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VOLUNTARY INTAKE AND FEEDING BEHAVIOR OF DAIRY COWS IN RESPONSE TO RUMEN FILL FROM FORAGE FIBER

By

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Major Professor: Michael S. Allen

AN ABSTRACT OF A DISSERTATION

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ABSTRACT

VOLUNTARY INTAKE AND FEEDING BEHAVIOR OF DAIRY COWS IN RESPONSE TO RUMEN FILL FROM FORAGE FIBER

By

Richard Gary Dado

Understanding factors that affect voluntary feed intake and mechanisms associated with intake control is vital to improve efficiency of milk production by dairy cows. Three experiments were conducted to address the hypothesis that forage fiber, as defined by neutral detergent fiber (NDF), and indigestible forage NDF limit intake by cows in early stages of lactation because of rumen fill. Because cows consume multiple meals each day, within-day measurement of feeding behavior is required to adequately study intake. A computer data acquisition system was developed for continuous monitoring of feed and water intakes, chewing activity, reticular motility, and ruminal pH. In experiment one, measuring 12 cows for 5 d in crossover designs provided adequate statistical power to detect meaningful treatment effects during a preliminary feeding behavior study. In experiment two, 12 cows (17 days in milk) were challenged with rumen fill as dietary NDF or inert bulk to determine if filling characteristics of forage diets varied with fiber content. Inert bulk decreased intake for 35% but not for 25% NDF diets. Rumen volume was similar for 35% NDF diets whether or not inert bulk was present. These data support the hypothesis that high NDF diets limit intake because of rumen fill. Changes in feeding behavior or rumen function were insufficient to maintain intake during high rumen fill. In experiment three, 12 cows (13 days in milk) were offered one of two 35% NDF diets with alfalfa silages that initially contained similar NDF concentrations (40%) but different NDF digestibilities (40 vs. 45% after 24 h in vitro fermentation). Silage with higher NDF digestibility increased intake by 1.0 kg/d and milk production by 1.9 kg/d. During the study, diets differed in

both NDF content (1.8% units) and NDF digestibility (3% units), perhaps from loss of digestible NDF in the higher digestible forage during feed-out. Equal NDF intakes suggest that intake was limited by NDF content and not by indigestible NDF. If increases in NDF digestibility prior to ensiling promote decreases in NDF content after ensiling, benefits from high NDF digestibility may be substantial. Future research is needed to determine if other dietary factors influence rumen fill and if cows vary in their ability to accommodate fill.

This dissertation is dedicated to the memory of my friend, Mark Peters.

Your time here was short, but our friendship remains.

May we be able to fulfill the dreams you left behind.

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TABLE OF CONTENTS

LIST OF TABLES ix

LIST OF FIGURES xiv

LIST OF ABBREVIATIONS xvii

PROLOGUE 1

CHAPTER 1

Literature Review 4

IMPORTANCE OF FEED INTAKE 4
LONG-TERM INTAKE CONTROL IN RUMINANTS 7
Physical Control of Intake 8
Physiological Control of Intake 17
Integrated Theories of Intake Control 19
SHORT-TERM INTAKE CONTROL IN RUMINANTS 22
Control of Individual Meals 23
Dietary Modulation of Feeding Behavior 25
Methods of Measuring Short-term Intake and Behavior 29
A Model of Feeding Behavior 31
FORAGES, FIBER, AND INTAKE 34
Variation in Forage Consumption Due to NDF Concentration 35
Variation in Forage Consumption Due to NDF Digestibility 49
Plant Factors Affecting Fiber Digestibility 58
Future Directions 62

CHAPTER 2

Continuous Computer Acquisition of Feed and Water Intakes, Chewing, Reticular Motility, and Ruminal pH of Cattle 63

ABSTRACT 63
INTRODUCTION 64
MATERIALS AND METHODS 66
Acquisition System 66

Feed intake 66
Water intake 67
Chewing activity 67
Reticular motility 70
Ruminal pH 70
Data collection 71
Data interpretation 73
Validation 78
RESULTS AND DISCUSSION 82
CONCLUSIONS 89

CHAPTER 3

Variation In and Relationships Among Feeding, Chewing, and Drinking Variables for Lactating Dairy Cows 90

ABSTRACT 90
INTRODUCTION 91
MATERIALS AND METHODS 92
Cow Trial 92
Statistical Analysis 93
RESULTS 95
DISCUSSION 104
CONCLUSIONS 113

CHAPTER 4

Intake Limitations, Feeding Behavior, and Rumen Function of Cows Challenged with Rumen Fill from Dietary Fiber or Inert Bulk 114

ABSTRACT 114
INTRODUCTION 115
MATERIALS AND METHODS 117
Experimental Design and Data Collection 117
Sample and Statistical Analysis 120
RESULTS 123
Production and Nutrient Digestibility 123
Rumen Characteristics 127
Feeding Behavior 132
DISCUSSION 135
CONCLUSIONS 147

CHAPTER 5

Harvesting Alfalfa Forages with Similar Fiber Contents but Different Fiber Digestibilities from Production-Scale Fields 148

ABSTRACT 148
INTRODUCTION 148
MATERIALS AND METHODS 150
RESULTS AND DISCUSSION 153
CONCLUSIONS 162

CHAPTER 6

Enhanced Intake and Production of Cows Offered Ensiled Alfalfa with Higher Neutral Detergent Fiber Digestibility 163

ABSTRACT 163
INTRODUCTION 164
MATERIALS AND METHODS 166
Forage Harvest and Selection 166
Experimental Design and Data Collection 167
Sample and Statistical Analysis 171
RESULTS 174
Forage and Diet Composition 174
Cow Response 178
DISCUSSION 182
CONCLUSIONS 191

EPILOGUE 192

LIST OF REFERENCES 195

APPENDIX 212

LIST OF TABLES

CHAPTER 1

Table 1. Summary of studies where various forms and quantities of inert bulk have been added to the reticulo-rumen to examine the effect of decreased rumen capacity on voluntary intake of ruminants..... 10

Table 2. Empirical equations developed with stepwise multiple regression to predict DMI for lactating cows..... 21

Table 3. Summary of studies that examined the effect of dietary NDF concentration or source as part of complete rations on intake and production of relatively high producing lactating dairy cows. Different NDF concentrations were obtained by changes in fiber source, forage quality, or forage:concentrate ratio..... 37

Table 4. Summary of studies that examined the effect of dietary NDF digestibility as part of complete rations with constant NDF concentrations on intake and production of lactating dairy cows. Different NDF digestibilities were obtained by changes in fiber source or forage quality..... 55

CHAPTER 2

Table 1. Monitoring equipment..... 66

Table 2. Computer, software, and data acquisition boards..... 72

Table 3. Output from the feeding behavior data interpretation program generated for eating, ruminating, and drinking bouts for one cow measured for 1 d..... 79

Table 4. Intake and chewing activity of 10 cows measured for 3 d using computer acquisition and manual observation..... 82

Table 5. Relationship of intake and chewing activity of 10 cows measured with computer acquisition and interpretation (independent data) and manual observation (dependent data)..... 84

CHAPTER 3

Table 1. Summary statistics for milk production and feeding behavior of six primi- and six multiparous lactating Holstein cows measured for 10 d..... 96

Table 2. Pearson correlation coefficients among feeding behavior variables for individual eating, ruminating and drinking bouts..... 99

Table 3. Pearson correlation coefficients among feeding behavior variables for 12 cow means averaged across 10 d of measurement..... 101

Table 4. Pearson correlation coefficients among feeding behavior variables for six primiparous and six multiparous cow means averaged across 10 d of measurement..... 102

Table 5. Variance component estimates for feeding variables using three linear models..... 103

Table 6. Estimated cow numbers required for 80% probability of detecting significant contrast differences between two treatment means for feeding variables for random and complete block designs..... 105

Table 7. Estimated cow numbers required for 80% probability of detecting significant contrast differences between two treatment means for feeding variables for covariate and Latin square designs..... 106

CHAPTER 4

Table 1. Ingredient and nutrient composition of 25% NDF, low fiber diet (LF) and 35% NDF, high fiber diet (HF) offered to 12 cows during the first 14 wk of lactation..... 118

Table 2. Nutrient composition of forages and concentrates used to formulate low fiber (LF) and high fiber (HF) diets..... 119

Table 3. Milk production and feed intake for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 125

Table 4. Apparent total tract digestibility of nutrients, fecal output, fecal composition, and fecal fiber particle size from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 126

Table 5. Rumen digesta characteristics for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 128

Table 6. Concentration and molar proportion of VFA in rumen fluid from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 129

Table 7. Rumen digestion kinetics of NDF and rumen apparent digestibility of NDF from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 131

Table 8. Eating, ruminating, and drinking activities for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.. 133

Table 9. Reticular contractions and ruminal pH for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 134

CHAPTER 5

Table 1. Characteristics of alfalfa forage harvested during the 1992 growing season from two adjacent 8 ha fields..... 155

Table 2. Composition of alfalfa forages before and after ensiling..... 158

Table 3. Correlation matrix among descriptors of forage quality for all five forage silages..... 159

Table 4. Potential improvement in intake and milk production in early lactation cows because of an increase in NDF digestibility between forages D and E..... 161

CHAPTER 6

Table 1. Characteristics of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages prior to commencement of animal experiment..... 168

Table 2. Ingredient and nutrient composition of low digestible fiber (LDF) and high digestible fiber (HDF) diets offered to 12 cows during the first 10 wk of lactation..... 169

Table 3. Nutrient composition of forages and concentrate sampled during animal experiment and used to formulate low digestible fiber (LDF) and high digestible fiber (HDF) diets..... 175

Table 4. In vitro NDF digestion characteristics of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages and diets sampled during animal experiment..... 176

Table 5. Milk production and body characteristics of 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 178

Table 6. Nutrient intake, fecal composition, fecal output, and apparent total tract digestibility for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 180

Table 7. Eating, ruminating, and drinking activities for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 181

Table 8. Rumen digesta characteristics for 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 183

Table 9. Rumen fluid pH and VFA concentration of digesta from 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 184

Table 10. Rumen digestion kinetics of NDF and rumen apparent digestibility of NDF from 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 185

APPENDIX

Table 1. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: computer board assignments in Labtech Notebook software setup..... 212

Table 2. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: channel characteristics of algorithm functions for data acquisition run under Labtech Notebook..... 213

Table 3. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: channel assignments for a complete acquisition run under Labtech Notebook. Setup is designed for monitoring all five activities for 12 stalls.. 217

Table 4. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: feeding behavior data interpretation computer program for summarizing individual cow data into bouts of eating, ruminating, and drinking..... 221

Table 5. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: probability values for effects used to describe variation in experimental variables..... 228

Table 6. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: apparent total tract digestibility of nutrients using acid detergent lignin as an internal marker from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 232

Table 7. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: rumen digesta parameters 2 h prefeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.. 233

Table 8. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: rumen digesta parameters 2 h postfeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.. 234

Table 9. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: concentration and molar proportion of VFA in rumen fluid 2 h prefeeding from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 235

Table 10. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: concentration and molar proportion of VFA in rumen fluid 2 h postfeeding from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 236

Table 11. Enhanced intake and production of cows offered ensiled alfalfa silage with higher neutral detergent fiber digestibility: probability values for effects used to describe variation in experimental variables..... 237

Table 12. Enhanced intake and production of cows offered ensiled alfalfa silage with higher neutral detergent fiber digestibility: apparent total tract digestibility of nutrients using acid detergent lignin as an internal marker for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets..... 240

LIST OF FIGURES

CHAPTER 1

Figure 1. Intake model illustrating the physical limitation and physiological regulation theories of intake control with constant energy consumed along line a-b and constant rumen fill obtained along line b-c in the general case (a) and for a 600 kg cow producing various quantities of 4% FCM (b)..... 20

Figure 2. Feeding behavior model for sheep (Forbes, 1980). Objectives of the model were to predict meal size and frequency during eating as determined by physical and physiological satiety factors. MER = metabolizable energy requirements..... 33

Figure 3. Modified model from Dado and Allen (1993) illustrating ruminal volume and passage compensation as concentrations of dietary NDF increase. Passage from the rumen increases when maximum rumen volume is reached. Intake of NDF is constant and DMI decreases only when both rumen volume and passage are maximum. The level of dietary NDF concentration where thresholds occur are both diet and animal dependent..... 50

Figure 4. Ruminal digestion curve of NDF. Y values represent the percentage of original NDF that remains after a given length of microbial fermentation. Fiber with faster fractional rates of digestion ferment more quickly. Fiber with higher maximum extents of digestion have less fiber remaining after extended periods of digestion. Fiber digestibility is time dependent..... 52

CHAPTER 2

Figure 1. Scaled output of feed manger, water meter, and pH monitors throughout 1 d for a cow fed twice daily..... 68

Figure 2. Analog output from chewing and reticulum motility monitors during episodes of eating and ruminating. Values presented are scaled pressure transducer output..... 69

Figure 3. File output of feeding behavior data from Labtech® Notebook in ASCII format..... 74

Figure 4. Frequency of inter-period intervals for eating and ruminating activity of twelve cows measured for twelve days. Data are expressed as survivorship curves with percent frequency determined cumulatively and backwards (Metz, 1975). The chosen minimum inter-bout interval of 7.5 minutes is indicated..... 76

Figure 5. Frequency of inter-drinking intervals of twelve cows measured for twelve days. Data are expressed as a survivorship curve with percent frequency determined cumulatively and backwards (Metz, 1975). The chosen minimum inter-bout interval of 4 minutes is indicated..... 77

Figure 6. Relationship between reticular contractions determined by manual observation of signal waveform and computer algorithm interpretation for 88 observations. Data are expressed as total number of contractions within a 30-min period. The line represents perfect correlation..... 87

Figure 7. Relationship between ruminal pH determined in vitro by manual sampling and in vivo by computer acquisition for 40 observations. The line represents perfect correlation..... 88

CHAPTER 3

Figure 1. Distribution of chewing time within a day expressed as the mean of 12 cow means. Feed was offered when cows were away from stalls for milking..... 98

Figure 2. Distribution of DMI within a day expressed as the mean of 12 cow means. Bars represent the standard error of each mean. Feed was offered when cows were away from stalls for milking..... 108

CHAPTER 4

Figure 1. Mean milk production and DMI by week of experimental period for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 136

Figure 2. Rumen digesta plus inert bulk volume 2 h prefeeding and 2 h postfeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 140

Figure 3. Rumen digesta volume as a function of rumen NDF pool size for 12 cows receiving low or high fiber diets without or with added rumen inert bulk..... 141

Figure 4. Model of NDF and DM intake response to increases in dietary NDF content. Intake of NDF increases until maximum rumen volume, at which point DMI decreases. Based on a maximum rumen volume of 100 L, maximum NDF intake of 6.5 kg/d, and baseline DMI of 22.8 kg/d, the threshold for intake limitation is 28.5% NDF..... 142

