate Professor of
Animal Science

Date

DEDICATION

This thesis is dedicated to my parents, Dr. and Mrs. Henry Poore, who have supported my interests in biology from the time they gave me my first microscope.

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Thanks are extended to my major professor, Dr. R. Spencer Swingle, for inspiring and helping with this study. Without his help in interpreting the data and editing the manuscript, a thesis of this quality would not have been possible. In addition, I wish to thank Drs. M. E. Wise and J. T. Huber for serving on my committee, and Drs. R. C. Wanderley and W. H. Hale for many valuable conversations. Special thanks goes to Dr. C. B. Theurer, who hired me for my first job in animal science research. His influence on me goes back many years and will persist many years into the future.

Last, but most importantly, I thank my wife, Jeannette Moore, for helping me with this project. She was beside me during all phases of the work, and helped support me through the tough times.

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ABSTRACT

Six ruminally cannulated steers were used to evaluate the influence of dietary concentrate level on digestion of fiber, rumen pH and fill, and liquid and particulate passage rates.

Total tract digestibility of potentially digestible fiber, but not total fiber, was decreased with each increase in concentrate level. Digestion coefficients suggest that potentially digestible fiber is a more appropriate expression of diet fiber than is neutral detergent fiber in studies on effects of concentrate level on fiber digestion.

Passage rate of feed components was not changed from 30 to 60% concentrate. Passage rate of roughages, but not milo or liquid, were decreased at the 90% concentrate level.

Ruminal digestibility of fiber was not decreased for any ingredient from 30 to 60% concentrate, but decreased for all components at 90% concentrate. These data indicate that roughage fiber digestibility may be more severely influenced by high concentrate level than grain fiber digestibility, but that grain fiber may account for the majority of fiber digestion depression associated with feeding high concentrate diets due to its high potential digestibility, and its large contribution to total diet fiber.

INTRODUCTION

The most important goal of ruminant nutrition is to develop methods for maximizing efficiency of meat and milk production. Over the past 20 years many feed additives and other growth promotants have been used for this purpose. Recent research on ionophores in beef cattle diets has shown that productive efficiency can be increased by altering rumen fermentation. A more thorough understanding of the rumen environment would allow its alteration through dietary manipulation to increase efficiency of feed utilization.

One area which has potential for improvement is fiber utilization. In underdeveloped countries most ruminant feeds consist of forages since most grain production is needed for human consumption. In these countries optimizing fiber utilization is extremely important. Even in developed countries, a high percentage of energy in beef, dairy and sheep diets is from pasture, range or harvested forages. Most research with forage quality and fiber utilization has been with high- or all-forage diets, while comparatively little has been with high-concentrate diets. More information is necessary in this area since higher concentrate diets are typically used in intensive production systems.

Addition of soluble carbohydrate to ruminant diets may lead to decreased digestion of fiber. Depressed digestion does not always occur, but may be substantial as in the experiments of Mulholland et al. (1976) where fiber digestion coefficients were reduced 50% by starch addition. Primary theories used to explain the depressed fiber utilization are: 1) decreased rumen pH (inhibiting microbial cellulase activity), and 2) competition for nitrogen between cellulolytic and amylolytic bacteria causing a change in the rumen bacterial population. More recent evidence suggests that soluble carbohydrate addition increases the lag phase (time before fiber digestion begins) and may not appreciably affect the rate of digestion or potential degradability of the fiber (Mertens and Lofton, 1980). This increased lag time may be due to decreased rate of bacterial attachment to feed particles (Hoover, 1986).

Ruminal digestion is dependent on the rate of digestion and the rate of passage of individual dietary particles. Mathematical models have been developed which predict digestion of particles based on rates of passage and digestion. Estimates of passage and digestion rates may prove valuable in evaluating the digestion of specific feed particles (Miller and Muntifering, 1985; Okeke et al., 1983; Erdman et al., 1987).

When fiber digestion is studied in mixed diets, the fiber represents a mixture of fiber from the different diet components. Conventional digestion measurements measure only total fiber, and do not allow observation of individual feed ingredients. Feed ingredients vary greatly in both particle size and density, both of which affect rate of passage (Ehle, 1983; Faichney, 1986) and may have different fiber digestion rates (Mertens and Lofton, 1982; Robles et al., 1980; Varga and Hoover, 1982). Application of models to predict digestion of mixed diets therefore requires passage and digestion rate estimates for all major dietary components.

The objectives of this study were:

1) to measure the effect of diet concentrate level on digestion of neutral detergent fiber (NDF) and potentially digestible NDF, rumen pH, rumen fill, and particulate and liquid passage rates.

2) to partition the digestion of total fiber into its component parts, allowing evaluation of concentrate level effects on digestion of each component.

LITERATURE REVIEW

The following literature review will cover the effect of increasing concentrate level of ruminant diets on fiber digestion and feed passage rates, and the relative passage rates of different feed components. The review will begin with a summary of techniques used to measure rates of passage.

Review of Marker Methodology

Passage (turnover) of particles and liquid from the rumen are poorly understood processes which are important variables affecting extent of ruminal digestion (Bull et al., 1977). Passage has been measured by a variety of methods, and the markers and techniques used may have an impact on the values obtained. A brief summary of techniques used is given to familiarize the reader with the methods commonly found in the literature. The interested reader is refered to the review by Ellis et al. (1982) for more information on marker methods and a discussion of the relative value of common models used to calculate rates of passage.

Stained feed particles and polyethylene glycol were the classical materials for measuring particulate and liquid passage (Ellis, Matis and Lascano, 1979). After feeding, the passage rate of stained particles was determined by sieving feces and manually counting the stained particles retained on the sieve (Balch, 1950). Problems with quantification led to criticism of this technique (Ellis and Houston, 1967). Polyethylene glycol (PEG) was mixed with water and poured into the rumen, or mixed with the diet. The turbimetric determination of PEG is subject to time and temperature variation which has decreased its acceptance as a liquid passage marker (Ellis et al., 1982).

In the 1960's, new methods were introduced for marking liquids and particulates. Rare earth metals were found to bind tightly to feed and to resist migration during passage through the digestive tract (Ellis and Houston, 1968). Radioisotopes of the rare earths were extensively used in early studies due to the ease of counting samples (Ellis et al, 1979), but due to the problems with disposal of radioactive waste, most current studies utilize cold rare earths with analysis by atomic absorption spectrophotometry, or by neutron activation analysis (Pond et al. 1985).

Chromium mordanted fiber (Cr-mordant) was recently proposed as a particulate marker (Uden, Colluci and Van Soest, 1980). Stability and indigestibility of the mordanted fiber were viewed as desirable characteristics. The marker rapidly gained acceptance, but more recent research shows that increased density of the marked particles may result in underestimated passage rates of the unmarked particles (Ehle, 1983; Mader, Teeter and Owens, 1984). Pond et al. (1981) compared the passage of Cr-mordant with that of a rare earth (applied by immersion) attached to the mordanted fiber. Passage of the rare earth was consistently, but only slightly, faster than passage of Cr-mordant.

Research has shown that most metals that form stable complexes with ethylenediaminetetraacetic acid (EDTA) can be used for measuring rumen liquid passage rate (Teeter and Owens, 1983). One major advantage of the EDTA complexes over PEG is that they are easily measured by diluting rumen fluid and aspirating directly into an atomic absorption spectrophotometer (Hart and Polan, 1983). Chromium-EDTA has been most widely used but prevents concurrent use of Chromium oxide and Cr-mordant as additional nutritional markers. Recent development of Cr-mordant prompted proposal of Cobalt (Co) EDTA as a rumen liquid marker (Uden et al., 1980). The two markers can be used simultaneously to measure liquid and particulate passage rates.

There has been much discussion concerning the optimum method of marking and dosing as well as the regimen used to sample liquid and particulates. Rare earths have been applied to feedstuffs either by spraying with a concentrated solution or by soaking in a more dilute solution followed by several washings. Both methods are in current use, but the soaking and washing procedure seems to be more desirable (Mader et al., 1984). Soaking in rare earth solution, rather than spraying, reduces migration of rare earth from marked particles to unmarked particles by eliminating loosely bound rare earth. The soaking procedure does have the disadvantage of partially removing the soluble fraction of the feed to be marked which may change the rate of digestion and passage of the particles. The error caused by this physical change is judged to be less of a problem than the high amount of migration which can occur when feeds are marked by spraying (Mader et al., 1984; Cooker, Clark and Shanks, 1982).

Dosing with particulate markers has been achieved by either mixing the marked feed in a meal (Colucci et al., 1982) or by mixing it directly in the rumen (Uden et al., 1980). Mixing in the rumen may bias rate estimates in that a meal may not immediately mix uniformly with rumen contents and that the particle size reduction, moistening and mashing associated with mastication is eliminated. Dosing with Co- or Cr-EDTA has been achieved by pouring the EDTA solution via rumen cannula into several rumen areas (Teeter and Owens, 1973).

Samples for liquid and particulate turnover have been obtained from the rumen, duodenum and/or feces. There is little consistency among studies in site and frequency of sampling. One recent study showed the importance of sampling site in interpretation of passage rate constants (Goetsch and Owens, 1985). Passage constants were significantly different when estimated from samples from the rumen, duodenum, ileum and feces. Robinson and Sniffens, (1983) sampled from the rumen, duodenum and feces and showed that passage rates tended to be faster when determined at the rumen or duodenum. As a general observation, most liquid turnover data is obtained by rumen sampling at frequent intervals (1-4 h) for 1 or 2 days. Fecal sampling has been the primary method for determining particulate turnover, with a sampling interval of about 6 h for 5 to 7 days. The recommendations of Teeter et al. (1984) make the extended sampling times questionable when rare earths are used due to migration. Most recent studies have used 5 days of fecal grab sampling (at various intervals) for determination of particulate passage rates.

Methods for estimating passage time from excretion curves in ruminants have been described by Balch (1950), Castle (1956), Blaxter (1956), Brandt and Thacker (1958), Patton and Krause (1972), Grovum and Williams (1973) and Ellis et al. (1979). Most recent studies use the two-compartment models of Grovum and Williams (1973) or Ellis et al. (1979). Both models describe two compartments, one with a fast turnover rate and one with a slow turnover rate. According to Grovum and Williams the slower of the two rates represents passage from the rumen and the faster passage from the hindgut. Ellis et al. (1979) believe that both compartments exist within the rumen. These workers interpret the slow rate to represent mixing of the large particle rumination pool, and the fast rate to represent passage of particles from the rumen.

Interpretation of the rates derived from the two models receives much discussion, but recent studies show that the rates predicted by each model are similar (Goetsch and Galyean, 1985; Prange, Jorgensen and Satter, 1982). Current understanding is that the slow rate describes rumen passage, and the faster rate is a combination of events occurring in the rumen, abomasum and hindgut (Goetch and Owens, 1985; Prange et al. 1982).

Depression of Fiber Digestion

Studies on fiber digestion depression have been of two types: those establishing digestion coefficients for fiber when starch or grain are added to diets, and those attempting to discover the mechanisms of the depression. The first category will be divided into those studies using added starch and those using grain additions.

Effect of Starch Addition on Fiber Digestion

Burroughs et al. (1949) demonstrated that addition of starch to a diet of corn cobs decreased dry matter digestion of the cobs. The diets fed to steers consisted of 4 lb corn cobs, 1.6 lb dry skim milk, and 0, 1.6, 3.2 or 4 lb corn starch. Corn cob dry matter digestion fell from 57% with no starch to 35% with 4 lb added starch. The authors also looked at the effect of starch addition on the digestion of alfalfa hay diets containing 5 lb alfalfa hay and 0, 2, 4 or 6 lb starch. The digestion of alfalfa hay was not depressed the first year, but when the experiment was repeated the next year a small decrease in digestibility of the hay components did occur. The authors give no explanation for this, but it is characteristic of the variability which occurs in the literature.

Kane, Jacobson and Damewood (1959) established the importance of adaptation to starch-containing diets. Three cows were fed alfalfa hay alone or with 6 lb added corn starch. Digestibility of alfalfa hay components was depressed when starch was added to the diet with a short (4 day) adaptation period. With a 20 day adaptation, however, the digestion of alfalfa hay was not depressed. The authors concluded that some of the digestibility depression seen in this type of experiment may be due to inadequate adaptation of animals to experimental diets.