Figure 5. Distribution of individual meal sizes expressed as a percentage of the total number of meals within each treatment for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 144

Figure 6. Distribution of DMI within a day expressed as a percentage of total daily DMI for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk. Bars within a time period with different letters differ ($P < .05$)..... 145

Figure 7. Distribution of rumination within a day expressed as a percentage of total time spent ruminating for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk..... 146

CHAPTER 5

Figure 1. Dimensions of alfalfa plots from which forage was sampled and harvested..... 151

Figure 2. Concentration of NDF in alfalfa forages sampled at various days prior to harvest. Objectives were to obtain forage with 40% NDF at day 0..... 154

Figure 3. Neutral detergent fiber concentrations and NDF digestibility for loads of chopped alfalfa obtained pre- and post-ensiling from harvests D and E. Digestibility of NDF was determined from 24 h in vitro fermentation with buffered rumen fluid..... 157

CHAPTER 6

Figure 1. Digestion of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silage NDF determined from in vitro fermentation in buffered rumen fluid for time indicated..... 177

Figure 2. Concentration of digestible NDF (DNDF) and indigestible NDF (INDF) for low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages following 120 h in vitro fermentation for samples taken prior to commencement of the lactation study (Pre) and samples taken during the lactation study (Post)..... 187

Figure 3. Contribution to digestible DMI from digestible NDF (DNDF) intake and digestible neutral detergent solubles (DNDS) intake for low digestible fiber (LDF) and high digestible fiber (HDF) diets offered to 12 early lactation cows..... 190

APPENDIX

Figure 1. Schematic of complete data acquisition system for continuous monitoring of feed intake, water intake, chewing activity, reticular motility, and ruminal pH of cannulated cows at Michigan State University Dairy Teaching and Research Farm..... 241

LIST OF ABBREVIATIONS

+0 = No added rumen inert bulk.
+B = Added rumen inert bulk.
ADF = Acid detergent fiber.
BW = Body weight.
CP = Crude protein (N x 6.25).
CV = Coefficient of variation.
DHIA = Dairy Herd Improvement Association.
DIM = Days in milk.
DM = Dry matter.
DMI = Dry matter intake.
FCM = Fat-corrected milk (usually 4%).
HDF = High digestible fiber.
HF = 35% NDF diet.
HPLC = High performance liquid chromatography.
k_d = Fractional rate of digestible NDF digestion in the rumen.
k_p = Fractional rate of NDF passage from the rumen.
LDF = Low digestible fiber.
LF = 25% NDF diet.
MIBI = Minimum inter-bout interval.
NDF = Neutral detergent fiber.
NE_L = Net energy for lactation.
NRC = National Research Council.
OM = Organic matter.
P = Probability that difference was due to chance alone.
r = Correlation coefficient.
RIB = Rumen inert bulk.
RMSE = Root mean square error.
SAS = Statistical Analysis System.
SCM = Solids-corrected milk.
SD = Standard deviation.
TDN = Total digestible nutrients.
TMR = Total mixed ration.
VFA = Volatile fatty acids.

PROLOGUE

Dairy cows efficiently convert large quantities of nutrients to milk components that supply valuable food products for human consumption. A sustainable dairy industry is possible because benefits from milk production outweigh input costs. Among domesticated animal species, dairy bovines supply the majority of milk for human food because of large milk output in relation to their maintenance requirements. High levels of feed intake are a major component of such efficiency.

Feed intake sets limits to production of dairy cows in early stages of lactation. Increasing feed consumption during this period not only improves milk production but also minimizes the negative health consequences associated with severe negative energy balance. Greater feed consumption in early lactation also increases milk output throughout the entire lactation period of the cow, since the shape of milk production curves is relatively constant across different levels of production. Higher producing cows convert nutrients to milk more efficiently than lower producers, because fixed nutrient requirements for body maintenance are diluted across more units of milk output. Such improvements in gross efficiency reduce production costs and environmentally challenging waste excretions associated with each unit of milk produced. Finally, increased intake capacity allows more flexible ration formulation and greater potential utilization of more fibrous forages and by-product feeds that are not suitable for human consumption. Undoubtedly, higher levels of feed intake by cows is beneficial to the entire dairy industry and to human society in general.

Understanding limits of feed intake and mechanisms associated with its control remains an intense area of dairy cattle nutrition research. Several mechanisms work in

concert with one another to produce a number of signals that are summarized by intake centers of the central nervous system that ultimately determines commencement and cessation of eating. Potential signals previously investigated include distention of the gastrointestinal tract, accumulation of digestion endproducts, such as VFA, hydrogen ions, peptides, or glucose, and concentration of circulating hormones or neurotransmitters. Lactating cows consume multiple meals per day, thus daily intake is the summation of many individual meals. To accurately assess the influence of diet on feed intake control mechanisms, quantitative examination of within-day feeding behavior is essential. Knowledge of other within-day animal responses to feeding also may contribute to a more complete description of diet/intake relationships.

Forages serve as major components of dairy cattle diets. Not all forages are consumed to the same degree, perhaps due to an intrinsic property that varies among forages. Concentration of cell wall (fiber) in forage plants has been implicated as a major factor associated with intake. In early lactation, feed intake by dairy cows may be limited by the rumen-filling properties of forage fiber. Under this scenario, forages with high concentrations of fiber are consumed to a lesser degree than those with low concentrations. If maintenance of feed intake is a high priority, cows may adjust their feeding behavior to accommodate diets with high concentrations of fiber.

Just as all forages are not consumed equally, all types of forage fiber may not be consumed equally. Forage fiber consists of different molecules, whose number and interactions differ between forage species and maturity. These variations contribute to differences in digestion of fiber in the rumen and may alter the rumen-filling effects of fiber, and forage intake. Fiber digestibility varies widely in forages of the same species; however, this characteristic is not currently measured in routine forage analyses. Before fiber digestibility is adopted for use in ration formulation, it must be demonstrated that differences in forage fiber quality influence animal performance.

Objectives of this research project relate to the influence of forage quality on feed intake by cows in early stages of lactation and were to:

1) Develop, validate, and implement a computer data acquisition system for the continuous monitoring of feed intake, water consumption, chewing activity, reticular motility, and ruminal pH of stall-housed dairy cows.

2) Challenge early lactation cows with rumen fill in the form of dietary NDF and rumen inert bulk to determine if limitations to intake from ruminal fill vary with NDF content.

3) Measure feeding behavior and rumen activity of early lactation cows to determine if within-day behavior changes allow cows to adapt to higher fill conditions and maintain normal daily feed intakes.

4) Harvest production-sized fields of alfalfa with similar NDF concentrations but different NDF digestibilities in sufficient quantities to conduct a lactation study.

5) Determine the effect of forage fiber digestibility on intake and milk production of early lactation dairy cows.

An overview of past research and current theories on intake as they relate to rumen fill in ruminants is presented as a literature review in Chapter 1. Description of a computer data acquisition system to quantitatively measure feeding behavior and rumen function is reported in Chapter 2. Chapter 3 describes an experiment with lactating cows receiving a common diet, that examined relationships among feeding variables. Such information was useful in designing and conducting subsequent experiments where feeding behavior was measured. Objectives 2 and 3 were addressed in a lactation study with 12 cows that is reported in Chapter 4. The harvesting of alfalfa forages with differences in NDF digestibility is described in Chapter 5, and the results of a 12 cow lactation study using these forages is presented in Chapter 6.

The overall hypothesis of this research is that forage fiber and rumen indigestible fiber limit voluntary feed intake in early lactation dairy cows because of rumen fill. To test this hypothesis, intake must be shown to be limited independently by both high fiber content of the diet and low fiber digestibility. Secondly, adequate measurements must be made to quantitatively evaluate whether these intake limitations were caused by physical filling of limited reticulorumen capacity.

CHAPTER 1

Literature Review

IMPORTANCE OF FEED INTAKE

The objective of domestic dairy cattle production is to optimize milk production, usually defined as maximum milk output per unit cost. Because cost of digestible nutrients is high, maximum production per unit of digestible nutrient is desired. Initial increments of digestible nutrients are utilized to maintain body tissue and basal metabolism. Such use is considered constant for a given animal regardless of production (Bauman et al., 1985). Any additional increments are available for productive processes, including growth, fetal development, and milk production. Optimal milk production, therefore, results from maximizing total milk output to decrease the percentage of total digestible nutrients used for maintenance.

High milk production requires large quantities of digestible nutrients. The genetic correlation between milk production and estimated net energy consumption was .82 for 548 cow lactations over a nineteen-year period (Miller et al., 1972). Cows with different genetic abilities to produce milk were found to have similar metabolic efficiencies (Custodio et al., 1983; Bauman et al., 1985), suggesting that a constant ratio exists between digested/absorbed nutrients and milk production. In early lactation, conversion of body tissue to milk allows cows to temporarily achieve production levels in excess of digestible nutrient consumption. However, there are limits to tissue mobilization. In addition, cows must return body stores to levels present before lactation commenced by increasing digestible nutrient consumption in later lactation.

Thus, higher total lactation production must be accompanied by greater digestible nutrient consumption across the lactation.

Consumption of digestible nutrients is a function of the rate of nutrient intake and its corresponding digestibility. Of these two, nutrient intake appears to hold greater importance. From 50 to 70% of the variation in digestible nutrient consumption between animals is due to differences in nutrient intake (Mertens, 1985). Intake has a coefficient of variation of 50% among different feedstuffs while digestibility has variation of 30% (Van Soest, 1982). Reid (1961) suggested that improvements in accurate determination of forage digestibility and nutrient content could increase efficiency of ration balancing by only 1 to 5%, but accurate determination of forage intake would increase efficiency of balancing by 40 to 50%. Finally, there is a mathematical limit to the extent that digestibility can be improved (e.g., cannot exceed 100%), but there is no theoretical limit to the extent that nutrient intake can increase.

Nutrient consumption may be increased one of three ways: increased daily consumption of DM (DMI), increased nutrient density of the DM, or increased DMI and nutrient density. Often an increase in nutrient density of the diet will increase DMI as well, especially with poor quality diets (Waldo, 1986). Increased nutrient density is commonly achieved by replacing less digestible forage with highly digestible concentrates. Such substitution not only increases energy density but also improves energy digestibility and possibly DMI. There are limits, however, to the extent to which forages may be replaced by concentrates (Kesler and Spahr, 1964). Rumen fermentation rates that are too fast result in digestive and metabolic problems for the cow, an animal not designed by nature to survive on extremely low forage/fiber diets. As with digestibility, there is also a mathematical limit to the degree that concentrate can substitute for forage; there is no known limit to DMI.

Intake and milk production are positively correlated, both phenotypically and genetically (Freeman, 1975). Brown et al. (1977) developed multiple regression

equations to describe intake and milk yield for 492 cows and found that DMI was a significant determinant of milk yield. Maximizing feed intake is especially critical for cows in early lactation. Of interest among researchers is the phenomenon where increases in intake lag behind increases in milk production immediately following parturition. Because cows are in negative energy balance in early lactation, increased DMI could prevent large losses of body tissue reserves or allow for increases in milk production. Performance may be improved not only for this period but also for the entire lactation (Broster, 1972).

Improving voluntary DMI requires a thorough understanding of factors involved in the control and influence of intake for ruminants in general, and for early lactation cows specifically. Several mechanisms that may control intake have been previously investigated and reviewed (Baile and Forbes, 1974). Physical fill and physiological control are two major mechanisms commonly cited. Because energy requirements are not met by nutrient consumption in early lactation, it is believed that physical limitations to intake predominate during this period. Daily intake of lactating cows usually involves consumption during discreet meals. A thorough study of those factors limiting intake must examine factors responsible for initiation and termination of individual meals. Forages provide the majority of nutrients to ruminants world-wide. Even for high producing dairy cows, forage quality may be crucial during limitations in intake and digestible nutrient consumption, especially since forage cannot be completely removed from their diets. Examination of forage quality in relation to intake is warranted.

Objectives of this literature review are to discuss past research and current theories on intake limitations as they relate to rumen fill in ruminants. Part I of this review will discuss the long-term control mechanisms of intake in ruminants, including physical, physiological, and integrated control mechanisms. Part II will address short-term intake control, including control of individual meals, modulators of feeding

behavior, and methods of measuring short-term intake. Finally, part III will focus on forages and fiber as they relate to intake and rumen fill. Variation in forage consumption, factors affecting forage composition, and the role of fiber digestibility as an influence on intake will be examined.

LONG-TERM INTAKE CONTROL IN RUMINANTS

Regulation of feed intake under ad libitum feeding has been differentiated into those factors affecting long-term control versus those affecting short-term control (Baile and Forbes, 1974). Long-term regulation involves maintenance of energy inputs and outputs to achieve balance in BW and productive function. Short-term regulation involves within-day activity that defines meal initiation, termination, and distribution. Undoubtedly, short-term controls contribute to long-term balance and may more accurately describe daily fluctuations in intake. However, long-term regulation has been utilized more in models to predict intake because of more sufficient data to support such theories (Illius and Allen, 1993). As additional within-day data are accumulated, perhaps short-term regulation will replace traditional theories used to describe intake. Regardless of relative factors, the ultimate coordinator of feeding behavior and intake control is the central nervous system, and more specifically, the lateral and ventromedial portions of the hypothalamus (NRC, 1987). Several reviews have discussed how such coordination may take place (Wyrwicka and Dobrzecka, 1960; Baile and McLaughlin, 1987; Miner, 1992).

Long-term regulators of intake have been categorized into three major mechanisms: factors associated with physical limitation, factors associated with physiological control, and factors associated with psychogenic adjustments (Mertens, 1985). Physical regulation implies that cows will consume a diet until the physical capacity of the digestive tract is exhausted, or until the maximum rate of a physical process associated with digestion (e.g., rumination) is reached. Physiological regulation commences when a cow has consumed sufficient nutrients to meet energy requirements.

Such a process implies that products of digestion (e.g., metabolites, hormones) send feedback to the hypothalamus to indicate energy balance. Psychogenic adjustment considers other intake control factors associated with environmental conditions (e.g., heat or cold stress), behavior mechanisms (e.g., social interaction), or disease states that are difficult to assign to general categories of intake control. Among these, palatability may be the most important factor, especially under conditions of imprinted feeding behavior. Nevertheless, palatability may exert an influence only for short periods of time and may be more appropriately considered a short-term regulator of intake. In general, one might consider psychogenic adjustments as "fudge factors" to describe intake observations that do not fit model expectations. The major mechanisms of physical and physiological control will be briefly examined as they relate to intake of early lactation dairy cows.