Chappell and Fontenot (1968) fed sheep purified diets containing corn starch and cellulose in varying proportions. Diets investigated included 0, 2, 4, 6, 8, 16, 32, 33.3, 40 or 48% corn starch. Cellulose digestibility tended to be highest at the 8% starch level and was decreased only when starch exceeded 32% of the diet.

Mulholland, Coombe and McManus (1976) fed sheep pelleted oat straw diets containing 0, 5, 10, 15, 20, 30 or 40% wheat starch. Cellulose digestion was not depressed except on the 30 and 40% starch diets. The authors conclude that starch additions of up to 10% have no effect on fiber digestion.

Prouty et al. (1979) fed 12 steers (3/treatment) alfalfa hay diets containing 0, 20, 40 or 60% isolated corn strach. Neutral detergent fiber digestion was not significantly decreased but tended to be lower on the two high starch levels (47.4, 47.8, 42.9 and 43.7% for 0, 20, 40 and 60% respectively). Dry matter intake was also decreased at 40 and 60% starch, which might have offset decreased fiber digesting activity in steers fed those diets.

Wedekind, Muntifering and Barker (1986) fed four abomasally fistulated adult wether sheep semipurified diets containing fescue hay with 0, 20, 40 or 60% of a concentrate composed of corn starch and soybean meal with or without sodium bicarbonate. Total tract and ruminal digestibilities for neutral and acid detergent fiber (NDF and ADF) were reported. In this experiment, total tract digestion of ADF and NDF were not significantly decreased, but ruminal digestion was depressed for both fiber fractions. This is an example of how hind gut digestion might compensate for depressed digestion in the rumen. Also, addition of sodium bicarbonate was shown to stabilize rumen pH to increase ruminal digestion of fiber.

Effect of Grain:Forage Ratio on Fiber Digestion

In 1959, Elliot and Loosli conducted a study with 12 high producing lactating cows to study the effect of increasing concentrate level on the digestion of crude fiber in diets containing alfalfa hay and concentrate (primarily corn and oats). Crude fiber digestibility was 46.6, 47.9 and 48.7 when concentrate level was 40, 60 and 80% respectively. The digestibility of crude fiber was not different in this study.

Kane, Jacobson and Moore (1961) studied digestion of forage components in six dairy cows fed diets with varing hay to grain ratios. The ratio of alfalfa hay to grain mixture (corn, wheat bran, oats and soybean meal) for the three diets was 1:1, 3:1 and 10:1, and intake was kept constant. No depression in the digestion of forage components was observed. The authors concluded that grain levels of up to 50% are not detrimental to the digestion of hay in the diet.

Montgomery and Baumgardt (1965) measured cellulose digestibility when heifers were fed diets of pelleted alfalfa meal and ground corn in ratios 100:0, 80:20, 60:40 or 40:60. Cellulose digestion decreased from 45.3% for the 100:0 diet to 31.5% for the 40:60 diet. Pelleting alters both intake and passage characteristics of feeds, and experiments with pelleted feeds may not apply to non-pelleted diets.

Bines and Davey (1970) used four dry cows in a 4x4 Latin square to compare diets containing 0, 20, 40 or 60% barley straw with concentrate (barley, corn, wheat bran, peanut meal and palm seed cake). Digestion coefficients for cellulose were 58.5, 42.9, 47.1 and 49.9% respectively. The authors also used rate of digestion of cotton thread as an index of rumen cellulolytic activity. Time required for 25% digestion of the thread was >120 h for the 0% straw, >60 h for the 20%, 28.5 h for the 40% and 29.6 h for the 60% diet. The high cellulose digestibility on the 0% straw diet is suprising considering the fact that the cotton thread experiment suggests a decreased capacity to digest cellulose. This suggests that cellulose in the concentrate mix was not as severely affected by high concentrate as cellulose in cotton thread.

Cole, Johnson and Owens (1976a) utilized four steers in a 4x4 Latin square to study two corn processing methods (steam flaked vs dry rolled) and two levels of roughage (0 or 21% cottonseed hulls). Cellulose digestibility was not different for the processing methods but was higher on the 100% corn diet than the 79% corn diet (72.2 vs 57.8%, $P<.01$). The authors offered no explanation for this increased cellulose digestion at the high grain level but it is possible that the cellulose in cottonseed hulls has a lower potential for digestion than the cellulose in corn. This would mean that when hulls were added a "more digestible cellulose" was replaced by a "less digestible cellulose."

In a companion study (Cole, Johnson and Owens, 1976b) four steers were used in a 4x4 Latin square disign to study the effect of adding 0, 7, 14 or 21% cottonseed hulls to whole corn diets on site and extent of diet digestion. Total tract digestion of cellulose was 78.2, 65.7, 54.1 and 66.0% for the four respective diets. Authors attributed the high cellulose digestion on the all-corn diet to differences in cellulose level or source.

Prouty et al. (1979) fed 12 steers (3/treatment) alfalfa hay diets containing 0, 20, 40 or 60% steam processed and flaked milo. Intake was similar for all treatments. Digestion coefficients for NDF were 48.3, 49.9, 50.3 and 53.9 for the 0, 20, 40 and 60% grain diets, respectively.

Zinn and Owens (1980) fed three steers rolled corn:prairie hay diets containing 20 (1.5% body wt/day intake) or 40% (1.5 and 2.0% body wt/day) hay. Acid detergent fiber digestibility was 53.5, 43.1 and 52.6% for the respective diets.

Ledoux et al. (1985) utilized four steers to study digestibility of whole shelled corn diets containing 4, 8, 16 or 24% chopped fescue hay. Total tract digestion of NDF was not different among diets (64, 74, 67 and 65%, respectively).

Joanning, Johnson and Barry (1981) studied the depression of neutral detergent fiber (NDF), and acid detergent fiber (ADF) digestibility when corn grain was mixed with corn silage. The five diets consisted of 1) all mature silage, 2) all immature silage, 3) 1:2 immature silage:corn grain, 4) 1:2 mature silage:corn, and 5) all corn grain. The depression of fiber digestibilities for the mixed diets was calculated using the actual digestibilities and the theoretical digestibilities predicted from the all-corn and all-silage diets. For the immature silage diets, NDF and ADF digestibilities were depressed 12.8% and 11.4% respectively. For the mature silage diets, NDF and ADF digestibilities were depressed 27.0% and 15.6%. This study indicates that the degree of depression in fiber diegestin may be related to the maturity the forage, at least when corn silage is fed.

Brink and Steele (1985) studied ruminal and total tract digestibility of NDF in five steers fitted with abomasal cannulae. The steers were fed diets containing 50, 70 and 90% cracked corn with the remainder of the diet as corn silage. Total tract digestibility of NDF was not changed (77.4, 77.1 and 74.5%) but ruminal digestibility was decreased (74.9, 69.4 and 34.8) with increased cracked corn. Ruminal digestion accounted for 89.9, 76.0 and 39.3% of the total tract digestibility. This study shows that decreases in ruminal fiber digestion associated with increased concentrate may be compensated for by hind gut fiber digestion.

DeFaria and Huber (1984a) studied the digestion of alfalfa haylage diets containing 0, 30 or 60% ground corn (dry basis), and fed to six steers in a double 3x3 Latin square. Apparent digestion of ADF was not significantly changed and was 51.0, 57.0 and 55.9% for the 0, 30 and 60% corn diets, respectively. In a companion study (DeFaria and Huber, 1984b) using the same steers and diets, 24-, 48- and 72-h dry matter disappearance of alfalfa hay, grass hay and corn silage was not affected by grain level.

Woodford, Jorgensen and Barrington (1986) studied the effect of alfalfa hay level on utilization of dairy diets in a 4x4 Latin square design with four lactating cows. Treatments consisted of 28, 36, 45 or 53% prebloom alfalfa hay fed with a mixed dairy concentrate. The NDF digestion coefficients were not significantly different for the four treatments (45.6, 47.5, 48.5 and 50.8% respectively). This study shows that when high quality roughage such as alfalfa hay is fed, fiber digestion may not be depressed with added concentrates.

Merchen, Firkins and Berger (1986) measured ruminal and total tract digestibility of NDF in four wethers fitted with ruminal and duodenal cannulae. Diets consisted of 75 or 25% chopped alfalfa hay with the concentrate portion composed of ground corn and soybean meal, and were fed at 1.6 or 2.6% of body wt/day. Total tract digestibility of NDF was not significantly affected by alfalfa hay level but was lower ($p<.05$) for the high level of intake, and averaged 60.5, 63.9, 61.1 and 63.2 for the high intake, low intake, high forage and low forage diets respectively. Proportion of total tract NDF digestion occurring in the rumen was not affected by intake, was lower for the 25% hay diet than the 75% hay diet ($p<.10$), and averaged 66.8, 74.5, 84.5 and 56.8% for the high intake, low intake, high forage and low forage diets, respectively.

Decreased fiber digestion due to increased grain in the diet has been more difficult to demonstrate than when purified starch was added. This may be due to more rapid digestion of purified starch resulting in a less stable rumen environment. Another possible factor is that grains contain substantial amounts of fiber which may differ in potential digestibility from roughage fiber. Fiber from concentrate sources may be high in potential digestibility relative to forage fiber (Van Soest, 1982) and increasing grain level in a diet may result in a dietary fiber with higher potential for digestion. In addition, depressed digestion in the rumen may be compensated by digestion in the hindgut.

Mechanisms of Fiber Digestion Depression

El-Shazly, Dehority and Johnson (1961) studied the mechanisms involved in decreased fiber digestion when starch was added to an in vitro rumen system. Four major theories of rumen fiber digestion depression were proposed: 1) inhibition of cellulolytic bacteria due to production of a toxic substance by amylolytic bacteria; 2) inhibition of microbial cellulases due to the low rumen pH associated with rapid starch digestion; 3) decreased activity of cellulolytic bacteria due to competition with amylolytic bacteria for critical nutrients (nitrogen being the most important); and 4) reduction of the rumen cellulolytic population to a level which would be limiting to fiber digestion. Experiments by these authors showed that no inhibitors were produced and that there was a viable cellulolytic population even when concentrate level was high. The rumen pH fluctuation and competition for nitrogen were the major factors involved in the depression of fiber digestion.

Mertens and Lofton (1980) measured the effect of adding 0, 40, 60 or 80% starch on in vitro digestion kinetics of alfalfa, fescue, orchardgrass, and bermudagrass hays. Digestion rate for potentially digestible fiber, averaged across forage, did not change and was 7.6, 7.2, 7.5, and 7.4%/h for the four treatments, respectively. The time before any digestion occurred (lag phase) increased when starch was added. Lag times were 1.1, 2.7, 3.1 and 3.1 h for the four treatments, respectively. The biological significance of this small change in lag time in vitro is not known, but such a change should not result in a dramatic decrease in fiber digestibility in vivo. Potential extent of NDF digestion was 67.8, 64.7, 64.6 and 62.2% for 0, 40, 60 and 80% starch.

Solaiman et al. (1982) utilized four rumen fistulated dry cows to measure the in situ rate of fiber digestion of orchard grass hay. Treatments were orchard grass alone, orchardgrass plus soybean meal, or orchardgrass plus soybean meal and starch. Fiber digestion rate was increased when soybean meal was added (2.2 to 2.6%/h) and increased further when starch was added (up to 3.0%/h). This is another example of starch addition affecting digestion characteristics in a direction different from what might be expected.

Miller and Muntifering (1985) conducted a study with five Holstein steers in a 5x5 Latin square design to evaluate the effect of corn addition on the rumen digestion of fescue hay NDF. The diets contained 0%, 20%, 40%, 60% or 80% corn. The model of Mertens (1977) was used to estimate the apparent extent of rumen digestion of fescue hay, which decreased from 32.4% on the 0% grain diet to 16.7% on the 80% grain diet. Total tract digestibility of NDF was not reported. The study is an interesting approach but the use of Cr-mordanted particles, which can cause biased passage rate estimates, short adaptation periods (14 days), and use of constant time for defining potentially digestible fiber may limit the interpretation of the estimates.