Physical Control of Intake

The concept that feed intake might be limited by its bulkiness was initially proposed by Lehmann (1941) more than fifty years ago. He suggested that ruminants can consume only a certain amount of indigestible matter. Consequently, poorly digested feeds would be consumed to a lesser extent than more digestible feeds. Since then a number of reviews have been published supporting this basic concept (Balch and Campling, 1962; Bines, 1971; Grovum, 1987). This mechanism is based on the premise that the gastrointestinal tract has a finite volume and that feed material must be digested and absorbed or passed out of the tract before additional intake can occur. Although the abomasum and intestines probably have finite volumes, there is general consensus that filling of these organs does not limit voluntary intake (Van Soest, 1982; Grovum, 1987), primarily because fecal output does not remain constant over various levels of intake. Ruminant digestion requires fractionation and fermentation of dietary components before they can pass through the omasal orifice and leave the rumen. Accumulation of

digesta within the reticulorumen is thought to be where fill limits intake. The presence of baroreceptors within these organs supports this possibility (Leek, 1969).

Several studies have investigated this mechanism by adding various quantities of inert bulk to the rumen via permanent cannulae. The general hypothesis of these studies is that inert bulk in the reticulorumen decreases utilizable space in the organ. Lower rumen volume should result in decreased intake if intake is limited by rumen capacity. A summary of results obtained from these experiments is presented in Table 1. A total of 38 treatment comparisons were identified from 11 published studies. Variables of interest included species, animal number, physiological state, BW, form of bulk, diet, amount of bulk addition, DMI, and DMI depression due to bulk addition. Experiments were conducted with sheep and cattle, with more recent studies conducted with lactating dairy cows (Johnson and Combs, 1991; 1992). Water-filled bladders, air-filled bladders, and polystyrene cubes have served as sources of inert bulk. Total added bulk varied from a low of .2 L for a sheep experiment to 48 L for a study with Holstein steers.

Intake achieved during each bulk treatment was compared to intake for controls. Depression in DMI due to bulk addition was calculated as the decline in intake, expressed in grams, per liter of added bulk (Table 1). Not all treatments resulted in depressions in DMI, although 92% of all treatments did. Average intake depression was 94 ± 78 g of DM/L of bulk, with a minimum of -39 and a maximum of 300 g/L (excluding studies involving reticular and abomasal filling; Grovum, 1979).

If the existence of a finite rumen capacity limits intake, then intake should decrease for every treatment in proportion to the amount of inert bulk added. Obviously, this was not the case. Measurement of rumen volume may help explain such discrepancies. Unfortunately, very few studies examined changes in digesta and total rumen volumes as a result of bulk addition to see if bulk actually lowered utilizable space in the rumen. Seven treatment groups included measurements for rumen volume (Table 1). Rumen digesta volume was lower upon bulk addition in every study,

Table 1. Summary of studies where various forms and quantities of inert bulk have been added to the reticulo-rumen to examine the effect of decreased rumen capacity on voluntary intake of ruminants.

Reference	Species	Number of animals	Physiological state	BW	Form of bulk	Diet	Amount of bulk	DMI	Decrease in DMI	Digesta volume	Total volume
Campling and Balch 1961	cattle	3	non-pregnant non-lactating cows	...	water-filled bladders up to 20 lb.	hay for 1 meal 6% CP 36% CF	0 23 L 34 L	10.0 kg/meal 8.8 kg/meal 8.2 kg/meal	 52 g/L 53 g/L	... ...	... ...
Mowat 1963	cattle	4	growing Holstein steers	295 kg	water-filled balloons	chopped hay 20% CP 29% CF	0 L 16 L 27 L 48 L	8.5 kg/d 7.6 kg/d 6.6 kg/d 4.3 kg/d	 56 g/L 70 g/L 88 g/L	54 kg 47 kg 45 kg 40 kg	54 kg 63 kg 72 kg 88 kg
Mowat 1963	cattle	4	growing Holstein steers	230 kg	air-filled balloons	chopped hay 9% CP 38% CF	0 L 9 L 24 L	6.4 kg/d 5.3 kg/d 3.6 kg/d	 122 g/L 117 g/L	... ...	... ...
Carr and Jacobson, 1967	cattle	8	"of dairy breeding"	about 500 kg	polyethylene cubes	chopped hay for 3 h meal	0 about 1.7 L	8.5 kg 8.2 kg	 176 g/L	... ...	... ...
Carr and Jacobson, 1967	cattle	8	"of dairy breeding"	about 500 kg	water-filled bags	chopped hay for 3 h meal	0 about 5.2 L	8.4 kg 7.9 kg	 96 g/L	... ...	... ...
Carr and Jacobson, 1967	cattle	6	"of dairy breeding"	about 500 kg	water-filled bags	chopped hay for 3 h meal	0 about 8.7 L	9.4 kg 9.3 kg	 11 g/L	... ...	... ...
Egan 1972	sheep	4	mature	40-55 kg	water-filled bladders	50:50 lucerne/ barley pellets	0 L 1 L 2 L 3 L	1.32 kg/d 1.11 kg/d 1.16 kg/d .92 kg/d	 210 g/L 80 g/L 133 g/L	... ...	... ...

Table 1. (cont.)

Reference	Species	Number of animals	Physiological state	BW	Form of bulk	Diet	Amount of bulk	DMI	Decrease in DMI	Digesta volume	Total volume
							0 L	.72 kg/d		...	...
Egan	sheep	4	mature	40-55 kg	water-filled	chopped	1 L	.42 kg/d	300 g/L	...	...
1972					bladders	wheat	2 L	.26 kg/d	230 g/L	...	...
						straw	3 L	.01 kg/d	237 g/L	...	...
Bines			dry		water-filled		0	9.4 kg/d		...	...
et al.	cattle	1	cow	...	bladders	medium	33 L 1-6 wk	7.3 kg/d	64 g/L	...	...
1973					11 L each	quality	33 L 7-12 wk	7.3 kg/d	64 g/L	...	...
						hay	33 L 13-17 wk	5.6 kg/d	115 g/L	...	...
						pelleted lucerne	0	.37 kg		...	...
						hay for 30 min	.2 L	.33 kg	200 g/L	...	...
Grovum	sheep	5	mature	82 kg	water-filled	meal	.4 L	.22 kg	375 g/L	...	...
1979			wethers		balloons	14% CP, 40% ADF	.6 L	.18 kg	317 g/L	...	...
						Bulk in reticulum	.8 L	.24 kg	162 g/L	...	...
Grovum	sheep	5	mature	82 kg	water-filled	same as previous	0	.39 kg		...	...
1979			wethers		balloons	Bulk in rumen	.8 L	.42 kg	-37 g/L	...	...
						pelleted lucerne	0	.37 kg		...	...
						hay for 30 min	.25 L	.26 kg	440 g/L	...	...
Grovum	sheep	5	mature	82 kg	water-filled	meal	.50 L	.34 kg	60 g/L	...	...
1979			wethers		balloons	14% CP, 40% ADF	.75 L	.28 kg	120 g/L	...	...
						Bulk in abomasum	1 L	.21 kg	160 g/L	...	...
Adams and					water-filled	complete pellet for 3 h	0	.27 kg/meal		...	...
Forbes	sheep	3	mature	...	bladders	0 mmol/min	1 L	.22 kg/meal	50 g/L	...	...
1981						acetate infused	2 L	.05 kg/meal	110 g/L	...	...

Table 1. (cont.)

Reference	Species	Number of animals	Physiological state	BW	Form of bulk	Diet	Amount of bulk	DMI	Decrease in DMI	Digesta volume	Total volume
Adams and Forbes 1981	sheep	3	mature	...	water-filled bladders	complete pellet for 3 h 2 mmol/min acetate infused	0 1 L 2 L	.24 kg/meal .14 kg/meal .04 kg/meal	 100 g/L 100 g/L	... ...	... ...
Adams and Forbes 1981	sheep	3	mature	...	water-filled bladders	complete pellet for 3 h 4 mmol/min acetate infused	0 1 L 2 L	.12 kg/meal .06 kg/meal .09 kg/meal	 60 g/L 15 g/L	... ...	... ...
Baumont et al. 1990	sheep	6	non-pregnant non-lactating ewes	50 kg	expanded polystyrene 3•4•5.5 cm	orchardgrass hay 11% CP, 70% fiber	0 1 L 2 L	1.10 kg/d .98 kg/d .75 kg/d	 120 g/L 175 g/L	8.5 L	8.5 L ... ...
Baumont et al. 1990	sheep	6	non-pregnant non-lactating ewes	50 kg	expanded polystyrene 3•4•5.5 cm	lucerne hay 14% CP, 51% fiber	0 1 L 2 L	1.76 kg/d 1.63 kg/d 1.34 kg/d	 130 g/L 210 g/L	7.6 L	7.6 L ... ...
Waybright and Varga 1991	sheep	4	mature wethers	65 kg	water-filled 115 L trash bags	75% conc. 25% chopped alfalfa 11% CP, 22% NDF	0 L 2.1 L 4.2 L 6.3 L	1.51 kg/d 1.38 kg/d 1.47 kg/d 1.38 kg/d	 62 g/L 10 g/L 21 g/L	7.8[1] L 5.5[1] L 3.6[1] L 2.5[1] L	 7.6[1] L 7.8[1] L 8.8[1] L
Johnson and Combs, 1991	cattle	6	28 DIM Holstein cows	645 kg	water-filled inner tubes	silage and conc. 21% CP, 26% NDF	0 24.2 L	23.5 kg/d 21.1 kg/d	 99 g/L	102 L 90 L	102 L 115 L
Johnson and Combs, 1991	cattle	8	21 DIM Holstein cows	650 kg	water-filled inner tubes	silage and conc. 23% CP, 28% NDF	0 21.4 L	24.4 kg/d 21.7 kg/d	 126 g/L	98 L 93 L	98 L 114 L

Table 1. (cont.)

Reference	Species	Number of animals	Physiological state	BW	Form of bulk	Diet	Amount of bulk	DMI	Decrease in DMI	Digesta volume	Total volume
Johnson and Combs, 1992	cattle	8	229 DIM Holstein cows	717 kg	water-filled inner tubes	silage and conc. 18% CP, 28.7% NDF	0 19.5 L	21.6 kg/d 21.5 kg/d	5 g/L	89 L 85 L	89 L 105 L
Johnson and Combs, 1992	cattle	8	53 & 185 DIM Holstein cows	705 kg	water-filled inner tubes	silage and conc. 17% CP, 33.6% NDF	0 23 L	22.6 kg/d 23.2 kg/d	-26 g/L	104 L 98 L	104 L 121 L
Johnson and Combs, 1992	cattle	8	53 & 185 DIM Holstein cows	705 kg	water-filled inner tubes	silage and conc. 17% CP, 27.3% NDF	0 23 L	25.1 kg/d 26.0 kg/d	-39 g/L	99 L 94 L	99 L 117 L

[1]Rumen liquid volume.

although not every decrease was statistically significant. Likewise, every study indicated that total rumen volume (digesta + bulk) increased upon bulk addition. Therefore, rumen space did appear to decline after bulk addition, however, expansion of the rumen compensated to some degree in order to decrease the extent of this volume decline (Mowat, 1963; Waybright and Varga, 1991; Johnson and Combs, 1991, 1992). Finite rumen capacity probably exists; however, no rumens were at capacity prior to bulk addition for any of these studies.

Besides failing to be at maximum rumen volume prior to bulk addition, other conditions may help explain why bulk does not elicit proportional declines in intake. Many authors have been quick to point out that physical fill is not the cause of limits in intake (Carr and Jacobson, 1967; Ketelaars and Tolkamp, 1992). However, other reasons for failing to achieve intake declines after bulk addition must first be discarded before such a broad statement can be made. Variation in rumen capacity has been observed frequently. Capacity varies with body size across species (Demment and Van Soest, 1983), stage of lactation (Remond, 1988), extent of fattening and pregnancy (Forbes, 1969), and time after feeding (Wright and Grainger, 1970; Aitchison et al., 1986). Because of such variation, it is plausible that different thresholds for maximum capacity exist for ruminants in different physiological states (Egan, 1972). Therefore, it must be shown that maximum capacity has been reached before one can expect added bulk to decrease intake. In addition to variation in rumen digesta volume, there may be variation in the volume of the gaseous head space above the digesta in the rumen. Such volumes have not been reported but need to be considered when defining maximum capacity available to hold digesta.

Multiple regression analysis was performed with data from Table 1 to determine what factors might contribute ($P < .01$) to variation in intake depression due to bulk. Intake depressions for sheep were 114 g/L greater than for cattle. In addition, animals of relatively smaller BW within species had greater depressions in intake. Finally,

animals that tended to be in physiological states with higher nutrient requirements (growing or lactating) had intake depressions 79 g/L greater than animals in maintenance states. Factors not significant included the relative amount of fiber in the diet, the amount of added bulk (as a % of BW), and the level of intake (as a % of BW). These estimates support the concept that animals differ in their susceptibility to intake declines because of added bulk and in the extent that maximum capacity has been filled, even when all were under ad libitum feeding conditions. Smaller animals under higher states of production appear more likely to have rumen fills near maximum capacity. Future studies with rumen bulk can improve their odds of reaching maximum capacity by utilizing smaller animals under high levels of production. Relatively small early lactation dairy cows provide such a model.

Two other reasons may explain why bulk does not elicit equivalent declines in intake. First, the degree of rumen fill depends not only on animal differences in rumen capacity but also on characteristics of digestion and passage in the rumen. Addition of rumen inert bulk increased the fractional dilution rate of liquid in the rumen of sheep (Waybright and Varga, 1991) and the fractional passage rate of fiber from the rumen of lactating cows (Johnson and Combs, 1991; 1992). Increased removal rates may allow these animals to maintain intake even though rumen volume has diminished. Second, animals challenged with rumen bulk may adjust their feeding behavior or rumen activity to compensate for the added fill. Baumont et al. (1990) reported that eating and ruminating bouts increased when bulk was added to the rumen of sheep and time spent eating and ruminating remained unchanged even though intake declined. Okine et al. (1989) placed 24 kg of mass in the ventral rumen of steers and observed 15% increases in the duration of reticular contractions and 46% increases in fractional passage rates of digesta from the rumen. Changes in ruminating and reticular activity may increase digesta flow, providing additional space in the rumen. Increases in eating and

ruminating frequencies may serve to keep the rumen full for as much of the day as possible and allow for normal intakes in spite of limiting rumen capacity.

Not all forages or diets produce the same level of rumen fill. Blaxter et al. (1956) calculated "ballast", or indigestible DM in the rumen using meal patterns, digestibility, and passage data and found more digestible feeds resulted in less ballast and greater appetites. Feeds that ferment and pass more quickly through the rumen are believed to be less filling because they occupy space within the rumen for a shorter period of time (Aitchison et al., 1986). Consequently, these feeds must differ in some component that produces varying degrees of rumen fill. Various components of ruminant diets have been implicated. Several recent models that predict intake consider rumen DM as the component of fill (Forbes, 1980; Fisher et al., 1987; Illius and Gordon, 1991; Hyer et al., 1991). Others use rumen OM (Pienaar et al., 1980), rumen fiber (Mertens and Ely, 1979; Bywater, 1984) or dietary fiber content (Mertens, 1987). In some instances, it is the indigestible portion of the rumen fiber pool that is considered as fill (Mertens and Ely, 1979; Lippke, 1986).

Bulk studies comparing air- and water-filled balloons indicate that digesta volume, not digesta mass, is the characteristic of digesta which results in fill (Mowat, 1963). Van Soest (1982) has elaborated on this concept by suggesting that cell wall, or NDF, is the fill agent because of its relationship with diet bulk density and volume. The relationship between diet NDF content and intake has been well investigated (Mertens, 1973) and will be discussed in greater detail in part III. However, few NDF studies have measured rumen volume to assure that it is rumen fill that links NDF and intake. It is likely that no one dietary component can be used to predict rumen fill because fill is a concept based on dynamic properties of digestion and passage. As improvements are made to existing rumen kinetic models, perhaps estimates of "rumen fill content" and "intake potential" can be appropriately defined from routine analyses and assigned to feeds for dairy cattle.

Physiological Control of Intake

Physiological control of intake is based on the premise that animals will consume nutrients until energy balance is achieved, and has been the subject of many reviews (Jones, 1972; Journet and Remond, 1976; De Jong, 1986). Once balance is attained, intake will cease. This mechanism requires three basic assumptions. First, it must be assumed that the basic urge to eat remains until the maximum genetic capacity for productive purposes has been fulfilled. Recently this premise has been scrutinized by Ketelaars and Tolkamp (1992), who believe that animals seek to maximize the efficiency of oxygen utilization, not energy. Second, if energy is the indicator of balance, then energy intakes should be constant for a given animal regardless of the energy density of the diet. Data supporting this argument have been reported by Conrad et al. (1964) and Montgomery and Baumgardt (1965). However, in a review on intake control, Grovum (1987) cited several studies conducted with sheep, beef cattle, and dairy cattle where digestible energy intakes were relatively constant at moderate diet energy densities but declined at high dietary energy concentrations. He suggests that maintenance of rumen function receives priority over maintaining energy intake under high concentrate feeding. Third, if energy balance is a threshold, it is implied that it can be measured in the animal. Because "energy receptors" do not exist per se, some other molecules associated with energy status must be monitored by receptors in the ruminant. Two classes of energy status mediators have been identified (De Jong, 1986): metabolites associated with energy metabolism, and hormones associated with homeoretic and digestive control.

Rumen fermentation produces large quantities of VFA that are related directly to total energy intake. Consequently, acetate, propionate, and butyrate have been thoroughly studied as possible mediators of energy intake. The most common method of studying VFA has been by ruminal or portal vein infusion. Early reviews suggested that acetate receptors exist in the rumen and propionate receptors in the rumen wall

(Baile and Forbes, 1974). A more recent review suggests that this is not the case (Grovum, 1987) and argues that depressions in intake from VFA infusion in earlier studies were confounded because of changes in osmolarity. Changes in rumen pH associated with VFA infusions must also be considered, since pH receptors are known to exist in the rumen. Concentrations of VFA may be more important during conditions of slug feeding compared to ad libitum-fed ruminants (De Jong, 1986). Lactate may be produced during fermentation of high concentrate diets and has also been suggested as a modulator of intake (Baile and Forbes, 1974). Other potential metabolites include glucose, free fatty acids, and amino acids.

Two types of hormones have been studied as regulators of energy status. They are hormones associated with peripheral energy metabolism (insulin, glucagon, glucocorticoids) and gut hormones associated with feeding (gastrin, secretin, cholecystokinin). Interactions among these hormones probably play the most important role in monitoring energy status and intake. Any perturbation in metabolism will likely initiate a hormonal response that, in conjunction with neural responses, ultimately signals the hypothalamus and controls intake. However, the numerous levels of hormone action and complexity of interaction will keep even the best future researchers challenged indeed. Continued examination of metabolism at this level is required if an understanding of intake regulation is to be obtained. Failure to understand relationships at this level has forced intake control to be modeled at more aggregated levels.

Other possible mediators of energy status may play a role in certain situations. They include rumen fluid pH and osmolarity (Carter and Grovum, 1990), placental lactogen (Byatt et al., 1992), melatonin, somatotropin, and insulin-like growth factor I. These, like any additional mediators that may someday be discovered, are associated with digestion or metabolism of nutrients in some manner. As with physical control mechanisms, threshold values for any of these mediators is likely to vary with animal and physiological state of production. Integrating these concepts into mechanistic

models of intake control may be the most efficient means of understanding these relationships.

Integrated Theories of Intake Control

Cessation of eating implies that satiety has been invoked by the hypothalamus and the brain. Lack of any one mechanism that induces satiety in all feeding situations suggests that satiety may result from the summation of many individual inputs. Grovum (1987) listed several possible contributors, many of which have already been discussed. They include distention of the reticulum, rumen, or other part of the digestive tract; effects of VFA in the stomach, ruminal veins, and liver; effects of ionic strength in the blood or digesta; effects of digesta pH; effect of gut contents and peptides on smooth muscle tone in the digestive tract; effects of circulating hormones; and the effects of various neurotransmitters. In many studies, supraphysiological levels of these factors were required to achieve depressions in intake. Few studies have examined possible cooperation or synergism among these many possible factors. Acetate infusion with or without rumen distention in sheep indicated suppression in intake with either two factors alone and an additive effect when combined at various levels (Adams and Forbes, 1981). With Friesian cattle, 7.5 L of rumen distention, 250 g/h of acetate infusion into the rumen, and 167 g/h of propionate infusion resulted in no significant intake suppression individually, but did depress intakes of hay under various combinations of all three factors (Anil et al., 1987). More investigation into interactions among multiple satiety signals is required before a comprehensive understanding will be achieved.

Attempts have been made to combine the main mechanisms of physical fill and physiological regulation to determine which mechanism dominates and to predict intake. Conrad et al. (1964) were one of the first groups to combine these ideas and suggested that intake was limited by undigested material in the digestive tract when diet DM digestibility was below 66% and limited by physiological controls at higher energy densities. Since then, other workers have integrated these concepts into static,

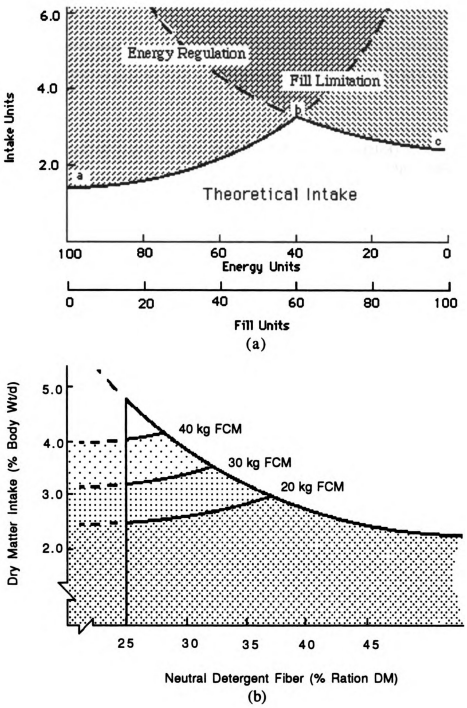


Figure 1. Intake model illustrating the physical limitation and physiological regulation theories of intake control with constant energy consumed along line a-b and constant rumen fill obtained along line b-c in the general case (a) and for a 600 kg cow producing various quantities of 4% FCM (b).

Table 2. Empirical equations developed with stepwise multiple regression to predict DMI for lactating cows.

Reference	Prediction equation
Chandler and Walker 1972	DMI (kg/d) = [3.62 + .076(FT) - .17(BW) + .01017(MY x MF) - .026(CF)] x BW
Brown et al., 1977	LnDMI (kg/d) = .52 - .00083(DIM) + .148(LnDIM) + .00068(BW) + .339(LnMY) + .0993(MFd) + .018(CF) - .00056$(CF)^2$
Vadiveloo and Holmes 1979	DMI (kg/d) = -4.14 -.095(WL) + 4.0401(log WL) + .015 (BW) + .208(MY) + .43(C)
Yungblut 1981	DMI (kg/d) = 3.37 + .34(LN) + .0096(BW) + .3362(MY) + .528(MF) - .106(ADF)
NRC, 1989	DMI (kg/d) = -.293 + .372(FCM) + .0968$(BW)^{.75}$
Kertz et al. 1991	DMI (kg/d) = .2286(DIM) - .00218$(DIM)^2$ + .00000705$(DIM)^3$ + .00804(BW) + .3134(FCM)
Rayburn and Fox, 1993	DMI (DIM < 84; kg/d) = .0117(BW) + .0749(DIM) + .281(FCM) DMI (DIM > 70; kg/d) = .023(BW) + .0201(DIM) + .286(FCM) - .0979(NDF)

where:

ADF = acid detergent fiber (% of diet DM)
BW = body weight (kg)
C = concentrate intake (kg/d)
CF = crude fiber (% of diet DM)
DIM = days in milk
FCM = 4% FCM (kg/d)
FT = type of feeding (+1 = winter, -1 = summer)
LN = lactation number
MF = milk fat (%)
MFd = milk fat (% as a decimal)
MY = milk yield (kg/d)
NDF = neutral detergent fiber (% of diet DM)
WL = week of lactation

mechanistic models to predict intake (Forbes, 1980; Bywater, 1984; Mertens, 1987; Fisher et al., 1987); these models have been summarized by Illius and Allen (1993). Most predictions are based on the premise that intake will vary according to energy demands (Forbes, 1977) but will be constrained to a maximum based on rumen capacity and dietary fill. Components associated with predictive equations vary with the model. One such model proposed by Mertens (1985, 1987) uses NDF as a common currency for both the "fill" content and energy content of the diet. Intake capacity of the animal is based on maximum NDF intake and energy requirements are based on maintenance and production requirements. An illustration of intake responses to various diet qualities based on this model is presented in Figure 1. Other systems have been developed that consider the filling effect of forages in different ways (Jarrige et al., 1986).

Many intake prediction equations for lactating cows have been reported that are based on empirical relationships rather than mechanistic relationships (Table 2). Under most practical applications of ration formulation, these equations tend to be used more often than their more complicated mechanistic model counterparts (NRC, 1989). Routine use requires that inputs to the equations be known; during ration balancing seldom does one have access to all the information required by most mechanistic models. Intake has been shown to be most related to daily milk production, BW, DIM, and dietary fiber content in these multiple regression equations (Table 2). Their accuracy of prediction depends on the extent that conditions during predictive use deviate from conditions used during equation generation.

SHORT-TERM INTAKE CONTROL IN RUMINANTS

As previously stated, long-term intake regulation seeks to obtain balance between maintenance and production requirements and energy inputs. Overall balance is essential if BW is to be maintained and survival assured. Long-term intake measurements are frequently defined in terms of the amount of feed consumed during a one day period (Forbes, 1986). Lactating cows under ad libitum feeding conditions,

however, do not consume feed continuously throughout the day, nor do they consume their entire daily intake in one meal. Intake within a day consists of a varying number of individual eating bouts (meals) whose frequency, duration, and intensity of consumption ultimately determine average daily intake (Bines, 1976). A more complete understanding of intake control may be obtained if factors affecting short-term meals can be defined. Short-term measures also are essential to understand interactions between particular diets and animal response.

Control of Individual Meals

Any study of individual meals requires an adequate definition of a meal. Meals are generally defined by the minimum size of eating required to be considered a meal, the maximum amount of time during which the minimum meal size must be consumed, and the minimum amount of inactivity required between two periods of eating (Heinrichs and Conrad, 1987). Not all meals are easily defined because of variation in eating intensities and variation in frequency and duration of breaks taken by animals during eating. Minimum intermeal intervals are often defined, with eating separated by intervals of time less than these values considered as part of the previous meal (Forbes, 1986). Wangsness et al. (1976) studied feeding of sheep and defined a meal as eating activity of at least 1 min after an intermeal interval of 20 min. A study with only two lactating cows found the appropriate meal definition for their animals was a minimum eating length of 2.5 minutes and an 8 min intermeal interval (Heinrichs and Conrad, 1987). Meal definitions should not be arbitrarily assigned, but selected only after analysis of a frequency plot of intermeal intervals (Savory, 1979). Extrapolation of meal definitions across species or across studies within the same species may lead to inappropriate meal descriptions.

Ruminants begin to consume food when in a state of hunger and stop when satiated. Unfortunately, these two states have no precise physiological meaning (Forbes, 1986) and cannot be verbally described by cows to curious researchers. Most

research has focused attention on regulation of intake via satiety mechanisms since these are more easily observed (Gallouin and Focant, 1980). In the central nervous system, satiety appears to be associated with the ventromedial hypothalamus and hunger with the lateral hypothalamus (Baile and McLaughlin, 1987). Lesions of the ventromedial hypothalamus usually produce excessive eating (hyperphagia) and lesions of the lateral hypothalamus produce aphagia (NRC, 1987). Whether cows commence eating because of hunger or because of lack of satiety has not been determined. If a high degree of correlation exists between meal size and length of preceding intermeal interval, a satiety mechanism controlling intake is implied; if the correlation is between meal size and length of postmeal interval, a hunger mechanism initiates intake (Savory, 1979). Metz (1975) conducted feeding behavior experiments with seven non-lactating cows and found meal size was correlated more positively with its preintermeal interval than with its postintermeal interval, suggesting that meals stop once a fixed level of repletion is reached. This supports the concept that satiety, and possibly rumen fill, is controlling meal size. Relationships between intermeal intervals and meal size vary diurnally (Metz, 1975), indicating that different mechanisms may be influencing intake at different times of the day.

Short-term regulators of meal size and meal distribution are not unlike those described for long-term intake control, although short-term regulators must respond more rapidly. Many of the same factors affecting long-term intake have been implicated as playing a role in meal regulation (Baile and Forbes, 1974). They include factors such as palatability, ruminal distention, rumen fluid and body osmolarity, ruminal pH, VFA, other blood metabolites, and hormones. For example, rumen fill was measured before and after feeding two qualities of forage to three cows (Freer and Campling, 1963). Rumen pool sizes of DM differed between the two diets prior to feeding (9.5 vs 5.2 kg) but were similar after feeding (16.2 vs 14.7 kg). They suggested that each feed was consumed until satiation from physical distention occurred and that rumen capacity was

limiting meal size for both diets. This conclusion is also supported by a summary of data compiled by Baile and Forbes (1974). Other measures of rumen volume before and after feeding have not resulted in such consistency of fill (Campling et al., 1961; Bines and Davey, 1970), suggesting that other measures of satiety may have occurred, especially with more digestible diets.