Mould, Orskov and Mann (1983) used eight ruminally cannulated sheep to study the digestion of different forage sources supplemented with various types and levels of concentrate. The authors observed that some types of concentrate depressed forage digestion more than others. They divided the depression into: 1) "the pH effect," which could be totally overcome by infusion of buffers that stabilized rumen pH, and 2) "the carbohydrate effect," which could not be overcome by the buffer infusion. Authors concluded that competition for nitrogen was not a factor, so the carbohydrate effect may have been due to the production of inhibitor or a decrease in the cellulolytic population. The pH effect was the major cause of the depression in all cases, and the authors concluded that rumen cellulolysis would be almost totally inhibited by pH lower than 6.0.

Mould and Orskov (1983) fed chopped hay or a pelleted concentrate (pelleted barley and fish meal) to six ruminally fistulated sheep (three each diet). Rumen pH in the hay-fed sheep was depressed by infusion of a combination of mineral acids, while ruminal pH in the concentrate-fed sheep was increased by infusion of sodium and potassium bicarbonate. Decreasing pH to about 6.2 had only a small effect on hay intake and in situ degradation of hay and cotton thread. When pH was further decreased to about pH 6.0, DM intake decreased and in situ degradation of hay and cotton thread was almost totally inhibited. At this pH there was destruction of the normal hay digesting population of the rumen. For the concentrate-fed group, increasing rumen pH from about 5.5 to 6.5 had little effect on either microbial population or the in situ degradation of hay or cotton thread. In situ degradability of hay and thread was near zero regardless of the ruminal pH. The authors concluded that that the critical pH for forage fiber digestion is between 6.0 and 6.2, and is associated with destruction of cellulolytic organisms. With the concentrate diet the absence of cellulolytic activity was not a direct result of low pH. The concentrate diet either resulted in reduced activity of fibrolytic bacteria, or led to very small numbers of fibrolytic bacteria, even at the higher pH levels.

In an attempt to determine the optimum pH for fiber digestion Shriver et al. (1986) used continuous in vitro cultures fed a 65% concentrate diet. The pH of fermenters was maintained at 5.8, 6.2, 6.6 or 7.0 (+.1 pH unit) by the infusion of NaOH or HCl. Digestion of NDF was severly depressed at pH 5.8 (8.1%), was increased at pH 6.2 (33.1%), but was not subject to further increase at pH 6.6 or 7.0 (32.4 and 32.0, respectively). At pH 5.8 there was a large decrease in the proportion of total microbes attached to particulate matter (>43um), as compared to the higher pH levels. This study indicates that depression of fiber digestion may not occur if rumen pH does not remain below 6.2 for a sufficient time. Depression of fiber digestion at pH 5.8 (moderately low) may be due to inhibition of the microbes ability to attach to particulate matter.

In vivo, ruminal pH is not constant (as in in vitro cultures) but is cyclic in nature even in animals fed ad libitum (deFaria and Huber, 1984a). Rumen pH may fall shortly after feeding (below 6.0) but return to the range of optimum fiber digestion (6.2 to 7.0) for much of the day. To establish the relevancy of different measurements of rumen pH, Istasse and Orskov (1983) fed a 67% barley, 33% hay diet to three ruminally fistulated sheep and correlated in situ hay degradation with ruminal pH. Variables presented were minimum pH, h below pH 6.0, and pH-h below 6.0 (area under the pH-time curve). Correlation coefficients of the four variables were -.88, -.76 and -.90 for the 3 pH variables, respectively.

Wedekind, Muntifering, and Barker (1986) examined the relationship between ruminal fiber digestion and ruminal pH. Diets were composed of fescue hay and 0, 20, 40 or 60% of a semipurified concentrate (corn starch and soybean meal with or without 7.5% sodium bicarbonate). The pH variables determined were mean pH, minimum pH, hr below pH 6.7 and pH-hr below pH 6.7 (area of pH curve under 6.7). Digestibility of fiber fractions was not correlated with pH parameters, except that ruminal hemicellulose digestibility was negitively correlated with pH-h below 6.7 ($p<.05$), and total tract digestibility of hemicellulose was negitively correlated with minimum pH ($p<.05$). Use of pH 6.7 as a reference in this study is questionable since pH can go well below 6.7 without affecting fiber digestion (Shriver et al., 1986).

The mechanisms of fiber digestion depression when concentrates are added to diets are as yet unclear. It can be said, however, that low rumen pH, decreasing microbial attachment and cellulase activity, is probably the major factor operating in vivo. Evidence that microbial population changes and preferance for easily fermentable energy sources may be involved, however, does exist. For further information on activities of isolated cellulase systems, and readily fermented carbohydrate effects on pure cultures of rumen organisms the reader is refered to the recent review of Hoover (1986).

Passage Rates for Different Feeds and Different Concentrate Levels

This section of the review will be divided into those studies which measured the effect of concentrate addition on rumen passage rates, and those which measured the passage rates for two or more dietary components in mixed diets.

Effect of Concentrate Level on Feed Passage Rates

Balch et al. (1955) studied the passage of stained hay particles in two lactating cows. Dietary treatments were: 1) 16 lb hay, 20 lb concentrate; 2) 2 lb hay, 24 lb concentrate or 3) 2 lb hay, 24 lb concentrate and 5 lb straw pulp. Rumen retention time was 58 h, 142 h and 128 h for treatments 1, 2 and 3 respectively. Hindgut retention time was 22 h, 37 h and 35 h for treatments 1, 2 and 3 respectivly. This study shows the general trend toward longer retention times at higher concentrate levels although results are confounded by changes in dry matter intake.

Eng et al. (1964) utilized 20 mature wethers fed cracked corn and chopped (coarsly ground) coastal bermuda hay diets to study the effect of dietary concentrate level on the passage of the hay and grain. Diets consisted of 100, 75, 50, 25 and 0% corn with the balance as hay. Stained particles of hay and corn were used to estimate the retention time of each type of feed. Retention time of the hay was 71, 87, 94 or 131 h for the diets containing 100, 75, 50 and 25% hay, respectively. Retention time of the corn was 77, 77, 97 and 78 h for the diets containing 25, 50, 75 and 100% corn. Retention time of the hay increased with increasing grain level, but the retention time of the grain was unaffected, indicating there may be differences in the way passage of various feeds respond to changes in concentrate level.

Montgomery and Baumgardt (1965) studied passage of stained corn and alfalfa meal in eight Holstein heifers fed pelleted diets with alfalfa meal to corn ratios of A) 100:0, B) 80:20, C) 60:40 and D) 40:60. Rumen retention times for corn, corrected for intake by covariance, were 33.4, 34.6 and 40.9 h for diets B, C and D respectively (B=C<D with $P<.05$). Corrected rumen retention times for alfalfa meal were 27.4, 27.7, 32.0 and 37.1 h for diets A, B, C and D respectively.

In 1973, Grovum and Williams studied the effect of concentrate level on hay passage using a model describing two independent compartments and radiocerium as a particulate marker. Passage parameters derived from the model included transit time (TT, time of first fecal appearance), passage rate from the first compartment (K_1, thought to represent the rumen) and passage rate from the second compartment (K_2, thought to represent the hindgut). Three sheep were fed diets which consisted of: 1) 800 g alfalfa hay, 2) 300 g alfalfa hay and 400 g wheat, and 3) 100 g alfalfa and 500 g wheat. One sheep died before receiving the third diet, so data presented are the average of two sheep. Average TT, K_1 and K_2 were 721 min, 6.4 and 17.6 %/h for diet 1; 657 min, 6.5 and 14.4 %/h for diet 2; and 1344 min, 4.7 and 6.9 %/h for diet 3.

Prange et al. (1979) measured passage rate of grain, forage and liquid from the rumen of six lactating cows fed diets (19 kg DM/d) containing hay to grain ratios of 83:17, 66:34, 47:53 or 29:71. Type of forage and grain were not reported, and rare earths (presumably applied by spraying) and Cr-EDTA were used as markers. Passage of liquid, hay and grain were not affected by forage level.

Colucci et al. (1982) studied the effect of forage to concentrate ratio on passage of concentrate and forage components using 16 dairy cows. Chromium-mordanted particles of the forage and concentrate portions of the diet were fed in succession to estimate rumen passage rates. Diets contained 1) 32% forage, 68% concentrate or 2) 83% forage, 17% concentrate, and were fed at maintenance (dry cows), or ad libitum (lactating cows). The forage portion of the diet contained half corn silage and half alfalfa haylage, and the concentrate was primarily corn and soybean meal. At low intake rumen passage rate of concentrate was 3.8 and 5.3%/h, while passage rate for forage was 2.3 and 4.1 %/h for diets 1 and 2 (both comparisons different at $P<.05$). At the high level of intake, rumen passage rate of concentrate was 7.0 and 6.8%/h, while passage rate of forage was 4.2 and 4.9%/h for diets 1 and 2, respectively (neither comparison different). This research indicates that the effect of concentrate level on particulate passage may not be as great when animals are at high levels of intake as compared to when they are fed at maintenance.

Okeke, Buchanan-Smith and Grovum (1983) studied passage rate of Cr-mordanted soybean meal particles in eight steers fed diets of 50% or 20% corn silage plus cracked corn and soybean meal concentrate and contained 0, .75, 2.5 or 5.0% sodium bicarbonate. Rumen passage rates were higher for the two high bicarbonate levels but were unaffected by diet concentrate level. Rumen passage rates were 5.3, 5.3, 6.5 and 6.6 %/h for the medium concentrate with 0, .75, 2.5 and 5.0% $NaHCO_3$, respectively and 5.0, 5.0, 6.6 and 6.7 %/h for high concentrate.

Miller and Muntifering (1985) measured the effect of forage:concentrate on the passage of Cr-mordanted fescue hay with five holstein steers in a 5x5 Latin square design. Diets consisted of 100, 80, 60, 40 or 20% fescue hay with the remainder as cracked corn grain. The rumen passage rate for the Cr-mordanted hay was 2.1, 2.7, 2.3, 2.4

and 1.9 %/h for the 100, 80, 60, 40 and 20% hay diets, and were differed only between the 80 and 20% hay diets. This study shows that passage of hay may not be linearly related to the concentrate level of the diet. The use of Cr-mordanted hay for this study may have affected the results since changes in density of the hay particles might cause them to pass differently than unmarked feed particles (Ehle, 1984).

Ledoux et al. (1985) studied the passage rate of whole corn in diets containing 4, 8, 16 or 24% chopped fescue hay (four steers in 4x4 Latin square). Rumen passage rates were determined from both rumen and fecal samples. Fecal sampling resulted in passage estimates of 2.3, 2.7, 2.7 and 2.9%/h for the respective diets, and no significant treatment effects were detected. Rumen samples resulted in rates of 2.3, 1.7, 2.4 and 2.8%/h for the respective diets, showing linear and cubic effects ($p<.05$).

Woodford et al. (1986) conducted an experiment with four lactating cows in a 4x4 Latin square design to measure the passage rates of liquid, hay and concentrate in diets containing: 1) 28%, 2) 36%, 3) 45% or 4) 53% alfalfa hay plus concentrate. Passage rates of hay and concentrate were measured using rare earth markers applied by spraying feed, and liquid rate was measured with Co-EDTA. For diets 1, 2, 3 and 4, rumen passage rate of liquid was 11.1, 11.6, 11.8 and 12.2 %/h, rumen passage rate of hay was 5.0, 6.0, 6.3 and 5.9 %/h, and rumen passage rate of concentrate was 9.7, 10.0, 11.2 and 10.5 %/h. Passage rate of each was unaffected by increasing concentrate level of the diet. The authors concluded that for high-producing dairy cows fed high quality alfalfa hay, changing concentrate level had little effect on passage rates of dietary components or liquid. The spraying technique for preparation of rare earth markers may result in a high level of marker migration (Mader, 1984), which could mask treatment differences.

Merchen et al. (1986) studied passage of liquid and particulates in diets containing 75 or 25% chopped alfalfa hay with corn and soybean meal concentrate fed at high or low intake to four wethers. Particulate passage rates were not affected by level of intake (4.4 vs 4.4 %/h, for high and low) but were significantly slower ($p<.05$) for the 25% hay than the 75% hay (4.2 vs 4.6 %/h, respectively). Fluid dilution rate was not affected by treatment, and averaged 6.5, 5.8, 6.6 and 5.7 %/h for the high intake, low intake, high alfalfa and low alfalfa, respectively. The authors give little explanation of how they applied the Yb marker used, except to say "the morning feed was marked with 200 mg Yb" giving little basis to judge adequacy of their marker technique.