Regardless of the actual mechanisms that control meal sizes and distributions, it is often useful to measure within day eating activity (i.e., feeding behavior) to examine how dietary manipulations alter behavior and ultimately affect intake. Effects of diet on ruminating activity may also lead to differences in meal patterns and are useful measurements. An understanding of how diet affects intake is valuable because diet manipulation provides the primary tool in which to improve animal performance. With adequate data, perhaps a complete model of feeding activity can be developed to describe the occurrence and size of individual meals.

Dietary Modulation of Feeding Behavior

Before discussing how diet affects feeding behavior, a review of general aspects of eating, rumination, and digestion is warranted. These comments are specific for stall-housed dairy cows and are based on reviews by Campling and Morgan (1981), Beauchemin (1991b), and Albright (1993). Cows consume between 6 and 20 meals per day, with larger meals occurring immediately following feed offering. Rate of consumption is most rapid at the beginning of the meal and slows until meal end. Meal size is highly variable, but total eating time is less variable, with 4 to 7 h spent each day eating. Comminution during eating is adequate to permit swallowing of food boluses and to add small amounts of saliva. Whether there is an upper limit to meal size based on physical abilities to process feed during eating is unknown; nevertheless, oropharyngeal metering is considered to be improbable (Baile and Forbes, 1974).

Rumination occurs during 10 to 20 individual ruminating bouts throughout the day, with each bout lasting from 1 min to 2 h or more. Total time spent ruminating

ranges from 5 to 10 h/d. Each rumination bolus consists of longer fiber portions of digesta near the reticular cardia and is chewed for 45 to 60 s at a relatively constant rate (1 chew/s). The primary purpose of rumination is to decrease digesta particle size, increase particle surface area, and increase saliva in the digesta pool. Total time spent chewing ranges from 9 to 16 h/d during which 30,000 to 50,000 chews occur. Requirements for rest from chewing may limit the maximum amount of time spent chewing each day. If such is the case, intake may be restricted to that which can be physically processed during eating and rumination. Once ingested and hydrated, feed particles are fermented by growing rumen microorganisms which produce VFA that must be buffered by saliva. The rate of fermentation and absorption in the rumen and the rate of passage out of the rumen determine the residence time of feed particles. Clearance from the rumen enables consumption of more feed. Motility of the reticulorumen enhances fermentation and plays a role in nutrient removal from the rumen.

Feeding behavior may be affected by two types of dietary manipulation; they are feeding management and diet formulation. Feeding management involves those aspects of feed consumption associated with physical aspects of supplying feed, and includes issues like animal housing, feed availability, and feeding frequency. Behavior of confinement-fed cows differs from pasture-fed cows (O'Connell et al., 1989). Pasture feeding occurred predominantly during daylight hours and rumination during darkness. In confinement, these same mid-lactation cows consumed feed and ruminated throughout all hours of the day, with no indication of diurnal variation. Harb et al. (1985) compared eating rates for cows housed in individual stalls compared to group housing and feeding. Eating rates increased when cows competed during group feeding. Other studies examining group feeding demonstrated that socially dominant cows ate first compared to more submissive animals. As feeding space was reduced, dominance tended to be more positively related to total daily intake (Friend and Polan, 1974; Friend

et al., 1977). Time spent ruminating tends to increase as time spent eating decreases during competitive feeding.

Shortening the time of access to feed from 24 h to 5 h/d has been shown to increase eating rates and rumination time and decrease DMI (Campling and Morgan, 1981). However, when feed access times were lowered to 8 h/d, DMI, time spent eating, and time spent ruminating did not change (Erdman et al., 1989). In a review on feeding management, Robinson (1989) stated that the sequence in which feedstuffs are offered and the frequency of feeding are potentially important contributors to intake and cow performance. His comments were based on the concept that more regular consumption of balanced nutrients would increase rumen microbial fermentation efficiency due to the more steady supply of nutrients. Such improvements in cow performance have been difficult to show experimentally (Gibson, 1984; Nocek, 1992), and few studies have included behavior measurements.

Gill and Castle (1983) observed that the number of eating bouts increased from 16 to 24 when feeding frequency increased from 2 to 22 times per day, however time spent eating and ruminating did not change. Ullyatt et al. (1984) fed sheep once or 24 times per day and noted increased DMI and eating times with multiple feedings, but no change in time spent ruminating. However, they forced eating patterns to be different between diets since sheep fed once daily only had access to feed for 3 to 4 h. This study emphasizes the difficulty of conducting behavioral work. If various feeding management factors are to be accurately studied as they relate to feeding behavior and intake, it is imperative that treatments and measurements be designed so experimental animals are free to alter their behavior for the correct reason. In other words, let the animals decide if treatments really work! Under ad libitum feeding, increased frequency of feeding does not automatically imply more numerous eating bouts.

The second type of diet manipulation is diet formulation, which consists of changes in the type and form of feedstuffs selected for inclusion in daily offerings to

cows. Variation in dietary concentrations of energy and fiber have been noted most often as feed components that alter feeding behavior. Baumgardt et al. (1973) found rate of eating was highly correlated with digestible energy content (.99) and bulk density (.93) of the diet with sheep. Rumination time has been associated with the roughage value of feeds (Balch, 1971) that is commonly defined in terms of fiber content. Cell wall intake and daily ruminating time was highly correlated in both sheep (.99; Welch and Smith, 1969) and cattle (.94; Welch and Smith, 1970). Beauchemin (1991b) summarized several studies where different concentrations of dietary NDF were offered to dairy cows. In general, eating and ruminating times increase as NDF content increases but chewing per unit of fiber remains relatively constant. Meal frequency has been shown to increase with increases in NDF content (Beauchemin and Buchanan-Smith, 1989), however, such results are not consistent (Colenbrander et al., 1991). Not all NDF elicits the same amount of chewing activity (Mooney and Allen, 1993). Chewing variation for fiber is likely due to differences in size of the fiber particles.

As forage particles increased in size, time spent ruminating increased (Woodford and Murphy, 1988; Colenbrander et al., 1991), and occasionally time spent eating increased (Jaster and Murphy, 1983; Grant et al., 1990). There is an upper limit to the ability of particle size to increase chewing activity. Therefore, chewing behavior is similar between coarsely chopped silages and long hay (Beauchemin, 1991b). Adequate particle size reduction is necessary to increase fermentation sites for rumen digestion and to allow for particle passage. Smaller particles were found to digest faster during in vitro fermentation (Cherney et al., 1988), and more dense particles were found to pass more quickly from the rumen (Ehle, 1984). Small particles tend to be more dense than larger particles (Hooper and Welch, 1985); sufficient specific gravity also is required for particle passage. Reduction in particle size may also decrease the effective volume of fiber, decreasing its rumen filling effect and stimulate greater intake. Campling and Freer (1966) noted increased intake when low digestible straw was ground but not when

a more digestible grass was ground. Eating and passage rates also increased with grinding. Whether particle size affects frequency or distribution of eating is generally not known.

Methods of Measuring Short-Term Intake and Behavior

Daily intake is typically measured by recording the mass of feed offered to cows and subtracting the mass of feed remaining the following day. Because cows consume multiple meals each day, more frequent weighing of feed is necessary to determine masses of individual meals. To measure eating and ruminating activity, chewing is typically monitored. Both feed and chewing measurements require continuous monitoring if complete data are to be obtained. Several methods of measurement have been developed in the past to obtain feeding behavior data for grazing, group-fed, or stall-fed ruminants. Some rely on manual observation, while others utilize automation.

Manual observation has been difficult. Although they may be great learning experiences, manual approaches are labor intensive, limited to short time periods, and somewhat subjective. Kertz et al. (1981) weighed feed every 4 min for 28 min following feeding of 10 cows to estimate eating rates of different forms of a diet. Nocek and Braund (1985) weighed feed hourly for 4 d with four cows to estimate eating rate and pattern of intake throughout the day. Unfortunately, timed weighing may not describe meal size accurately since cows may consume more than one meal an hour. In grazing experiments, meal sizes have been measured by weighing animals before and after grazing (Erlinger et al., 1990). Manual measurements of chewing activity have been made by recording cow activity periodically (every 5 min, Woodford and Murphy, 1988; every 15 min, Erdman et al., 1989). Such methods must assume that the same activity was present during the entire period represented by the sample observation. In all manual measurements it must also be assumed that the measurement process itself does not alter behavior. This may not be true, especially if feed mangers are being weighed periodically.

Automatic systems of measurement attempt to alleviate a part or all of the labor required for manual observations. They require a monitor on the feed manger or head of the cows and a data logging system to record signals from the monitors. Determination of meal size automatically during grazing is obviously extremely difficult. Chacon et al. (1976) attempted this by automatically monitoring bite number with a microswitch to detect jaw movement and a mercury head switch to differentiate grazing and ruminating activity. Meal size was calculated as the product of bite size and bite number, where bite size was estimated via weighing of food boluses from an esophageal fistula. Methods to measure chewing activity during grazing are considerably easier and have been summarized (Penning, 1983). Many different monitors have been developed to detect jaw movement. They include electrodes in the masseter muscle of the jaw, carbon-filled stretch electrodes, pneumatic bellows, and electronic microswitches, straingauges, and pressure transducers. Data collection devices have included strip-chart recorders, oscillographs, and analog/digital convertors for computer acquisition. Signal transfer between monitors and collection devices range from cassette tapes on the animals, long cords to a central location in the paddock, radiotelemetry, to static ram chips mounted on the chewing collars. Once collected, the signals have been interpreted either manually or via computer algorithm (Penning et al., 1984).

Intake and behavior of group-fed cows have been monitored with systems developed by Forbes et al. (1986) and Mason et al. (1991). Group-fed monitoring faces similar challenges to data collection as does grazing, in that there is not a one-to-one correspondence between cow and manger as their is in stall feeding, and that free-roaming animals cannot be hard-wired into a collection system. These problems have been overcome by using electronic identification systems and, as mentioned, use of radiotelemetry or animal-mounted recorders.

Automatic determination of meal size in stall-fed animals has been conducted using two basic methods. Multiple allocation of pre-weighed feed was used in systems

described by Minson (1966) and Wangsness et al. (1976). Continuous electronic weighing of feed mangers with load cells has been utilized by several groups (Suzuki et al., 1969; Metz and Borel, 1975; Heinrichs and Conrad, 1987). This second method has advantages in that meal weights are determined electronically and that it is not limited in the number of individual meals an animal can consume. To detect chewing activity, many of the same methods have been used in stall-feeding as in grazing. These are summarized by Beauchemin et al. (1989), who have developed one of the most automated systems to date. Pioneers in this field include Balch (1971), Sudweeks (Law and Sudweeks, 1975), and Welch (1982). Other unique ways of determining feeding behavior include use of time-lapsed photography (Vasilatos and Wangsness, 1980), insertion of pressure transducers in the esophagus (McLeod and Smith, 1989), and estimation of rumination via detection of the three phase contraction of the reticulum with internal balloons and pressure transducers (Norgaard, 1989).

The optimum system for measuring feeding behavior should be accurate, continuous, accommodating to a sufficient number of cows, automatic, and capable of recording several cow activities simultaneously for an extended period of time. Current developments in computer technology and electronic data acquisition make this possible.

A Model of Feeding Behavior

Qualitative description of factors involved in short-term eating patterns have limited usefulness if they cannot be quantitatively related to specific behavior variables. Integration of these factors into a simulation model to predict meal patterns and daily intake has been developed by Forbes (1980), and is the only model of its type known to this author. Forbes assumed that feeding commences in response to an insufficient quantity of absorbed substrates in relation to energy requirements and terminates when a relative excess of energy has been consumed or maximum gut fill has been reached. Consequently, the model incorporates both physical and physiological aspects of intake

control. Objectives of the model were to simulate minute-by-minute changes in digestion and metabolism of a lean mature sheep to drive satiety factors that explain the size and frequency of individual meals. An overview of the model is presented in Figure 2. Feed components consisted of a rapidly fermentable and absorbable soluble fraction, a more slowly fermentable insoluble fraction, and an indigestible fraction. At each iteration (1.0 min interval) energy available from previous bites are summated and compared to requirements. If absorbable energy is below a defined threshold, eating begins or continues, if above a slightly higher threshold, eating ceases or does not begin. Such thresholds are similar to a household thermostat, allowing an interval between on and off thresholds so eating is not rapidly turning on and off. Total gut capacity available to hold feed started at 12 L and decreased as abdominal fat or conceptus increased.

During simulation, both gut capacity and energy adequacy limited meal size at different times during the day (Forbes, 1980). The number of individual meals and total daily intake was similar to data from a living animal of similar size and state. Meal patterns were more difficult to predict; however predicted meal sizes were realistic. Eating patterns of actual sheep are not consistent day to day, that is, eating does not occur at exactly the same day after day for ad libitum fed animals. The model, however, did behave in this fashion, suggesting that other factors need to be considered when predicting meal distributions, or that a form of stochasticity should be incorporated. Other pertinent factors suggested by Forbes was rumen and blood concentrations of products of digestion, distention of different parts of the digestive tract, feed palatability, competing drives, and social interaction. The model also showed promise in predicting changes attributable to differences in growth, fattening, pregnancy, lactation, and feed quality. Although not perfect, this modeling attempt illustrated that the basic concepts associated with the control of meal size may be realistic. One might suspect that similar modeling of lactating dairy cow meal patterns would be considerably more complex,