Owens and Goetsch (1986) summarized the available literature on passage rates to evaluate concentrate level effects on concentrate and roughage passage rates. Concentrate level classifications were; <20%, 20-50%, 50-80%, and >80%. Passage rates for the different concentrate levels are as follows:

% Concentrate	N	Concentrate K_p	SEM	N	Roughage K_p	SEM
< 20%	5	5.0	0.5	70	3.1	0.2
20 - 50%	29	6.9	0.2	53	3.7	0.3
50 - 80%	17	3.4	0.3	6	3.5	0.3
> 80%	19	3.1	0.2	1	2.9	-

where K_p is rumen passage rate, and N is the total number of observations. Passage rate of concentrate seems to be more affected by concentrate level than passage rate of roughage. However, the relationship may not hold true in specific situations, since some of the rates represent a few actual data points.

The literature reviewed shows that passage rate of feed components may decrease as concentrate level of the diet is increased. Other studies have shown no influence of concentrate level on passage rate. High levels of intake (as with lactating dairy cows) may eliminate the effect of concentrate level on passage rate. In addition, the passage rate of all dietary particles may not be equally affected as in the studies of Colluci et al. (1982) who showed that at low intake, passage rate of concentrate and forage were decreased by 32 and 56%, respectively, as concentrate level increased from 17 to 65% of the diet.

Relative Passage Rates for Feed Components

Relative passage rates for roughage and concentrate portions of mixed diets have been measured in several experiments, most showing a faster passage of concentrate than roughage. The literature is incomplete, however, concerning relative passage rates for a wide range of roughage and grain types.

Eng et al. (1964) utilized 20 mature wethers in an experiment comparing the passage time of corn and hay in diets containing varied proportions of ground corn to chopped bermuda hay. Retention times were determined using stained particles, and the method for calculating rumen retention time was as described by Balch et al. (1950). Rumen retention times were 96 h for hay and 82 h for corn. The greatest difference between corn and hay occurred on the 75% corn diet, which had a retention time of 131 h for hay and 97 h for corn.

Montgomery and Baumgardt (1965) measured rumen retention times for alfalfa meal and corn in Holstein heifers fed pelleted alfalfa meal and corn diets which contained 0, 20, 40 and 60% corn. Rumen retention times, determined by stained particles and corrected for intake by covariance, were 31.1 h and 36.3 h for alfalfa meal and corn respectively, averaged across concentrate level. Rates of passage for the two components were different ($P<.05$) only for the 80% alfalfa meal diet which had retention times of 27.7 h and 33.4 h for alfalfa meal and corn respectively.

Prange et al. (1979) studied passage of liquid, hay and grain (types not reported) in dairy cows fed diets differing in hay to grain ratio. Hay level did not affect passage rates. Passage rate for liquid, hay and grain were 10.9, 7.9 and 5.41 %/h, respectively.

Hartnell and Satter (1979) measured passage rates for liquid, grain (ground corn, ground oats, soybean meal) and alfalfa hay using Holstein cows at four stages of lactation (dry, 12, 24 and 44 wk). Rare earths (spray technique) and Co-EDTA were used for determination of particulate and liquid passage rates, respectively, and the method of Grovum and Williams (1973) was used to calculate rumen passage rates. Rumen passage rates for liquid, grain and hay, averaged across sampling time, were 8.1, 4.4 and 3.9 %/h respectively. Passage rates for hay and grain were not significantly different.

Colucci et al. (1982) studied passage rates of concentrate (corn and soybean meal) and forage (half corn silage and half alfalfa haylage) in dairy diets fed at two forage levels and two intake levels. The investigators used Cr-mordanted concentrate and forage and calculated rates according to Grovum and Williams (1973). Rumen passage rates for concentrate and forage were 5.7 and 3.9 %/h averaged across treatments.

Lindberg (1985) fed diets consisting of 400 g chopped grass and 500 g crushed barley (maintenance) to six wether sheep. Passage rates were determined for Cr-mordants of hay, barley hulls, crushed peas, rapeseed meal and cottonseed meal. Mean retention times, calculated according to Blaxter (1956), were 53.5 h for hay, 52.3 h for barley hulls, 44.3 h for crushed peas, and 37.0 hr for rapeseed meal (pooled SEM=4.55 hr). Rumen passage rates calculated according to Grovum and Williams (1973) were 2.8, 2.5, 4.0, 4.9 and 4.0 %/h for hay, barley hulls, crushed peas, rapeseed meal and cottonseed meal respectively (SEM = 0.5 %/h). This study was the first attempt to establish relative passage rates for several feed types using a typical mixed grain and forage diet.

Rogers et al. (1985) utilized four Holstein cows in a 4x4 Latin square to measure the passage of concentrate (ground corn and soybean meal), long alfalfa hay and chopped alfalfa hay in diets containing 46% concentrate and 54% hay. Treatments were: 1) long hay, 2) long hay + 1.4% sodium bicarbonate, 3) chopped hay, and 4) chopped hay + 1.4% sodium bicarbonate. Samarium, Cerium or Lanthanum were sprayed onto the three feeds to determine passage rates which were calculated according to the model of Grovum and Williams (1973). Rumen passage rates, averaged across treatment, were 6.8, 6.1 and 4.5 %/h for concentrate, long hay and chopped hay respectively. The greatest difference between markers was on the chopped hay + bicarb diet which had passage rates of 7.8, 5.9 and 4.0 %/h for concentrate, long hay, and chopped hay (SEM=0.67 %/hr). The observation that passage rate was slower for chopped than long alfalfa hay is disturbing. Passage from the rumen can occur only after feed particles reach a certain threshold size (Faichney, 1986). This means that if the only difference between two marked feeds introduced into the rumen is particle size, the marker with smaller particle size should pass faster. The use of the rare earth spraying technique and a different rare earth for each feed in this study may explain the curious results. Spraying rare earth on feeds may lead to substantial migration, resulting in errant passage rates (Mader et al., 1984). Differences between rare earth markers also may exist so that marking each feed with a different rare earth may bias the passage rates for individual feed ingredients.

Woodford et al. (1986) conducted a study with four lactating Holstein cows in a 4x4 Latin square design to measure the passage rates of liquid, alfalfa hay and concentrate in diets containing 28%, 36%, 45% and 53% alfalfa hay. Passage rates (Grovum and Williams, 1973) were determined by rare earths sprayed on feeds, and Co-EDTA was used as a liquid marker. Rumen passage rates for the liquid, hay and concentrate were 11.7, 5.8 and 10.3 %/h respectively (pooled SEM=.59 hr). Differences between hay and concentrate (20 vs 10 h respectively) were greatest for the 28% hay diet.

Hunt, Klopfenstein and Britton (1986) measured the rumen passage rate of wheat straw and alfalfa hay using five steers (5x5 Latin square) fed wheat straw and alfalfa hay in ratios of 100:0, 75:25, 50:50, 25:75, 0:100. Increasing alfalfa in the diet linearly increased the passage rate of wheat straw ($P<.05$), an effect probably due to increased voluntary feed intake. Passage rate for alfalfa and wheat straw, averaged across treatments, were 2.2 and 3.0%/h, respectively.

Owens and Goetsch (1986) summarized available data on concentrate and roughage passage rates. Rumen passage rate of concentrate averaged 4.5 %/h while passage rate of roughage averaged 3.3 %/h. The greatest difference between the rates was for intakes of <1.25% of body wt, where passage rate of concentrates was 3.6%/h and roughage was 1.8%/h.

Erdman et al. (1987) studied the passage rates of concentrates and roughages fed to three lactating dairy cows. Cows were producing 18 kg milk/day and consumed about 15 kg/day of diets containing 30% corn silage, 10% alfalfa haylage, 10% chopped alfalfa hay and 17.6% ground corn (dry basis) plus three combinations of energy and protein concentrate sources. Feed ingredients were marked by spraying with either Ce, La or Sm. Passage rates (%/h) for forages were as follows; alfalfa hay, 3.7; alfalfa haylage, 4.5; and corn silage, 4.6 (SEM = 0.5). Passage rates for concentrates were; corn, 4.4; soybean meal, 4.8; wheat mids, 4.9; corn gluten feeds, 4.3; oats, 4.7; distiller's dried grains with solubles, 4.6; barley, 5.0; brewers dried grains, 4.7; and cottonseed meal, 4.9 (SEM = 0.5). None of the passage rates for the feeds were significantly different, possibly because of the relatively high level of intake (Colucci et al., 1982), or because marker migration biased the passage estimates.

The literature on relative passage rates shows that in general roughages pass slower than concentrate in mixed diets. It must be noted, however, that not all studies have shown marked differences in passage rates of forage and concentrates, indicating that the relationship may not hold for all roughage/concentrate combinations, and levels of intake. There is evidence that different types of concentrates (including grains and protein concentrates) have different passage characteristics (Lindberg, 1985). It is also likely that different roughage types have different passage rates (Hunt et al., 1986), but the literature is incomplete on this regard.

The use of the spraying technique for marking feeds with rare earths has been widely criticized (Mader et al., 1984; Cooker et al., 1983), but is still commonly used, especially in dairy research. Further validation, comparison and refinement of the various marker techniques is necessary for better understanding of differential rumen passage of individual feed components.

Summary

When purified starch is added to forage diets in vitro or in vivo, forage fiber digestion is usually depressed. Possible mechanisms for the depression include low pH (decreasing cellulase activity and microbial attachment), competition between amylolytic and fibrolytic bacteria for critical nutrients, or the production of inhibitors by amylolytic bacteria (Hoover, 1986).

Decreased total tract digestibility of fiber has been more difficult to demonstrate when grain to forage ratios are changed in mixed diets. This may be due to more stable rumen pH, to hindgut digestion compensating for decreased rumen digestion or to changes in the source (and possibly potential digestibility) of fiber in the diet. In addition, ruminal passage rates of diet components may be decreased with increased concentrate level, which would tend to offset decreased digestion rates. Which of these factors is most important for explaining data from a given experiment is unknown, and interpretation of NDF digestion data is difficult as a result. Further research in these areas is necessary to expand our understanding of rumen digestion.

Research to date has shown that roughages generally pass slower from the rumen than do concentrates. Studies have shown, however, that passage rate of alfalfa hay may be more similar to grain than other roughages. Research on passage rate in ruminants has been conducted with a wide variety of methods, all of which are open to criticism due to one or more limitations. More work comparing and validating existing techniques, as well as development of new techniques, will allow us to obtain more interpretable data in ruminant digestion experiments.

MATERIALS AND METHODS

Six ruminally fistulated crossbred steers with a mean wt of 509 kg were used to evaluate the effect of diet concentrate level on the differential passage and digestion of major dietary components. The steers were individually housed in 2.4 x 4.9 m concrete floored pens. The feed bunks and half of each pen were protected by an aluminum shade.

Three diets, containing 70, 40 or 10% roughage (table 1), were studied in two simultaneous 3x3 Latin squares, balanced to eliminate residual effects. The roughage was 50:50 chopped wheat straw:chopped alfalfa hay, while the concentrate portion was primarily steam processed and flaked milo. Steers were fed no more than 2% body wt/day (as fed basis) in two equal feedings at 12-h intervals. If voluntary intake was less than 2% body wt/d, steers were offered 110% of voluntary intake. Each experimental period consisted of a 28-d adaptation period, 5-d total fecal collection for determination of digestibility and particulate passage rate, and a 2-d period during which rumen pH and liquid turnover rate were measured. Rumen fill was determined by total evacuation on one of the last 2 d of each period.

Total tract digestion coefficients were determined by the total collection method. Feed samples and refusals were taken daily. Fecal samples were dried at 50 C, and all samples were ground through a 1-mm screen (Wiley mill) before analysis. Absolute dry matter of samples was determined in a 100 C vacuum oven. Neutral detergent fiber (NDF) was determined by the methods of Georing and Van Soest (1970) using an amylase modification (Robertson and Van Soest, 1977). Calcium, phosphorus and crude protein were determined using a Technicon Autoanalyzer. Potentially digestible neutral detergent fiber (PDF) was determined by incubating dacron bags (50 micron average pore

Table 1. Composition of Diets (Dry Matter Basis).