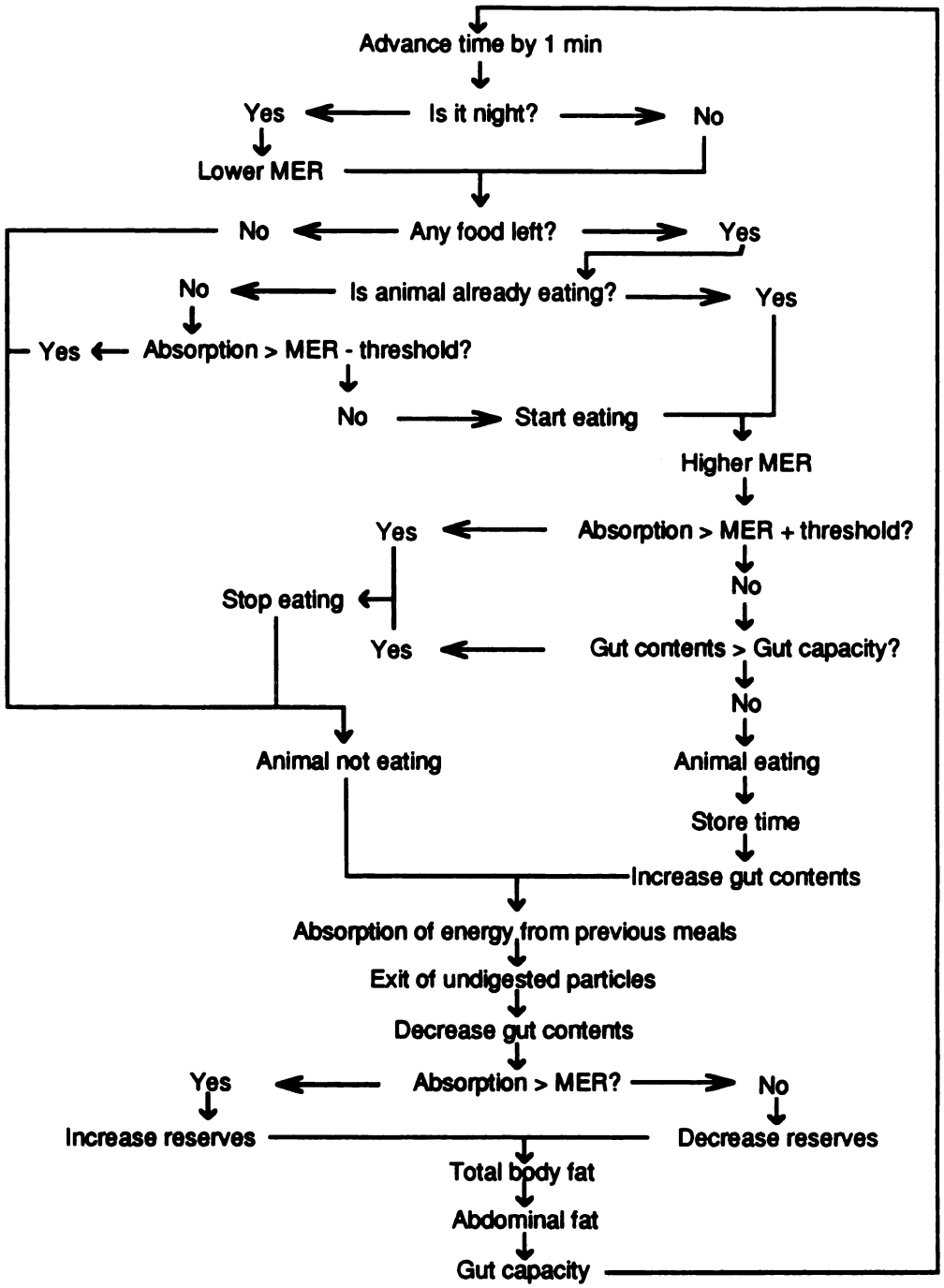


Figure 2. Feeding behavior model for sheep (Forbes, 1980). Objectives of the model were to predict meal size and frequency during eating as determined by physical and physiological satiety factors. MER = metabolizable energy requirements.

however, such attempts have not been made. Models will never simulate reality completely, but they certainly will continue to provide a mechanism to ask pertinent questions and design future experiments.

In conclusion, feeding behavior is a function of the interactions between hunger and satiety. To consider that any one factor is responsible for meal control under all situations is fallacious. Perhaps this concept was best stated by Forbes (1988):

> "We can no longer consider the various theories of intake control as alternatives but rather as complementary and contributing to a multifactorial control system. No single factor is essential for normal feed intake and many manipulations which stay within the physiological range have effects which can only be picked up by close attention to details of feeding behaviour."

Measurement of feeding behavior in dairy cattle is in its infancy. Continued efforts to measure short-term intake will enhance our understanding of and ability to improve animal performance.

FORAGES, FIBER, AND INTAKE

Dairy cattle, because they are ruminants, harbor a population of anaerobic microorganisms in their reticulorumen that live in synergy with their host animal. The ruminal environment provides a continuous supply of nutrients, warmth, moisture, anaerobiosis, and end-product removal for the microorganisms. In return, the microbes ferment cellulosic plant material that results in production of end-products which provide a substantial portion of the animal's energy needs. To sustain this symbiotic relationship, the animal must maintain a ruminal environment where variables such as pH, osmolarity, and oxidation-reduction potential are appropriate for microbial growth. The slow, continuous fermentation of roughage provides this type of environment; it is for this reason that dairy cattle have forage requirements.

Diets for dairy cattle typically contain 40 to 60% forage for lactating cows, and 60-100% forage for other types of dairy cattle. Forage consists of the entire vegetative portion of legume or grass plant species and is characterized by the composition and

structure of individual plant cells. Not all forages are utilized by dairy cattle to the same degree. Forages differ in rate of digestion, extent of digestion, and intake potential by cattle. Variation in forage quality, and how to measure it, has been the subject of investigation for many decades (Wolff, 1856; Goering and Van Soest, 1970). It was, and still remains, unfeasible to conduct a biological assay (i.e., animal trial) on every forage wishing to be fed to cattle, consequently, it was necessary to develop laboratory methods to measure characteristics of forages that were highly related to animal performance. The detergent fiber analysis system was originally developed to describe forage quality in terms of nutritionally available and unavailable plant components (Van Soest, 1967). Measurement of the plant cell wall, as estimated by the NDF assay, was considered effective in dividing forages into completely available (neutral detergent solubles) and partially available (NDF). Although not chemically homogenous, the NDF fraction has been useful in describing forage quality because of its negative relationship with digestibility and intake (Van Soest, 1965).

Variation in Forage Consumption Due to NDF Concentration

Dietary cell wall content has been suggested to be the most important single factor affecting ad libitum consumption of forages (Van Soest, 1982). Mertens (1973) collected data from trials where 187 forages were fed without supplementation to sheep and found the correlation between cell wall content of the forage and DMI was -.76. Cell wall intake, as a percent of metabolic BW, was also relatively constant, indicating that cell wall content reflects the ruminal fill characteristics of the diet, although rumen fill was never measured. Another study where standardized intake of sheep was determined also demonstrated a strong negative relationship between cell wall content and intake (Osbourn et al., 1974). If NDF content is directly related to rumen fill, a strong relationship between NDF content and intake indicates that rumen capacity was the predominant limitation to intake for these sheep.

A more vigorous test of the NDF/intake relationship would include not only studies solely with forage, but also those using mixed diets of forage and concentrate. Addition of more digestible, less fibrous concentrates will dilute the fill effect of forage fiber and allow limitations other than capacity to influence intake. One might expect intake to be correlated negatively with NDF content at high dietary NDF but correlated positively with NDF content at low dietary NDF. Such results would support the physical/physiological intake control mechanism proposed by Mertens (1987) as discussed in part I of this review. Mixed diets are much more common for lactating cows than are all forage diets. However, early lactation cows experience a period of negative energy balance where physical limits to intake are more likely. Examination of recent studies where lactating cows have received diets varying in NDF content may be useful.

A summary of 26 studies utilizing 673 animals conducted within the last ten years with lactating cows was compiled from the literature (Table 3). Cows were relatively high producing and averaged 29.6 kg/d of milk; cows ranged from 7 to 200 DIM at the start of their trial. Each experiment quantified dietary NDF concentrations from which forage NDF in the diet DM was calculated. Objectives of the experiments involved the study of forage quality (e.g., Beauchemin, 1991a), non-forage NDF sources (e.g., Clark and Armentano, 1993), or the interaction between a dietary component, such as fat (Grant and Weidner, 1992), and fiber level on animal performance. Different NDF concentrations were obtained by changes in fiber source, forage quality, or forage:concentrate ratio. The minimum dietary NDF content used was 19.6% and the maximum was 44.8%. Minimum DMI obtained was 12.9 kg/d and the maximum was 26.2 kg/d. Regression of DMI on dietary NDF concentration across all 103 treatment observations resulted in a negative relationship ($b = -.18$; $P < .002$; $r = .31$). Regression of DMI on forage NDF concentration resulted in a similar relationship ($b = -.15$) that was slightly stronger ($r = .37$), suggesting that non-forage NDF may not be as related to

Table 3. Summary of studies that examined the effect of dietary NDF concentration or source as part of complete rations on intake and production of relatively high producing lactating dairy cows. Different NDF concentrations were obtained by changes in fiber source, forage quality, or forage:concentrate ratio.

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources; diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
Clark and Armentano 1993	1	16	135		1	alfalfa silage(AS); forage(F)=30%	21.2	13.0	
					2	AS; F=44%	25.4	18.8	
					3	AS+dried distillers grains; F=31%	24.0	13.3	
					4	AS+whole cottonseed; F=30%	25.8	13.1	
Poore et al. 1993	2	22	64	585	1	alfalfa hay(AH)+slow starch; F=52%	29.2	21.8	
					2	AH+fast starch; F=52%	29.7	21.8	
					3	wheat straw (WS)+slow sch; F=31%	29.8	22.4	
					4	WS+fast starch; F=31%	30.7	22.4	
Grant and Weidner 1992	3	8	17	597	1	AS+corn silage(CS)+sbeans; F=39%	25.0		
					2	AS+CS; F=39%	25.5		
					3	AS+CS+soybeans; F=49%	28.8		
					4	AS+CS; F=50%	29.1		
Sarwar et al 1992	4	5	57	550	1	AH+CS; F=43%	31.7	25.4	
					2	AH+CS+soyhulls(SH); F=37%	31.6	22.1	
					3	AH+CS+SH; F=31%	30.6	18.4	
Beauchemin et al 1991	5	9	80	670	1	AH; F=33%	29.3	14.8	
					2	AH+alfalfa pellets; F=33%	31.9	14.8	
					3	AH+beet pulp; F=33%	31.9	14.8	
					4	AH+oat hulls; F=33%	31.9	14.8	
					5	AH; F=43%	31.4	19.1	

Table 3. (cont.)

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources: diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
Beauchemin 1991a	6	6	80	630	1	early cut(EC) AH; F=37%	31.5	14.5	
					2	mid cut(MC) AH; F=26%	32.1	12.5	
					3	EC AH; F=56%	33.7	21.2	
					4	MC AH; F=39%	34.8	18.8	
					5	EC AH: F=74%	36.2	29.4	
					6	MC AH; F=52%	37.3	24.7	
Poore et al 1991	7	24	72	640	1	WS:AH=0:3; F=49%	30.4	20.8	
					2	WS:AH=1:2; F=42%	31.3	20.1	
					3	WS:AH=2:1; F=34%	31.9	19.3	
					4	WS:AH=3:0 F=28%	30.2	18.6	
Bernard and McNeill 1991	8	16	180		1	CS control; F=46%	33.0		
					2	CS+corn gluten feed; F=40%	35.9		
					3	CS+SH; F=48%	42.6		
					4	CS+wheat middlings; F=41%	36.6		
Cameron et al 1991	9	8	147	505	1	AS+CS control; F=70%-all diets	34.1	29.8	
					2	AS+CS+20% alkali-treated WS	37.4	33.4	
					3	AS+CS+40% alkali-treated WS	40.8	36.9	
					4	AS+CS+60% alkali-treated WS	43.7	40.4	
Llamas-lamas and Combs 1991	10	6	45	600	1	AS; F=56%	28.3	21.1	
					2	AS; F=71%	31.0	26.8	
					3	AS; F=86%	33.4	32.4	
Llamas-lamas and Combs 1990	11	6	120	686	1	EC AH; F=66%	32.6	23.8	64.7 T=72
					2	MC AH; F=49%	32.6	25.3	51.7 T=72
					3	late cut(LC) AH; F=40%	27.9	20.7	41.5 T=72

Table 3. (cont.)

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources; diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
Weiss et al 1989	12	12	126	562	1	AS+barley; F=48%	30.9	19.2	
					2	AS+corn; F=67%	29.2	26.9	
Shaver et al 1988a	13	5	35	583	1	EC AH; F=60%	30.8	25.3	58.4 T=infin.
					2	MC AH; F=60%	35.0	32.6	44.1 T=infin.
					3	LC AH; F=60%	37.2	33.7	43.3 T=infin.
					4	bromegrass; F=60%	44.8	43.1	61.7 T=infin.
					5	CS; F=60%	32.7	26.8	42.4 T=infin.
Grummer et al. 1987	14	30	133		1	AS+CS; F=55%	30.7	25.5	
					2	AS+CS; F=27%	19.6	11.1	
Colenbrander et al 1986	15	24	7	590	1	AS; F=55%	32.7	25.5	
					2	CS; F=67%	32.3	28.2	
					3	AS+CS=1:1; F=62%	33.0	26.6	
DePeters and Smith 1986	16	24	7	primi parous	1	EC AH; F=50%	32.6	20.0	
					2	EC AH; F=70%	33.7	28.1	
					3	MC AH; F=50%	34.6	23.0	
					4	MC AH; F=70%	36.6	32.3	
DePeters and Smith 1986	17	44	7	multi parous	1	EC AH; F=50%	32.6	20.0	
					2	EC AH; F=70%	33.7	28.1	
					3	MC AH; F=50%	34.6	23.0	
					4	MC AH; F=70%	36.6	32.3	

Table 3. (cont.)

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources; diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
					1	EC AH; F=28%	21.2	12.9	
Woodford et al 1986	18	4	63	655	2	EC AH; F=36%	24.2	16.6	
					3	EC AH; F=45%	27.4	20.8	
					4	EC AH; F=53%	30.1	24.5	
Phipps et al. 1984	19	92	21	540	1	grass silage; F=35%	32.2	21.6	
					2	grass silage; F=50%	42.2	30.8	
					1	AH; F=50%	32.3	18.6	68.8 T=72
					2	AH; F=50%	32.0	18.0	65.3 T=72
					3	AH; F=50%	31.5	18.9	67.2 T=72
					4	AH; F=50%	35.6	20.3	57.2 T=72
Alhadhrami and Huber 1992	20	40	90	615	5	AH; F=50%	36.2	24.6	51.6 T=72
					6	AH; F=35%	30.0	13.1	
					7	AH; F=35%	28.6	12.6	
					8	AH; F=35%	29.0	13.2	
					9	AH; F=35%	34.1	14.2	
					10	AH; F=35%	34.3	17.3	
				590	1	EC AS; F=60%	27.6	22.7	
Nelson and Satter 1992a	21	48	15	578	2	LC AS; F=60%	32.1	27.2	
				526	3	EC AH; F=60%	31.5	26.6	
				557	4	LC AH; F=60%	34.2	29.3	
				590	1	EC AS; F=60%	26.9	23.1	
Nelson and Satter 1992a	22	48	15	578	2	LC AS; F=60%	31.3	27.2	
				550	3	EC AH; F=60%	27.7	23.8	
				566	4	LC AH; F=60%	31.9	27.7	

Table 3. (cont.)

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources; diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
Nelson and Satter 1992b	23	4	110	650	1	EC AS; F=60%	26.6	22.7	
					2	LC AS; F=60%	31.1	27.1	
					3	EC AH; F=60%	29.2	25.3	
					4	LC AH; F=60%	32.9	28.7	
Colenbrander et al. 1991	24	32	78	540	1	high fiber AS; F=50%	31.3	23.6	
					2	low fiber AS; F=50%	21.5	16.3	
Nelson and Satter 1990	25	55	40-200	624	1	EC AS; F=55%	31.1	22.1	
					2	MC AS; F=55%	37.6	28.6	
					3	LC AS; F=55%	39.3	30.2	
Nelson and Satter 1990	26	85	40-180	600	1	EC AS; F=55%	29.8	22.9	
					2	MC AS; F=55%	33.7	26.7	
					3	LC AS; F=55%	35.2	28.3	
					4	EC AH; F=55%	30.5	23.3	
					5	MC AH; F=55%	33.9	27.6	
					6	LC AH; F=55%	35.0	28.8	

Table 3. (cont.)

Ref. no.[1]	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Rumen: Digesta vol. (L)	Rumen: pH	Rumen: [VFA] mM	Rumen: Ac[7] M%	Rumen: Pr[7] M%	Rumen: Liquid[8] kp	Rumen: Solid[8] kp	Eat[9] time	Rum[9] time
	1	32.2	3.16	23.8	5.05						61.6	23.1			276	405
1	2	30.6	3.30	22.8	5.79						66.3	18.5			302	455
	3	32.5	3.27	24.3	5.83						61.6	22.9			262	389
	4	31.5	3.34	24.0	6.19						62.8	22.1			286	464
	1	28.6	3.53	21.1	6.16		39.2			77	68.5	17.5	.069	.101	286	376
2	2	31.3	3.02	20.6	6.12		37.5			68	64.9	20.7	.067	.093	262	383
	3	27.6	3.60	20.2	6.02		38.0			57	68.0	20.0	.043	.081	296	363
	4	31.6	3.37	20.0	6.14		37.0			62	62.8	25.0	.044	.081	259	340
	1	30.8	3.57	22.2	5.55										220	337
3	2	33.0	3.57	25.4	6.48										230	336
	3	32.0	4.01	22.0	6.34										246	599
	4	30.6	3.91	23.0	6.69										231	578
	1	24.7	3.46	19.4	6.15		48		5.87	113	57.0	23.5				
4	2	24.2	3.57	19.8	6.26		53		5.89	113	57.1	23.8				
	3	25.2	3.61	19.4	5.94		52		5.67	124	56.3	25.2				
	1	25.9	2.25	20.6	6.1				5.53	142	51.1	35.0			356	401
	2	26.0	2.81	21.2	6.7				5.57	150	53.6	33.2			339	373
5	3	25.3	3.00	21.0	6.7				5.58	141	56.1	31.1			326	386
	4	24.9	3.02	21.1	6.8				5.76	129	56.3	30.4			350	411
	5	25.8	3.17	21.1	6.6				5.74	138	57.0	27.4			340	420

Table 3. (cont.)

Ref.[1] no.	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Rumen: Digesta vol. (L)	Rumen: pH	Rumen: [VFA] mM	Rumen: Ac[7] M%	Rumen: Pr[7] M%	Rumen: Liquid[8] kp	Rumen: Solid[8] kp	Eat[9] time	Rum[9] time
	1	27.0	2.86	22.3	7.0				5.63	132	67.8	19.5			367	402
	2	26.8	2.50	22.5	7.2				5.57	124	64.8	23.2			331	434
	3	26.8	3.08	22.2	7.5				5.78	148	69.1	17.1			381	423
6	4	25.7	3.04	22.5	7.8				5.77	124	68.2	18.9			361	427
	5	25.0	3.30	21.4	7.7				6.08	147	71.9	14.9			447	443
	6	24.5	3.31	22.6	8.4				5.92	134	70.2	16.1			387	429
	1	38.4	3.22	22.5	6.84		43.5			64	64.1	21.7				
7	2	39.5	3.00	23.3	7.29		45.4			55	59.9	25.1				
	3	39.4	2.94	23.9	7.62		40.7			65	59.3	27.1				
	4	36.2	2.60	22.5	6.80		31.2			48	57.3	29.8				
	1	27.7	3.50	21.3	7.03	75.7	60.1									
8	2	28.6	3.50	22.0	7.90	74.9	58.1									
	3	27.7	3.67	22.5	9.58	76.1	65.1									
	4	27.9	3.47	21.2	7.76	72.6	53.9									
	1	26.9	3.72	21.6	7.37	66	44.4	77.1	6.14	128	64.9	17.9				
9	2	26.9	3.75	22.3	8.34	69	54.6	72.5	6.17	131	65.8	18.9				
	3	25.9	3.69	20.8	8.49	66	56.5	78.7	6.17	131	66.7	18.7				
	4	23.5	3.60	18.9	8.26	64	59.3	77.8	6.17	136	69.2	18.2				
	1	39.1	2.80	23.0	6.5	70.7	48.2	90.8	6.07		62.5	20.6	.083	.047		
10	2	35.8	2.99	21.4	6.6	69.9	48.8	99.3	6.12		64.0	19.8	.085	.047		
	3	35.7	3.12	21.3	7.1	67.5	47.7	97.0	6.29		65.3	19.3	.082	.052		
	1	33.6	3.41	26.1	8.5	71.5	55.0	110	6.23	103	68.4	18.1	.084	.052		
11	2	33.1	3.22	24.4	8.0	68.8	48.6	99	6.08	88	66.9	20.0	.083	.048		
	3	33.8	3.10	24.8	6.9	70.0	43.4	99	6.09	94	68.1	19.2	.078	.048		

Table 3. (cont.)

								Rumen								
Ref.[1] no.	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Digesta vol. (L)	pH	[VFA] mM	Ac[7] M%	Pr[7] M%	Liquid[8] kp	Solid[8] kp	Eat[9] time	Rum[9] time
12	1	22.9	3.41	20.7	6.40	70.0	46.3				58.2	24.5				
	2	23.3	3.75	21.2	6.19	70.1	48.9				61.1	20.8				
	1	38.0		23.3	7.18		46.5						.122	.052		
	2	32.6		20.2	7.07		42.8						.112	.049		
13	3	32.1		20.0	7.44		42.4						.115	.049		
	4	29.7		17.9	8.02		51.2						.096	.043		
	5	36.5		23.7	7.75		39.9						.105	.053		
14	1	29.5	3.39	19.2	5.9						43.4	24.9			201	458
	2	29.4	2.87	18.9	3.7						38.6	31.7			162	310
	1	32.2	3.45	21.1	6.90											
15	2	33.0	3.34	19.8	6.40											
	3	32.7	3.36	21.7	7.16											
	1	25.7	3.4	15.2	4.95											
16	2	23.5	3.7	14.7	4.98											
	3	23.0	3.7	13.7	4.68											
	4	20.6	4.1	14.0	5.08											
	1	35.4	3.3	19.5	6.39											
17	2	30.5	3.5	18.3	6.12											
	3	31.3	3.4	18.6	6.56											
	4	30.6	3.8	19.5	7.20											

Table 3. (cont.)

Ref.[1] no.	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Rumen: Digesta vol. (L)	Rumen: pH	Rumen: [VFA] mM	Rumen: Ac[7] M%	Rumen: Pr[7] M%	Rumen: Liquid[8] kp	Rumen: Solid[8] kp	Eat[9] time	Rum[9] time
	1	34.0	3.5	24.9	5.28	72.0	45.6		6.6		60.5	24.0	.111	.050	294	335
18	2	33.7	3.6	25.7	6.22	71.2	47.5		7.0		63.3	21.8	.116	.060	315	376
	3	33.4	3.9	23.8	6.52	70.4	48.5		6.8		66.2	19.0	.118	.063	370	396
	4	32.1	4.0	23.6	7.10	70.7	50.8		6.9		67.7	18.0	.122	.059	373	421
19	1	21.7	3.90	15.0	4.83	73.1										
	2	20.2	3.98	12.9	5.44	71.8										
	1	31.1	3.0	22.9	7.40	71	51								161	
	2	30.0	3.2	23.7	7.58	74	53								197	
	3	30.8	2.9	26.2	8.25	72	54								201	
	4	27.6	3.3	25.3	9.01	69	48								252	
	5	27.6	3.0	23.4	8.47	70	56								271	
20	6	32.4	3.0	22.3	6.69	68	42								145	
	7	29.2	3.3	24.3	6.95	73	47								188	
	8	30.0	2.7	23.1	6.70	72	48								158	
	9	29.3	3.1	25.7	8.76	71	47								227	
	10	30.0	2.8	23.3	7.99	72	53								217	
	1	34.3	3.37	20.2	5.51											
21	2	32.4	3.29	19.0	5.80											
	3	31.2	3.33	18.0	5.35											
	4	31.9	3.44	18.5	5.87											
	1	38.2	3.64	21.7	5.55											
22	2	36.8	3.45	22.6	6.73											
	3	34.3	3.53	22.6	5.90											
	4	35.9	3.55	21.9	6.69											

Table 3. (cont.)

								Rumen								
Ref.[1] no.	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Digesta vol. (L)	pH	[VFA] mM	Ac[7] M%	Pr[7] M%	Liquid[8] kp	Solid[8] kp	Eat[9] time	Rum[9] time
	1	30.1	3.90	20.7	5.51	62.4		98							390	292
23	2	27.5	3.78	21.9	6.81	56.6		108							430	392
	3	30.0	3.60	23.8	6.95	61.2		114							428	389
	4	30.5	3.83	23.3	7.66	56.0		118							414	469
24	1	26.7	3.33	19.8	6.33										232	532
	2	24.0	3.46	18.3	3.93										176	390
	1	23.5	4.26	22.5	7.00	68.2										
25	2	23.8	4.13	22.8	8.57	63.6										
	3	22.0	4.19	21.4	8.41	62.0										
	1	27.2	3.94	22.0	6.56	62.2									216	474
	2	27.0	3.82	22.3	7.32	61.3									252	450
26	3	27.7	3.96	22.5	7.67	57.2									222	510
	4	26.6	3.59	20.1	6.05	65.4									300	456
	5	25.5	3.78	18.7	6.10	61.6									360	438
	6	25.5	3.73	19.1	6.42	60.2									384	426

[1]References 1 to 19 include diets with varying sources of NDF or varying forage:concentrate ratios. References 20 to 26 include diets with the same forage source and forage:concentrate ratios but different forage fiber contents.

[2]NDF content of diet DM (%).

[3]NDF content of diet DM from forage (%).

[4]NDF digestibility of forage after (T) hours of fermentation as measured by in situ analysis.

[5]units of kg/d.

[6]dig = apparent in vivo digestibility.

[7]Ac = acetate; Pr = propionate.

[8]Fractional rate of passage from the rumen (h^{-1}).

[9]Time (min/d) spent eating (Eat) or ruminating (Rum).

DMI as forage NDF. Multiple regression that included the study number in both of these models greatly increased model fit, however, parameter estimates for the effect of NDF concentration on intake did not change appreciably. To examine effects in early lactation only, regression of DMI on NDF concentration was performed for studies where cows were less than 100 DIM at the start of their trial. The linear fit of DMI on dietary NDF content was more strongly negative (b = -.30; r = .40), as was that for DMI on forage NDF content (b = -.21; r = .45). Fifty treatment observations had cows starting their experiment at less then 80 DIM. Regression of DMI on dietary NDF content was once again more strongly negative (b = -.42; r = .59).

Results from this analysis support the concept that DMI decreases in early lactation as NDF concentration of the diet increases. Approximately 35% of the variation in DMI for cows starting treatments less than 80 DIM can be explained by differences in dietary NDF content. Conducting forage studies to examine NDF effects is extremely challenging. Analysis for NDF content of mixed forage/concentrate diets is difficult because of starch contamination of the residual fiber (Van Soest et al., 1991). Often researchers have little ability to control the quality of forages harvested on experimental farms and have to use what is available. Even if they know forage characteristics prior to cutting, the potential for these parameters to change during harvest, storage, and feeding is immense (McGechan, 1990). Animal selectivity when offered high or low fiber diets is also very common. Therefore, what one thinks they are feeding may not be what is being consumed. Just measuring DMI as affected by dietary factors can be difficult. Abrams et al. (1987) used the intake of a standard forage as a covariant to reduce the error of estimating DMI and suggested that differences in physiological state, production, body condition, environment, genetics, and experimental error can all contribute to difficulties in measuring DMI precisely. Consequently, it may be surprising that any linear relationships can be observed between DMI and NDF content at all!

Several mechanisms may allow cows to compensate for increases in NDF content of the diet without decreases in DMI. Some of these thoughts have previously been suggested by Van Soest (1982). As mentioned in part I of this review, the rumens of cows consuming control diets may not be at maximal fill, so when NDF content of the diet increases, additional ruminal fill can be tolerated. This was found when forage NDF concentrations increased across maturities of alfalfa (Nelson and Satter, 1992b). Additional distention may be tolerated by cows if they have a greater drive to eat or are consuming poor quality diets, such that their intake of digestible energy is farther from their physiological set point. Such ideas have been included in intake models. Williams et al. (1989) modified the intake model of Mertens (1987) by allowing rumen capacity for NDF to vary between .8 and 1.2% of BW as energy demands increased. They also adjusted intake upward by 10% of the difference between the physical and physiological intake estimates (Mertens, 1987) if the latter was greater. Rate of passage of digesta from the rumen may increase as NDF intake and distention increase (Woodford et al., 1986; Llamas and Combs, 1991). Cows may also increase their eating and ruminating activity (Woodford et al., 1986; Grummer et al., 1987) to allow for faster diet digestion and passage from the rumen. These changes would allow faster clearance of digesta from the rumen and enable cows to consume diets with higher concentrations of NDF.

Limits to DMI from ruminal fill of NDF might imply that NDF intake is constant. Based on the observations from Table 3, this may not be the case. For these cows, NDF intake ranged from 3.7 to 9.6 kg/d. Rayburn and Fox (1993) examined the variation in NDF intake from production studies and found that NDF intake as a percent of BW was related positively to DIM, FCM, and dietary NDF concentration. The positive relationship between NDF intake and NDF concentration was also observed from regression of data in Table 3. This supports the concept that additional distention may be tolerated as diet quality declines.

Perhaps these concepts of rumen capacity, digestion, passage, and NDF intake can be summarized best by a modified model (Figure 3) originally proposed by Dado and Allen (1993). As the concentration of NDF in the diet increases, NDF intake and rumen volume increase until a maximum rumen volume has been reached at the capacity threshold. Beyond this point, rumen volume remains constant. Diet NDF content can continue to increase without a decrease in DMI because of passage compensation. During this period, eating, ruminating, and rumen motility activity increases to promote passage from the rumen. Eventually, the cow cannot increase these activities any further and reaches a point where no additional NDF can be consumed (NDF intake threshold). Any additional increases in diet NDF concentration results in a decrease in DMI. It is proposed that the level of diet NDF at which these thresholds occur are both diet and animal dependent. Such a mechanism would allow the cow to maintain DMI at the expense of digestibility in the rumen. However, maintaining DMI is more critical to total digestible energy consumption than digestibility because of potential post-ruminal digestion.