	Concentrate level, %		
Ingredient, %	30	60	90
Chopped alfalfa hay	35.0	20.0	5.0
Chopped wheat straw	35.0	20.0	5.0
Steam processed and flaked milo	20.6	50.7	80.5
Molasses	5.0	5.0	5.0
Tallow	2.0	2.0	2.0
Urea	0.9	0.8	0.7
Dicalcium phosphate	1.0	0.7	0.3
Limestone	-	0.3	1.0
Salt	0.5	0.5	0.5
Analysis, %			
Crude protein	10.5	10.2	10.7
Calcium	.78	.68	.59
Phosphorus	.34	.32	.35
NDF	41.6	28.1	15.3

size), containing duplicate 5 g samples of the diets, in the rumen of a fistulated steer fed 1.5% body wt/day (as fed) of the 60% concentrate diet. The fiber remaining after 72 h was termed indigestible neutral detergent fiber (IDF) and PDF was calculated as NDF - IDF. Total intake of PDF was calculated and digestion coefficients determined.

Wheat straw, alfalfa hay and milo were marked by the method of Goetsch and Galyean (1983) which consisted of 24-h immersion in rare earth solution, followed by four hourly rinses and drying at 50 C. Flaked milo was soaked for 12 h and rinsed prior to marking. Marked feeds were mixed with a small portion of the morning feeding such that the dose of rare earth was approximately 500 mg for milo and 1000 mg for the roughages. After 1 h, uneaten marked feed was removed and the balance of the meal fed. Europium (Eu), ytterbium (Yb) and dysprosium (Dy) were selected for this study due to relatively simple analysis by atomic absorption spectrophotometry, and the lack of any mutual absorptive interferences. The three feeds were randomly assigned to rare earths in a way such that each feed would be marked by a different rare earth each period. Thus wheat straw was marked with Yb, Eu and Dy in period 1, 2 and 3 respectively, alfalfa with Dy, Yb and Eu in period 1, 2 and 3, and milo with Eu, Dy and Yb in period 1, 2 and 3. This eliminated the possibility that a difference in markers could lead to bias in relative passage rates. Fecal samples were obtained prior to dosing and at 12-, 16-, 20-, 24-, 28-, 32-, 36-, 42-, 48-, 54-, 60-, 72-, 84-, 96- and 120-h post dosing. Feces voided since the previous sampling time (starting at 8 h for the first sample) were mixed and sampled, and the midpoint of the sampling interval was called the sample time. Rate of passage samples were dried at 50 C and ground through a 2-mm screen (Wiley mill) prior to lab analysis.

A modification of the method of Ellis et al. (1982) was used to extract rare earths from feces samples. Duplicate 2.5 g samples were weighed into tared 50 ml beakers, dried at 100 C for dry matter determination, and then ashed overnight at 500 C. Twenty mililiters 3N $HCl/3N\ HNO_3$ was added, and the beakers were placed on a hot plate and brought to a full boil to ensure complete extraction of the rare earths. Extracts were diluted to 50 ml, allowed to settle, and 150 mg of KCl was added to control ionization. Common matrix standards were made up from blank feces obtained prior to dosing. Standards and samples were analyzed on a Hitachi 80-70 atomic absorption spectrophotometer equipped with high temperature burner and nitrous oxide flame (Ellis et al., 1982; Goetsch and Galyean, 1983).

Immediately prior to feeding on the morning of day six, steers were dosed into four areas of the rumen via cannula with 13 grams of NaCobalt-EDTA (Uden et al., 1980) dissolved in 500 ml of water, using a funnel with a plastic tube attached to the end. Samples of rumen fluid were obtained using suction just prior to dosing and at 4-, 8-, 12-, 16-, 24-, 36- and 48-h post dosing. Rumen fluid pH was determined at 0-, 2-, 4-, 6-, 8-, 10- and 12-h post feeding using a pH meter. Fluid samples were strained through four layers of cheesecloth, centrifuged at 2000 G, and refrigerated pending analysis. Duplicate 1-ml aliquots of each sample were diluted to 10 ml with 0.5% acetic acid, and Co concentration was determined by atomic absorption using common matrix standards and an air-acetylene flame (Hart and Polan, 1985).

Rumen outflow constants were calculated according to the methods of Grovum and Williams (1973). Rumen outflow is the slope of the downsloping portion of the curve obtained by regressing the natural log of the marker concentration (in feces or rumen fluid) on sampling time. Rumen liquid volume was determined by dividing the total dose of cobalt administered by the concentration at time zero.

Ruminal digestion of NDF from wheat straw, alfalfa hay and milo was estimated using the methods proposed by Mertens (1977) and Van Soest (1982). Rates of passage used were those determined in the present study, while rumial digestion rates were those determined earlier by Urias (1986). Prior to feeding on either day eight or nine, the rumen of each steer was evacuated and separated into the raft phase (rumen digesta which was in a floating mass in the dorsal regions of the rumen) and liquid phase (liquid digesta remaining after all floating material was removed). Dry matter was determined on duplicate samples of each phase, and rumen dry matter and liquid distributions calculated.

Data were analyzed for concentrate level effects by analysis of variance for a double 3x3 Latin Square (Cochran and Cox, 1957). This method involves partitioning total variation among animals (5 degrees of freedom), periods (2 degrees of freedom), concentrate level (2 degrees of freedom) and residual (8 degrees of freedom).

Differences between feed and liquid passage rates were analyzed within concentrate level by analysis of variance with animals (5 degrees of freedom) as the only blocking criterion (Steele and Torrie, 1960).

When F-tests from the analysis of variance indicated significant effects, means were compared using the least significant difference test (Snedecor and Cochran, 1967).

RESULTS AND DISCUSSION

Effect of Concentrate Level on Intake and Digestibility of Dry Matter and Fiber

Intake and digestibility of dry matter (DM) and neutral detergent fiber (NDF) are presented in table 2. Dry matter intake was

Table 2. Intake and Digestibility of Dry Matter and NDF in Diets Containing 30, 60 or 90% Concentrate.

	Concentrate level, %			
Item	30	60	90	SE
Intake				
DM, kg/d	7.20^{a}	8.30^{b}	7.94^{b}	0.21
DM, % of body wt	1.44^{a}	1.64^{b}	1.55^{ab}	0.04
NDF, kg/d	2.91^{a}	2.32^{b}	1.20^{c}	0.10
Digestibility (%):				
DM	63.60^{a}	70.36^{b}	79.95^{c}	1.23
NDF	40.98	35.63	33.05	2.99

^{a,b,c}Means in the same row with different superscripts differ (P<.05).

lower (P<.05) for the 30% concentrate diet than the 60 or 90% concentrate diet but the magnitude of the difference was small (12% lower). Dry matter intake as a percent of body weight was higher (P<.05) for the 60% than the 30% concentrate diet but was not different (P>.10) for the 30 vs 90% or the 60 vs 90% concentrate diets.

Digestibility of dry matter increased with each increase in concentrate level (P<.05), while NDF digestibility was not changed. The lack of a depression of total NDF digestibility is consistent with much of the literature (Cole et al., 1976; Woodford et al., 1985; Ledoux et al., 1985; deFaria and Huber, 1984a), but is contrary to experiments in vitro (El-Shazley et al., 1961) or in vivo with purified diets (Chappell and Fontenot, 1968; Mulholland et al., 1976). This contradiction may be due to differences in the source of dietary fiber (Cole et al., 1976a,b). For example, several studies have found that total tract fiber digestion coefficient was highest at 100% concentrate, and was significantly decreased with roughage addition (Cole et al. 1976a,b; Bines and Davey, 1970).

Fiber from steam processed and flaked milo has higher potential digestibility than fiber from either alfalfa hay or wheat straw (Urias, 1986). Thus, as milo is increased in a diet with wheat straw and alfalfa as roughage sources, potential digestibility of fiber should increase. As concentrate level of the diet is increased, factors which inhibit fiber digestion come into play (low pH, substrate preference and/or microbial population changes). However, if potential digestibility of NDF in diets increases, the result could be no change in NDF digestibility.

Table 3 shows the potential digestibility of diet NDF predicted from 72-h in situ NDF disappearance of individual ingredients (Urias, 1986), potential digestibility of NDF (determined from 72-h incubation of the mixed diets) and the apparent digestibility of potentially digestible NDF (PDF) observed in our digestion trial. Potential digestibility of NDF determined in this study was slightly higher than predicted using Urias' (1986) values, probably because of differences in particle size of the substrates.

Table 3. Potential Digestibility of Fiber Predicted From 72-h In Situ Incubation of Individual Ingredients (Urias, 1986) or 72-h In Situ Incubation of Mixed Diets, and the Apparent Digestibility of PDF.

	Concentrate level, %			
Item	30	60	90	SE
Predicted potential digestibility of NDF, % [a]	40.9	46.2	62.8	--
Measured potential digestibility of NDF, % [b]	44.3[c]	50.8[c]	69.7[d]	1.5
Apparent digestibility of PDF, %	92.4[c]	70.3[d]	48.0[e]	5.3

[a] 72-h in situ incubation of individual ingredients (ground through 2-mm screen) in steers fed 60% concentrate diets (Urias 1986).

[b] 72-h in situ incubation of mixed feeds from each period in one steer fed the 60% concentrate diet (ground through 1-mm screen).

[c,d,e] Means in the same row with different superscripts differ ($P<.05$).

Apparent digestibility of PDF decreased with each increase in concentrate level ($P<.05$). Total tract digestion of PDF was high on the 30% diet, and illustrates the efficiency with which cattle can digest fiber when concentrate level and intake is moderate. In this study, PDF digestibility was a better measure of fiber digestion than was NDF digestibility, because increased potential digestibility of fiber compensated for decreased fiber digesting activity that occurred as diet concentrate increased.

Effect of Concentrate Level on Rumen pH

Rumen pH was decreased (P<.05) with each increase in concentrate level (table 4). Figure 1 shows average 12-h pH cycles for the three diets. Studies of pH effects on ruminal fiber digestion are often

Table 4. Effect of Dietary Concentrate Level on Rumen pH Parameters.

	Concentrate level, %			
Item	30	60	90	SE
Minimum pH	6.34^{a}	5.76^{b}	5.40^{c}	0.11
Hrs below pH (in 12 hr):				
6.2	0.73^{a}	4.32^{b}	7.10^{c}	1.06
6.0	0.33^{a}	3.25^{b}	6.50^{c}	1.04
pH-hr below pH (in 12 hr):				
6.2	0.13^{a}	1.68^{b}	4.27^{c}	0.63
6.0	0.02^{a}	0.81^{b}	2.92^{c}	0.43

^{a,b,c}Means in the same row with different superscripts differ (P<.05).

conducted at a defined and constantly maintained pH (Shriver et al., 1986; Mould and Orskov, 1983), and show that when pH is maintained below 6.0, fiber digestion is depressed. The effect of cyclic changes in

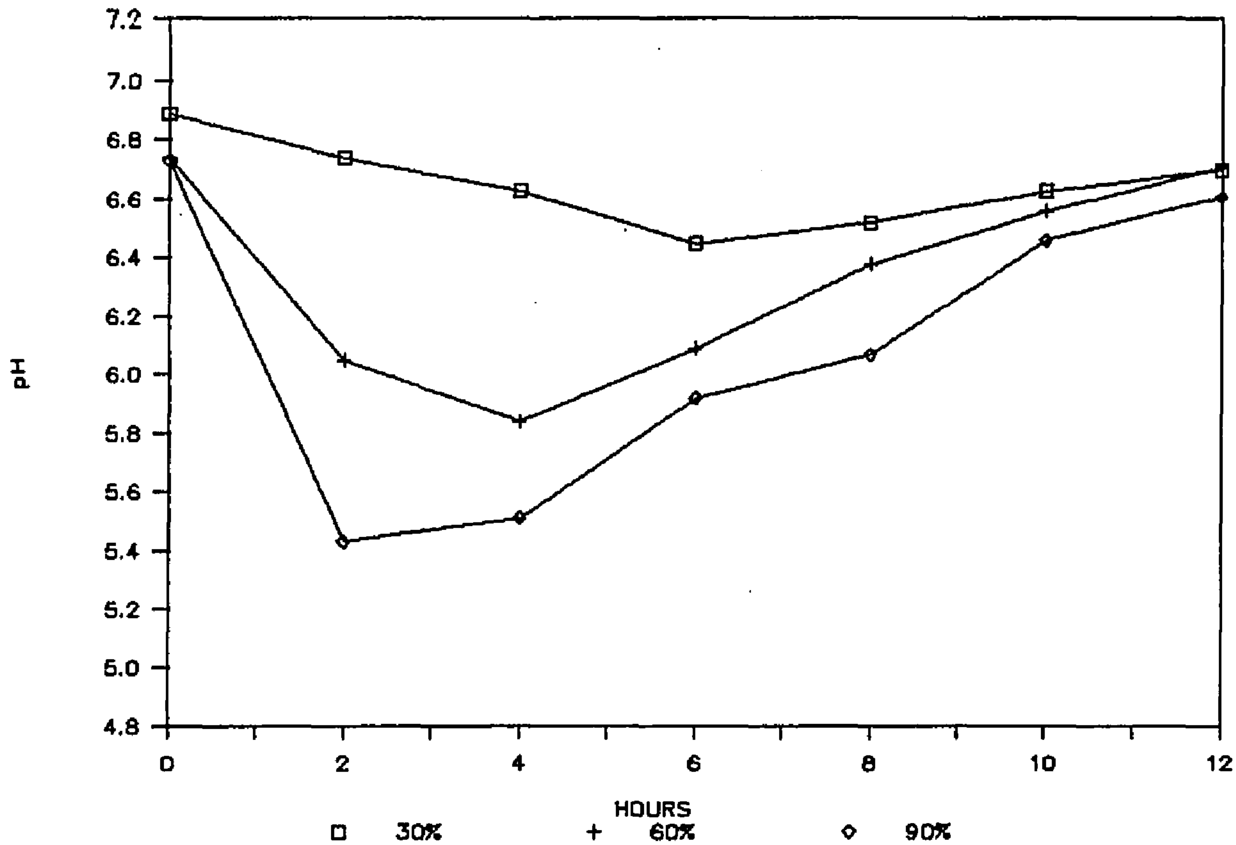

Figure 1. Effect of Dietary Concentrate Level on Ruminal pH. Animals Were Fed Immediately After the 0-h Sample.

rumen pH as occurs in vivo are not well understood, and may lead only to short term decreases in fiber digestion (Hoover et al., 1986). Table 4 shows minimum pH, hours below given pH and pH-hours below given pH. The pH-hour variable represents the area of the pH-time curve falling below a given pH, and is an attempt to integrate the time below a given pH, minimum pH achieved, and rates of decline and recovery from that minimum. Minimum pH and pH-hr are thought to be more closely related to fiber digestion than mean or hr below given pH (Istasae and Orskov, 1983).

Effect of Concentrate Level on Rumen Fill

The rumen of each steer was evacuated prior to the morning feeding to determine total liquid and dry matter fill, and the relative distribution of digesta in the raft and liquid phases (table 5). Ruminal digesta is not homogenous, but is stratified, associating into a dorsal dry "raft phase" and a ventral "liquid phase" (Dixon et al, 1982; Van Soest, 1982).

Some feeds, because of their natural bouancy or tendency to trap gases during digestion float into a dense mat in the dorsal regions of the rumen. More dense feeds, which may also lack the ability to trap gases, would tend to sink in the rumen and be found in the ventral, more liquid regions. The bouyant feeds would be expected to have slower passage rates than the nonbouyant ones, while feeds that are very dense (cottonseed hulls) may tend to sink to the ventral regions of the rumen posterior to the cranial piller, and may have a very slow passage rate.

Table 5. Effect of Dietary Concentrate Level on Ruminal Fill and Distribution of Dry Matter and Liquid.

Item	Concentrate level, % 30	60	90	SE
Total DM fill, kg	4.5	4.3	4.1	0.28
Raft Phase DM, kg	3.6[a]	3.3[a]	1.8[b]	0.44
Liquid phase DM, kg	0.9[a]	1.1[a]	2.3[b]	0.23
Total liquid fill, l	29.8	29.1	28.4	0.95
Raft phase liquid, l	20.2[a]	18.4[a]	10.5[b]	2.52
Liquid phase liquid, l	9.6[a]	11.5[a]	17.9[b]	2.07
Raft phase, % of total rumen digesta	69.2[a]	61.9[a]	34.9[b]	7.78

[a,b]Means in the same row with different superscripts differ ($P<.05$).

Implications of the raft phase are not completely understood, but it is agreed that presence of a raft stimulates rumination, which may stabilize rumen pH when higher concentrate levels are fed (Van Soest, 1982; Ulyott, 1986). As concentrate level increases the size of the raft diminishes, and at very high concentrate levels ruminal digesta may become homogenous (Van Soest, 1982). For this reason, roughage sources that have a high rafting ability may be advantageous in high concentrate diets (Van Soest, 1982).

Ulyott (1986) and Faichney (1986) discuss the rumen raft as a possible "filter bed" which holds particles in the rumen until they are comminuted to a size and density that will descend through the filter and into the liquid phase flowing from the rumen. Thus, roughage sources that form a well-defined raft may be useful in prolonging the retention time of feeds that would otherwise pass rapidly due to their size and density. On the other hand, if the small dense particles do not mix in the raft but enter the liquid phase, their passage rate may be rapid. How these different possibilities affect the efficiency of feed utilization is poorly understood, but it is likely that there are interactions related to roughage source and method of feed processing (Owens and Goetsch, 1986). Further research is required to determine how the rumen raft influences passage of specific feed particles.

In the current study, total rumen dry matter and liquid were not affected by concentrate level (P>.10). The percentage of total rumen digesta in the raft, however, was lower (P<.05) on the 90% concentrate diet. Dry matter (P<.05) and liquid (P<.10) in the raft were lower on 90% concentrate, while dry matter (P<.05) and liquid (P<.10) in the liquid phase were higher. Description of raft and liquid phases in terms of dry matter and liquid distributions may be inadequate. As concentrate level increased, dry matter concentration of the raft phase

Table 6. Effect of Dietary Concentrate Level on Dry Matter of Raft and Liquid Phase Digesta and the Relative Dry Matter Content of the Two Phases.

	Concentrate level, %			
Item	30	60	90	SE
DM % in Raft phase	14.97[a]	15.03[a]	13.47[b]	0.49
DM % in Liquid phase	8.89[a]	8.99[a]	11.28[b]	0.46
DM % Liq / DM % Raft	0.59[a]	0.60[a]	0.85[b]	0.04

[a,b]Means in the same row with different superscripts differ (P<.05).

and liquid phase converged (table 6), with two steers on 90% concentrate showing no stratification at all. Dry matter concentration of the raft phase decreased at the 90% concentrate level ($P<.10$) while dry matter concentration of the liquid digesta increased ($P<.05$). Changes in viscosity of the digesta might also be important; liquid phase digesta from the 90% concentrate diet appeared more viscous than that from the 30 or 60% diets. The dry matter of the liquid phase relative to the raft phase may be a good indicator of raft and liquid phase definition. Steers with no defined raft would have a value of 1.0 while a steer with liquid digesta containing half the dry matter concentration as raft digesta would have a value of 0.5. The ratios were .59 and .60 respectively, for the 30 and 60% diets and increased ($P<.05$) to .85 for the 90% diet, indicating that stratification of rumen digesta was obvious for 30 and 60% concentrate, but less well defined at 90%.

Effect of Concentrate Level on Rumen Liquid Kinetics

Rumen fluid dilution rate and liquid volume were not altered ($P>.05$) by treatment (table 7). This is in contrast to much of the literature (Cole et al., 1976c; Evans, 1981a; Teeter et al., 1984; Owens and Goetsch, 1986) which shows that liquid dilution generally increases with increased roughage level. The reason liquid dilution was not slower at the 90% concentrate level is not known, but if straw functions to stimulate rumination, high salivary secretion may have been a factor. Liquid outflow rate, which is the product of dilution rate and volume, was lowest for the 90% concentrate ($P<.05$). This is in agreement with Wanderly et al. (1986) who, using duodenally cannulated steers

Table 7. Effect of Dietary Concentrate Level on Liquid Passage Rate, Rumen Liquid Volume, and Liquid Outflow Rate as Estimated by Co-EDTA.

	Concentrate level, %			
Item	30	60	90	SE
Liquid passage rate, %/h	9.30	10.00	8.15	0.56
Rumen liquid volume, l	42.18	40.07	35.48	2.17
Liquid outflow rate, l/hr	3.81[a]	3.87[a]	2.68[b]	0.18

[a,b]Means in the same row with different superscripts differ ($P<.05$).

fed wheat straw, alfalfa hay and flaked milo mixed diets, showed less duodenal liquid flow with a high concentrate ration than high roughage.

Effect of Concentrate Level on Particulate Passage Rates

Rumen outflow rates for wheat straw, alfalfa hay and flaked milo are summarized in table 8. Passage rate of milo tended to decrease with increased concentrate. Passage rates for wheat straw and alfalfa were decreased at 90% concentrate but not at 60%. Eng et al., 1964, reported retention time of hay was increased with increasing concentrate but retention time of corn was unchanged. Colucci et al. (1982) showed that when cows were fed diets containing 12 or 68% concentrate at 1.25 % body wt/day, passage rates of both concentrate and forage were faster at the lower concentrate level (3.79 vs 5.28 %/h for concentrate, and 2.32 vs 4.14 %/h for forage). Owens and Goetsch (1986) reviewed literature that

Table 8. Effect of Dietary Concentrate Level on Rumen Passage Rates for Wheat Straw, Alfalfa Hay and Flaked Milo (%/h).

	Concentrate level, %			
Item	30	60	90	SE
Wheat straw	3.37^a	2.97^a	2.15^b	0.18
Alfalfa hay	4.63^a	4.72^a	4.10^b	0.15
Flaked milo	5.34	5.08	4.41	0.37

^{a,b}Means in the same row with different superscripts differ ($P<.05$).

showed passage rate of concentrate was slower for low concentrate (20-50%) than high concentrate (50-80%) diets (6.9 vs 3.4%/h) while passage rate of roughage was not different (3.7 vs 3.5 %/h). A possible explanation is that liquid passage rate also decreased with the increase in concentrate level, suggesting that concentrate passage rate may be more closely related to liquid passage rate than is roughage passage rate.

Mean passage rate for concentrate and roughage, from Owens and Goetsch (1986), were 4.5 and 3.3 %/h respectively, which were 63 and 48% of the liquid passage rate. Mean values from the present study were 5.0, 4.5 and 2.8 %/h for milo, alfalfa and wheat straw respectively, and were 55, 50 and 31% of the liquid passage rate. Particulate passage rate relative to liquid passage was decreased only for wheat straw as concentrate level of the diet increased (36, 30 and 26 % of liquid passage rate for 30, 60 and 90% concentrate diets, respectively, $P<.05$). Passage rate of flaked milo was 57, 51 and 55% of liquid passage, while passage rate of alfalfa hay was 51, 48 and 51% of liquid passage rate for the respective diets.

Evaluation of the Multiple Marker System

One of the objectives of the experiment was to evaluate the value of the marker system. An assumption generally made is that all rare earths have similar passage characteristics. There is little direct evidence that all rare earths pass at the same rate when bound on the same feed. Goetsch and Galyean (1982), showed that passage rate of alfalfa hay was the same when determined with either Dy or Yb in steers fed all alfalfa hay diets. Moore, Poore and Swingle (1986) showed that in vitro digestion characteristics of wheat straw, alfalfa hay, cottonseed hulls and steam processed and flaked milo were similar whether marked with Yb or Dy. In addition, migration of marker to unmarked stems and solubilization of marker was similar for the two rare earths.

The current study allows a comparison of the three markers used since each element was applied to each feed for two observations per treatment. Table 9 shows passage rates for the three feeds as determined with each rare earth. Average passage rates of the three rare earths was not different (using SEM pooled over all feeds), which suggests that each rare earth had similar passage characteristics when bound to the same feed.

Possible influence of markers should not be ignored in interpretation of passage data. Use of rare earths has been questioned

Table 9. Passage Rates of Each Feed as Determined by Each Rare Earth.

	Feed passage rate (%/h)		
Feed	Europium	Dysprosium	Ytterbium
Wheat straw	2.72	2.75	3.02
Alfalfa hay	4.40	4.58	4.46
Flaked Milo	5.37	4.87	4.59
	----	----	----
Mean (PSEM = 0.22)	4.16	4.07	4.02

because migration from marked feedstuffs could cause over- or under-estimation of passage rates (Cooker et al., 1982). The immersion technique, as used in this study, appears to be superior to spraying (Mader et al., 1984) and less migration should occur. Moore et al. (1986) used an in vitro system to show that during a 48-h incubation only about 2% of the total rare earth migrated from feeds marked by immersion to unmarked stems included in the incubation flask. From 10 to 30% of the total rare earth was in the soluble phase (passed through 50-um dacron filter), indicating that solubilization of the marker might have more impact on passage rate than migration. Solubilization of marker at 48-h was in the order of wheat straw > alfalfa > steam flaked milo which is the reverse of passage rate measurements in the present study. Solubilization of marker may cause overestimation of wheat straw passage rate relative to alfalfa and milo since wheat straw tends to show more solubilization and slower passage rate.

Application of Rumen Digestion Model To Partition Fiber Digestion

Passage rates determined in this study were used with digestion rate (K_d) and PDF estimates determined earlier (Urias, 1986) with these same diets (table 10) to partition ruminal digestion of fiber among diet components. The model described by Mertens (1977) as modified by Miller and Muntifering (1985) was used to calculate rumen digestion of wheat straw, alfalfa hay and flaked milo NDF. The model used was;

$AED = PDF \times [K_d / (K_d + K_p)]$ where

Table 10. Effect of Dietary Concentrate Level on the Rate and Potential Extent of Neutral Detergent Fiber Digestion (Urias, 1986).

	Concentrate level, %					
	30		60		90	
Ingredient	PDF	K_d	PDF	K_d	PDF	K_d
Alfalfa hay	41.9	6.1	43.2	6.3	21.4	4.3
Wheat Straw	38.9	4.1	36.2	4.6	10.4	3.8
Flaked milo	78.4	5.5	80.7	5.9	50.8	3.9

Table 11. Effect of Dietary Concentrate Level on the Apparent Extent of Ruminal Neutral Detergent Fiber Digestion (AED) of Feed Components.

	Concentrate level, %			
Ingredient	30	60	90	SEM
Alfalfa hay	24.0^a	24.9^a	11.1^b	0.3
Wheat straw	21.7^a	22.1^a	6.8^b	0.6
Flaked milo	40.6^a	44.1^a	24.4^b	1.3

[a,b]Means in the same row with different superscripts differ (P<.05).

AED is apparent extent of NDF digestion, PDF is the 72-h in situ fiber disappearance, K_d is the rate of digestion and K_p is rate of passage. Lag time was not included in the model.

No decrease in AED for any component was observed as diet concentrate level increased from 30 to 60%. However, at the 90% concentrate level, ruminal AED for wheat straw, alfalfa hay and flaked milo decreased (P<.05) by 70, 55 and 44%, respectively (table 12). Total ruminal fiber digestion for the 90% concentrate diet was 50% than that expected based on AED of components in the 60% diet. Wheat straw, alfalfa hay and flaked milo accounted for 22.1, 13.9 and 64.0% of the total decrease in fiber digestion, since at the 90% concentrate milo contributed 57% of total dietary fiber.

Table 12 shows the contribution of each diet component to total NDF and NDF digested in the rumen. The contribution of milo fiber to total fiber digested in this study substantiates the observations of Van

Soest (1982) and Wedekind et al. (1986) who recognized the significance of grain fiber in higher concentrate diets. Van Soest (1982) showed that fiber from concentrate sources (i.e. unlignified brans and hulls) may be higher in potential digestibility and prone to more extensive digestibility depression than forage fiber, and concluded that grain had been overlooked as a substantial source of fiber in mixed diets for

Table 12. Feed Ingredient Contribution to Dietary NDF and NDF Digested in the Rumen for Diets Containing 30, 60 or 90% Concentrate.

Conc %	Ingredient	% of NDF in diet	% of ruminal NDF digestion	SEM
30 %	Wheat straw	55.6	51.4	0.4
	Alfalfa hay	39.7	40.5	0.3
	Flaked milo	4.7	8.1	0.3
60 %	Wheat straw	48.2	39.6	0.4
	Alfalfa hay	34.4	31.9	0.3
	Flaked milo	17.4	28.5	0.3
90 %	Wheat straw	24.9	9.6	0.4
	Alfalfa hay	17.8	11.3	0.3
	Flaked milo	57.3	79.2	0.3

ruminants. Wedekind et al. (1986) used semi-purified diets without grain to evaluate concentrate level effect on forage fiber digestion without the interfering effects of grain fiber. Miller and Muntifering (1985) used the model technique of Mertens (1977) to evaluate effect of concentrate level on forage fiber digestion only, and effects of concentrate level on grain fiber digestion were not considered, even in diets containing 80% corn.

Grain fiber may be the most important contributor of potentially digestible fiber in high concentrate diets, so manipulation of grain fiber digestion may prove more rewarding than manipulation of forage fiber digestion in attempts to improve fiber digestion in these diets. Ignoring concentrate level effects on grain fiber digestion, and grain contribution to total diet fiber, leads to confusion concerning the nature and implications of fiber digestion depression associated with high concentrate levels.

Table 13 shows the amount of NDF digested in the rumen and in the total tract. Ruminal digestion accounted for 57.7, 79.3 and 58.6%

Table 13. Effect of Dietary Concentrate Level on Digestion of NDF in the Rumen and Total Tract.

	Concentrate level, %			
Item	30	60	90	SE
NDF digested in the Rumen, g/100g diet NDF	23.59^{a}	26.90^{b}	17.65^{c}	0.49
NDF digested in the Total tract, g/100g diet NDF	40.98	35.63	33.05	2.99
Proportion of total digestion occuring in the rumen, %	57.7	79.3	58.6	7.43

^{a,b,c}Means in the same row with different superscripts differ (P<.05).

of total tract NDF digestion for the 30, 60 and 90% concentrate diets, respectively. The low proportion of NDF digestion occuring in the rumen on the 30% diet is not in agreement with literature that shows the highest digestion occurring in the rumen in diets with the highest forage level. This suggests that hindgut digestion of NDF may be important on low concentrate diets where digestion and passage rates are such that considerable PDF exits the rumen, or that ruminal NDF digestion was underestimated for the 30% diet. Bines and Davey (1970) showed that when dry cows were fed (average 1.8% body wt/d) mixed concentrate diets containing barley straw, ruminal digestion of cellulose was 57.3, 56.9 and 28.4% of total tract digestion for 60, 40 and 20% straw, respectively. This confirms that hind gut digestion may be of importance when diets contain low quality roughages. The proportion of NDF digestion occurring in the rumen on the 60 and 90% concentrate diets was more consistent with other studies (Brink and Steele, 1985; Wedekind et al., 1986; Merchen et al., 1986). Brink and Steele (1985) reported that ruminal NDF digestion was 89.9, 76.0 and 39.3% of total tract digestion when diets contained 50, 70 and 90% concentrate, respectively. In a similar experiment, Wedekind et al. (1986) showed that the ruminal contribution was 81.1, 69.4, 56.6 and 57.8% of total tract NDF digestion when sheep were fed concentrate levels of 0, 20, 40 and 60%, respectively. Merchen et al. (1986) showed that when concentrate level was 25 or 75%, proportion of NDF digestion occuring in the rumen of sheep was 84.5 and 56.8% respectively.

Proportion of NDF digestion occuring in the rumen was quite variable, but since values were similar to those determined experimentally by other authors, it is suggested that the modeling approach yielded reasonable estimates of ruminal fiber digestion.

Summary

Increasing concentrate level from 30 to 90% resulted in increased dry matter digestibility but no change in the digestibility of NDF. As flaked milo was substituted for roughages, potential digestibility of dietary fiber increased, which compensated for the expected decrease in fiber digesting activity. Apparent digestibility of PDF was decreased with each increase in concentrate level. This confirms that PDF estimates are required to interpret NDF digestibility data when source of fiber in the diet varies.

Rumen pH decreased with each increase in concentrate level. On the 60 and 90% concentrate diets, pH fell well below levels known to decrease ruminal fiber digestion.

Total dry matter and liquid fill were not affected by diet, but digesta were stratified into large raft and small liquid phases on the 30 and 60% diets. On the 90% diet, the raft and liquid phases were of similar size.

Passage rates of roughages, especially wheat straw, were decreased at 90% concentrate while passage rate of milo and liquid were not changed. The marker system used in this study was adequate for identifying treatment effects on passage rates of dietary components. Comparison of passage rates determined with each element suggests that the three rare earths passed at similar rates when bound to the same feed.

Apparent extent of ruminal NDF digestion decreased for all feed ingredients at the 90% concentrate level with wheat straw being the most seriously depressed (70%) and milo the least (44%). However, since milo was the largest contributor of NDF in the 90% diet, it provided 80% of total ruminal NDF digestion, and accounted for 60% of the total fiber digestion lost when AED decreased as a result of increasing concentrate level from 60 to 90%.

Estimates of ruminal digestion of NDF, calculated from the passage and digestion rate model, appeared resonable compared to estimates from other studies. This modeling approach may prove valuable for evaluating rumen digestion of individual dietary components.

Results of this experiment show that as concentrate was increased in mixed diets rumen pH and digestion of PDF was reduced. Passage rate of feed components was reduced at high concentrate level, but not enough to compensate for decreased rate of digestion in the rumen. As a result, more potentially digestible fiber entered the hindgut and was subsequently lost in the feces.

APPENDIX

Appendix Table 1. Individual steer values, 30% concentrate diet.

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Experimental period-	2	2	1	3	3	1	-	-
Intake (kg/d)-								
Dry matter:	8.44	6.29	8.80	5.80	5.62	8.25	7.20	0.21
NDF:	3.35	2.34	3.74	2.32	2.25	3.46	2.91	0.10
PDNDF:	1.45	1.05	1.67	1.06	1.03	1.54	1.30	0.04
Digestion Coeff (%)-								
Dry matter:	62.77	65.36	62.93	66.46	59.77	64.28	63.60	1.23
NDF:	39.45	42.46	41.90	44.57	35.29	42.20	40.98	2.99
PDNDF:	91.85	98.52	94.12	97.85	77.48	94.81	92.39	5.34
Rumen pH								
0 hr	7.12	6.91	6.84	6.64	7.00	6.83	6.89	0.07
2 hr	6.80	6.91	6.79	6.65	6.64	6.67	6.74	0.12
4 hr	6.68	6.82	6.81	6.54	6.83	6.11	6.63	0.13
6 hr	6.58	6.58	6.54	6.45	6.72	5.85	6.45	0.12
8 hr	6.65	6.49	6.39	6.55	6.73	6.33	6.52	0.09
10 hr	6.73	6.48	6.59	6.45	7.03	6.51	6.63	0.07
12 hr	6.84	6.11	6.93	6.61	6.88	6.84	6.70	0.08
Minimum pH	6.58	6.11	6.39	6.45	6.64	5.85	6.34	0.12

Appendix table 1. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Hrs below pH								
6.7	5.8	7.1	6.0	12.0	0.9	9.8	6.72	0.82
6.4	0.0	1.6	0.4	0.0	0.0	6.1	1.35	1.11
6.2	0.0	0.5	0.0	0.0	0.0	3.9	0.73	1.05
6.0	0.0	0.0	0.0	0.0	0.0	2.0	0.33	1.04
5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.96
pH-Hrs below pH								
6.7	0.39	1.68	1.06	1.95	0.04	4.00	1.52	0.86
6.4	0.00	0.23	0.00	0.00	0.00	1.68	0.32	0.81
6.2	0.00	0.02	0.00	0.00	0.00	0.74	0.13	0.63
6.0	0.00	0.00	0.00	0.00	0.00	0.14	0.02	0.43
5.8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Rumen fill (kg)-								
Rumen DM:	5.13	4.68	4.28	6.00	3.11	3.91	4.52	0.28
Raft Phs DM:	4.41	4.04	3.36	5.15	1.92	2.71	3.60	0.44
Liq Phs DM:	0.72	0.64	0.92	0.85	0.74	1.20	0.85	0.23
Rumen H_2O:	32.77	26.40	34.85	33.37	20.98	30.18	29.76	0.95
Raft H_2O:	25.02	21.87	19.48	26.45	11.67	16.49	20.16	2.52
Liq Phs H_2O:	7.75	4.53	15.37	6.93	9.31	13.69	9.62	2.07
Raft % of total:	77.50	83.27	60.54	80.25	57.50	56.33	69.23	7.77
Dry matter content of digesta-								
Raft Phs % DM:	14.99	15.60	14.70	16.29	14.12	14.13	14.97	0.49
Liq Phs % DM:	8.45	12.26	6.20	10.98	7.34	8.04	8.89	0.46
LP % DM/ RP % DM:	0.56	0.79	0.42	0.67	0.52	0.57	0.59	0.04

Appendix Table 1. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Liquid kinetics-								
Passage rate (%/h):	8.2	8.9	12.9	5.2	9.9	10.7	9.30	0.56
Volume (l):	55.97	34.80	37.80	50.13	31.67	42.70	42.18	2.17
Outflow (l/h):	4.59	3.10	4.88	2.61	3.14	4.56	3.81	0.18
Feed passage rates (%/h)-								
Milo:	4.60	5.82	7.27	2.74	5.60	5.98	5.34	0.37
Alfalfa hay:	4.51	4.87	5.37	2.81	5.30	4.89	4.63	0.15
Wheat straw:	2.93	3.16	4.20	1.83	4.36	3.72	3.37	0.18
Particulate rate/ liquid rate x 100								
Milo:	56.1	65.4	56.4	53.7	56.6	55.9	57.2	3.30
Alfalfa hay:	55.0	54.7	41.6	54.0	53.5	45.7	50.8	1.54
Wheat Straw:	35.7	35.5	32.6	35.2	44.0	34.8	36.3	0.98
Ruminal AED of NDF (%)-								
Milo:	42.69	38.09	33.77	52.33	38.85	37.56	40.55	1.31
Alfalfa hay:	24.12	23.33	22.32	28.72	22.45	23.29	24.04	0.30
Wheat straw:	22.71	21.99	19.24	26.92	18.88	20.42	21.69	0.61

Appendix Table 2. Individual steer values, 60% concentrate diet.

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Experimental period-	1	3	2	1	2	3		
Intake (kg/d)-								
Dry matter:	8.96	7.81	8.80	7.97	7.60	8.74	8.30	0.21
NDF:	2.55	2.14	2.48	2.23	2.11	2.40	2.32	0.10
PDNDF:	1.24	1.07	1.34	1.09	1.13	1.20	1.18	0.04
Digestion Coeff (%)-								
Dry matter:	72.10	70.87	61.44	74.47	72.80	70.50	70.36	1.23
NDF:	38.25	33.95	21.52	43.07	43.50	33.46	35.63	2.99
PDNDF:	78.71	67.91	40.06	88.60	81.31	65.26	70.31	5.34
Rumen pH								
0 hr	6.82	6.52	6.95	6.21	6.94	6.79	6.74	0.07
2 hr	6.38	5.83	5.90	5.78	6.63	5.78	6.05	0.12
4 hr	5.84	6.32	5.64	5.56	6.36	5.34	5.84	0.13
6 hr	6.26	6.21	6.21	5.66	6.61	5.57	6.09	0.12
8 hr	6.50	6.22	6.60	5.95	6.78	6.22	6.38	0.09
10 hr	6.64	6.51	6.73	6.10	6.75	6.60	6.56	0.07
12 hr	6.75	6.79	6.97	6.13	6.75	6.89	6.71	0.08
Minimum pH	5.84	5.83	5.64	5.56	6.36	5.34	5.76	0.12

Appendix Table 2. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Hours below pH								
6.7	10.7	11.5	9.0	12.0	5.6	10.5	9.88	0.82
6.4	5.3	9.1	6.0	12.0	0.9	8.3	6.93	1.11
6.2	3.1	2.5	4.5	9.0	0.0	6.8	4.32	1.06
6.0	1.4	1.1	3.4	7.7	0.0	5.9	3.25	1.04
5.8	0.0	0.0	1.7	5.1	0.0	4.8	1.93	0.96
pH-hours below pH								
6.7	7.52	5.01	3.96	10.08	0.94	7.94	5.91	0.86
6.4	2.86	1.91	1.75	6.54	0.01	5.16	3.04	0.81
6.2	1.18	0.48	0.69	4.11	0.00	3.59	1.68	0.63
6.0	0.27	0.10	0.08	2.07	0.00	2.34	0.81	0.43
5.8	0.00	0.00	0.00	0.77	0.00	1.31	0.35	0.26
Rumen fill (kg)-								
Rumen DM:	4.18	3.46	3.59	6.96	3.14	4.75	4.34	0.28
Raft Phase DM:	3.07	2.36	2.28	5.94	2.19	3.85	3.28	0.23
Liq Phase DM:	1.11	1.10	1.32	1.02	0.95	0.90	1.06	0.23
Rumen H_2O:	32.87	21.91	29.87	38.50	23.02	28.21	29.06	0.95
Raft Phase H_2O:	17.50	12.64	14.88	29.47	11.79	23.99	18.38	2.52
Liq Phase H_2O:	15.37	9.27	14.98	9.03	11.23	4.22	11.46	2.07
Raft % of total:	55.52	59.14	51.19	77.90	53.34	74.24	61.89	7.77
Dry matter content of digesta-								
Raft Phase % DM:	14.91	15.72	13.26	16.78	15.66	13.82	15.03	0.49
Liq Phase % DM:	8.20	10.59	8.04	10.08	7.74	9.30	8.99	0.46
LP DM% / RP DM%:	0.55	0.67	0.61	0.60	0.49	0.67	0.60	0.04

Appendix Table 2. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Liquid kinetics-								
Passage rate (%/h):	9.1	13.0	12.4	5.9	10.4	9.3	10.00	0.56
Volume (l):	36.06	33.03	37.13	53.58	21.21	31.87	40.07	2.17
Outflow (l/h):	2.71	2.94	3.19	1.88	2.44	2.93	3.87	0.18
Feed passage rates (%/h)-								
Milo:	5.10	6.12	4.48	2.83	7.13	4.83	5.08	0.37
Alfalfa hay:	4.65	5.58	5.11	2.95	5.70	4.34	4.72	0.15
Wheat straw:	3.00	3.52	3.54	1.56	3.44	2.78	2.97	0.18
Particulate rate/ liquid rate x 100								
Milo:	56.0	47.1	36.1	48.0	68.6	51.9	51.28	3.30
Alfalfa hay:	51.1	42.9	41.2	50.0	54.8	46.7	47.78	1.54
Wheat straw:	32.7	27.1	28.5	26.4	33.1	29.9	29.61	0.98
Ruminal AED of NDF (%)-								
Milo:	43.35	39.68	45.94	54.60	36.61	44.44	44.10	1.31
Alfalfa hay:	24.89	22.94	23.89	29.45	22.71	25.61	24.92	0.30
Wheat straw:	21.82	20.41	20.36	29.96	20.61	22.47	22.10	0.61

Appendix Table 3. Individual steer values, 90% concentrate diet.

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Experimental period:	3	1	3	2	1	2	-	-
Intake (kg/d)-								
Dry matter:	7.65	8.59	8.41	6.81	7.42	8.53	7.94	0.21
NDF:	1.09	1.36	1.20	1.01	1.18	1.33	1.20	0.10
PDNDF:	0.79	0.89	0.86	0.73	0.77	0.96	0.83	0.04
Digestion Coeff. (%)-								
Dry matter:	76.45	81.07	79.01	80.30	80.96	81.88	79.95	1.23
NDF:	18.19	38.59	33.46	27.31	39.45	41.30	33.05	2.99
PDNDF:	26.35	59.24	46.34	38.03	60.59	57.56	48.01	5.34
Rumen pH								
0 hr	7.03	6.48	7.08	5.98	6.80	6.84	6.73	0.07
2 hr	5.21	5.39	4.72	5.53	6.49	5.23	5.43	0.12
4 hr	5.33	5.33	5.11	5.48	6.52	5.26	5.51	0.13
6 hr	5.70	5.34	6.38	5.81	6.62	5.68	5.92	0.12
8 hr	5.95	5.63	6.68	5.75	6.46	5.96	6.07	0.09
10 hr	6.76	6.26	6.86	5.60	6.59	6.68	6.46	0.07
12 hr	7.05	6.62	7.02	5.78	6.57	6.60	6.61	0.08
Minimum pH	5.21	5.33	4.72	5.48	6.46	5.23	5.41	0.12

Appendix Table 3. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Hours below pH								
6.7	9.4	12.0	7.7	12.0	11.5	11.8	10.73	0.82
6.4	8.4	10.6	5.5	12.0	0.0	10.0	7.75	1.11
6.2	7.7	9.3	5.0	12.0	0.0	8.6	7.10	1.06
6.0	7.0	8.3	4.5	12.0	0.0	7.2	6.50	1.04
5.8	5.5	7.3	4.0	11.0	0.0	5.6	5.57	0.96
pH-hours below pH								
6.7	9.00	11.53	7.68	12.40	1.36	9.39	8.56	0.86
6.4	6.31	8.05	4.52	8.82	0.00	6.67	5.73	0.81
6.2	4.69	6.05	3.51	6.40	0.00	4.95	4.27	0.63
6.0	3.18	4.26	2.70	3.94	0.00	3.41	2.92	0.43
5.8	1.88	2.66	1.94	1.61	0.00	2.08	1.70	0.26
Rumen fill (kg)-								
Rumen DM:	3.36	3.16	4.61	6.64	3.05	3.78	4.10	0.28
Raft Phase DM:	0.00	0.00	2.80	4.33	1.06	2.70	1.82	0.44
Liq Phase DM:	3.36	3.16	1.82	2.31	1.99	1.07	2.29	0.23
Rumen H_2O:	30.41	20.80	32.95	38.05	21.86	26.24	28.39	0.95
Raft Phase H_2O:	0.00	0.00	18.27	21.92	6.76	16.05	10.50	2.52
Liq Phase H_2O:	30.41	20.80	14.68	16.13	15.10	10.19	17.91	2.07
Raft % of total:	0.00	0.00	56.78	58.63	31.39	62.36	34.86	7.77
Dry matter content of digesta-								
Raft Phase DM%:	9.95	13.10	13.27	16.50	13.58	14.42	13.47	0.49
Liq Phase DM%:	9.95	13.10	11.02	12.47	11.65	9.48	11.28	0.46
LP DM% / RP DM%:	1.00	1.00	0.83	0.76	0.86	0.66	0.85	0.04

Appendix Table 3. (continued)

Item:	Steer # 4	5	6	7	8	9	Mean	SEM
Liquid kinetics-								
Passage rate (%/h):	7.5	8.9	8.6	3.5	11.5	9.2	8.15	0.56
Volume (l):	36.06	33.03	37.13	53.58	21.21	31.87	35.48	2.17
Outflow (l/h):	2.71	2.94	3.19	1.88	2.44	2.93	2.68	0.18
Feed passage rates (%/h)-								
Milo:	4.66	4.58	3.60	2.34	6.46	4.84	4.41	0.37
Alfalfa hay:	4.28	4.55	4.10	1.87	5.08	4.69	4.10	0.15
Wheat straw:	2.31	2.25	1.69	0.90	3.41	2.33	2.15	0.18
Feed passage rate/ liq passage rate x 100								
Milo:	62.1	51.5	41.9	66.9	56.2	52.6	55.20	3.30
Alfalfa hay:	57.1	51.1	47.7	53.4	44.2	51.0	50.75	1.54
Wheat straw:	30.8	25.3	19.7	25.7	29.7	25.3	26.08	0.98
Ruminal AED of NDF (%)-								
Milo:	23.14	23.36	26.42	31.75	19.12	22.67	24.41	1.31
Alfalfa hay:	10.66	10.34	10.89	14.86	9.75	10.17	11.11	0.30
Wheat straw:	6.47	6.53	7.20	8.41	5.48	6.45	6.76	0.61

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