Variation in Forage Consumption Due to NDF Digestibility

Not all sources of NDF may elicit the same response from dairy cattle as their concentrations are increased in the diet. Briceno et al. (1987) performed similar statistical comparisons between DMI and dietary NDF content using 20 experiments from the University of Florida that included 1688 cow-period observations from early to mid-lactation and various roughage sources. Dietary NDF content was related curvilinearly to DMI, however, there was a significant interaction between source of roughage and dietary NDF concentration. They suggested that NDF could only be used to formulate dairy rations within roughage source and postulated that differences in intake response were due, in part, to variation in NDF digestion characteristics among fiber sources.

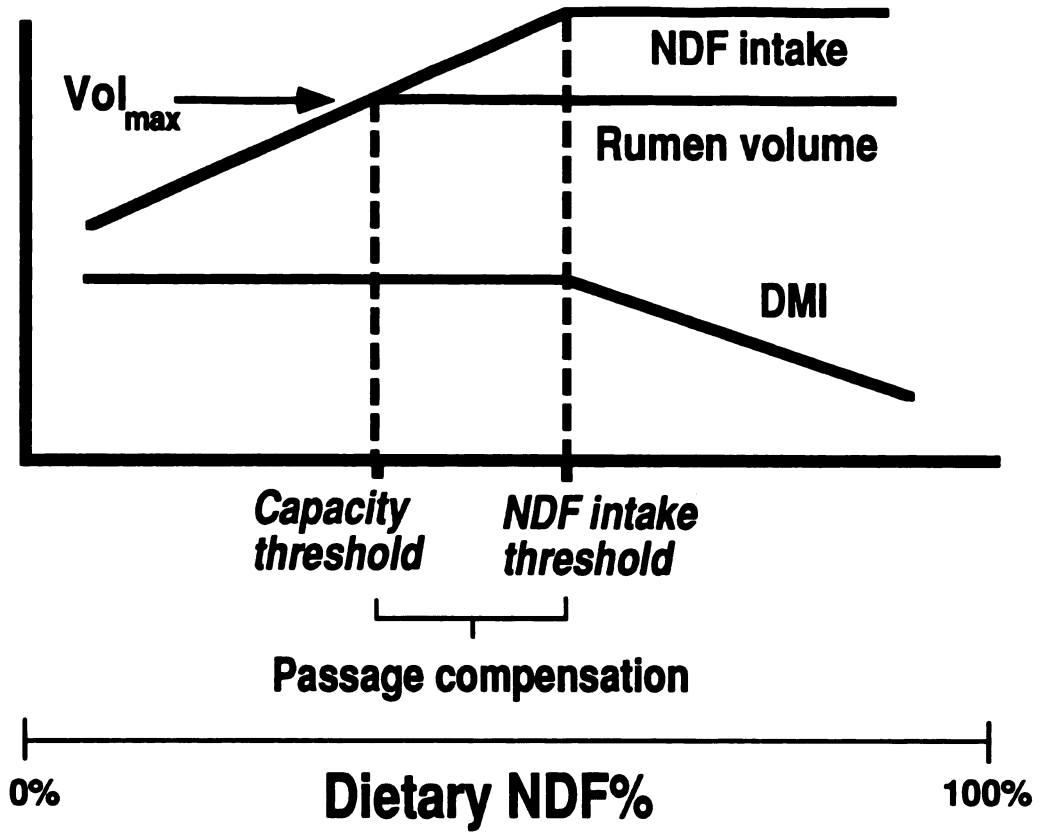


Figure 3. Modified model from Dado and Allen (1993) illustrating ruminal volume and passage compensation as concentrations of dietary NDF increase. Passage from the rumen increases when maximum rumen volume is reached. Intake of NDF is constant and DMI decreases only when both rumen volume and passage are maximum. The level of dietary NDF concentration where thresholds occur are both diet and animal dependent.

Not all NDF has the same composition. Availability of the NDF fraction to rumen microorganisms is variable and depends not only on the chemical composition of the NDF but also on the structural interrelationships between the components. Tremendous effort has been put forth by botanists and plant biochemists to describe plant cell wall structure and by nutritionists and physiologists to describe cell wall degradation and utilization by animals. A recent international symposium highlighted progress in these areas (USDA-ARS, 1993). Nutritionists have measured fiber digestibility either directly with in vivo digestion studies (Quicke et al., 1959), with in vitro fermentation methods that utilize rumen fluid (Goering and Van Soest, 1970) or enzyme preparations (Clarke et al., 1982), or with nylon bags placed in situ within the rumen of a fistulated animal (Marinucci et al., 1992).

Ruminal fiber digestion is a dynamic process. Extent of fiber digestion (i.e., digestibility) depends on the length of time spent in the rumen (or in vitro flask, or in situ bag). A typical digestion curve of two types of fiber is presented in Figure 4. Longer times of fermentation result in greater extents of digestion, except at very long times when a relatively indigestible residue of fiber remains and extent of digestion is complete. One of the first models to kinetically describe fiber digestion was developed by Waldo et al. (1972). Since then numerous other models have been developed (Illius and Allen, 1993), however, most utilize the same principles outlined by Waldo et al. (1972). Fiber digestion can be described in terms of the fractional rate of its digestion and the maximum extent of its digestion. Maximum extent of digestion is measured with very long times of fermentation; rate of digestion is generally determined as the negative slope of the natural log of digestible fiber remaining versus time. Such a calculation assumes fiber digestion is a first order chemical process with respect to digestible fiber pool size. Large variation in rate and maximum extent of fiber digestion in different forage species have been reported (Smith et al., 1972; Varga and Hoover, 1983). When fiber digestibilities are reported from in vitro or in situ measurements, the

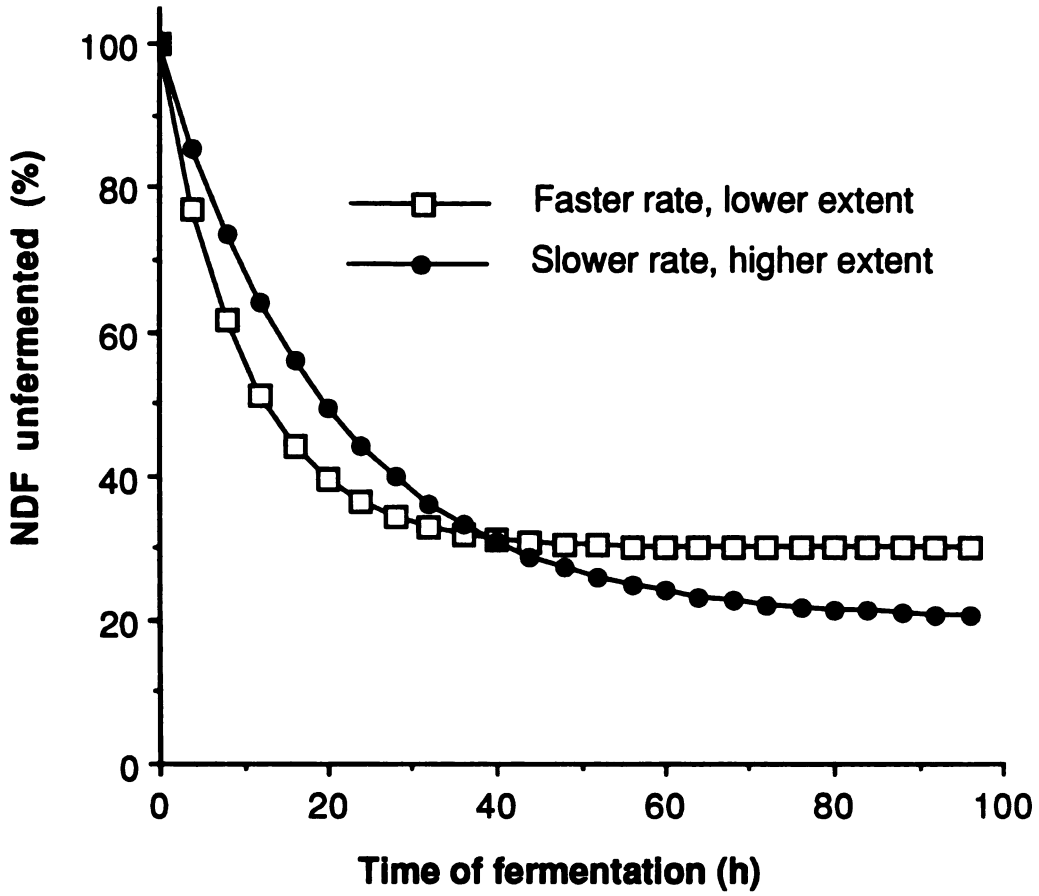


Figure 4. Ruminal digestion curve of NDF. Y values represent the percentage of original NDF that remains after a given length of microbial fermentation. Fiber with faster fractional rates of digestion ferment more quickly. Fiber with higher maximum extents of digestion have less fiber remaining after extended periods of digestion. Fiber digestibility is time dependent.

length of fermentation must also be reported. Typically, fermentation times are chosen which are hoped to represent the average retention time of fiber in the rumen. In vivo, fiber digestibility is a function of the proportion of fiber that is potentially digestible, the rate of fiber digestion in the rumen, and the rate of fiber passage from the rumen (Allen and Mertens, 1988b).

Digestibility of fiber has been shown to vary both across and within forage species (USDA-ARS, 1993). Because lactating dairy cows derive from 10 to 20% of their digestible energy from fiber (Galyean and Goetsch, 1993), an increase in fiber digestibility should result in additional energy for productive purposes. What is less well known is whether differences in fiber digestibility affect the voluntary intake of forages and their diets. A more rapid or greater extent of fiber digestion may enhance clearance of fiber from the rumen, stimulating an increase in DMI. Glenn and Waldo (1993) suggested that such an understanding is critical in improving the efficiency and performance of ruminants. Crampton and co-workers (Crampton et al., 1960; Donefer et al., 1960) developed a nutritive value index for forages based on the intake potential and digestibility of individual forages. They believed that previous forage quality indexes failed to predict animal performance because they did not include estimates of intake. They found both relative intake and the nutritive value index for sheep to be highly correlated ($r > .83$) with cellulose digestibility after 12 h of in vitro incubation, which suggests that fiber digestibility influences DMI. Muller et al. (1972) fed corn silage stover from normal or a brown mid-rib mutant variety to sheep. Both silages contained equal NDF concentrations (60%) but differed in NDF digestibility by 12% units (39 vs. 51%) after 36 h in vitro. Both in vivo DM digestibility (56 vs. 62%) and DMI (1.9 vs. 2.4% of BW) increased with high fiber digestibility. Steers were fed straws with varying maximum extents and rates of DM digestion; their intakes varied in relation to these digestion parameters (Orskov et al., 1988). Because the straws

contained similar and high concentrations of NDF (mean = 83% of DM), such intake responses were likely due to differences in fiber digestion.

Few attempts have been made to directly measure the affect of fiber digestibility on intake of lactating cows. A summary of six experiments where such measurements were made is presented in Table 4. To assess only the effect of fiber digestibility, it was imperative that these studies used dietary treatments with equivalent fiber concentrations. Studies 1 to 4 altered forage:concentrate ratios to achieve equivalent NDF contents, while studies 5 and 6 used forages that contained approximately equal fiber contents so ratios could remain constant. In only one study (Llamas-lamas and Combs, 1990) was DMI significantly greater ($P < .01$) with higher fiber digestibility. Cows on this experiment had substantially higher DMI than the other studies, which may have resulted in their ability to detect intake differences. Studies 1, 2, and 4 are difficult to interpret because of the wide variety of fiber sources utilized. They formulated rations based on the rate of fiber digestion of feedstuffs measured in situ (Varga and Hoover, 1983) to achieve diets with different rumen fill characteristics. Studies 5 and 6 were ideal to examine digestibility effects because they were not confounded by differences in fiber source and forage:concentrate ratio. Both of these studies showed improved milk production with greater fiber digestibility; however, their cows were not in early lactation so intake differences were not detected. Any of the studies investigating the effect of NDF content (Table 3) had the potential of having differences in fiber digestibility, unless shown to the contrary. Most studies never measure fiber digestibility so they do not know if their NDF content differences are confounded by differences in NDF digestibility. To isolate fiber digestibility, the ideal approach is that of Robinson and McQueen's (1992); however, improvements might include use of higher fiber diets (40% NDF is not high for a study using grass forage) and cows in negative energy balance limited by rumen capacity. Comparison of

Table 4. Summary of studies that examined the effect of dietary NDF digestibility as part of complete rations with constant NDF concentrations on intake and production of lactating dairy cows. Different NDF digestibilities were obtained by changes in fiber source or forage quality.

Reference	Ref.[1] no.	Cow no.	DIM	BW (kg)	Diet no.	Primary NDF sources; diets	Diet[2] NDF	NDF[3] from forage	NDF[4] digestibility
Feng et al. 1993	1	4	147	614	1	VNS; F=0%; low fill-39% NSC	34.1	0	fast digestion
					2	VNS; F=16%; high fill-39% NSC	34.1	6.6	slow digestion
					3	VNS; F=28%; low fill-29% NSC	34.1	11.7	fast digestion
					4	VNS; F=55%; high fill-29% NSC	34.0	23.9	slow digestion
VNS=various non-forage NDF sources; F=percent forage; NSC=non-structural carbohydrate									
Miller et al. 1990	2	34	0	556	1	VNS; F=6%; low fill	33.9		51.5 T=24
					2	VNS; F=25%; high fill	32.1		32.8 T=24
Llamas-lamas and Combs 1990	3	6	120	686	1	early cut alfalfa hay; F=66%	32.6	23.8	64.7 T=72
					2	mid cut alfalfa hay; F=49%	32.6	25.3	51.7 T=72
Varga et al. 1984	4	28	0	535	1	VNS; F=22%; low fill	39.3		58 T=24
					2	VNS; F=23%; high fill	39.7		43 T=24
Robinson and McQueen 1992	5	16	mid lactation	630	1	100% poor timothy silage; F=57%	40.3	34	54 T=24
					2	66% poor timothy silage; F=57%	40.2	34	56 T=24
					3	33% poor timothy silage; F=57%	41.5	34	60 T=24
					4	100% good timothy silage; F=57%	40.6	34	62 T=24
Keith et al. 1979	6	12	past peak	675	1	brown mid-rib corn silage; F=75%	≈40.4	37.2	65.3 T=48
					2	normal corn silage; F=75%	≈41.8	38.6	54.8 T=48
					3	brown mid-rib corn silage; F=50%	≈34.3	24.8	(forage only)
					4	normal corn silage; F=50%	≈35.5	25.8	

Table 4 (cont.)

Ref.[1] no.	Diet no.	Milk[5] yield	Milk fat%	DM[5] intake	NDF[5] intake	DM[6] dig.	NDF[6] dig.	Rumen: Digesta vol. (L)	Rumen: pH	Rumen: [VFA] mM	Rumen: Ac[7] M%	Rumen: Pr[7] M%	Rumen: Liquid[8] kp	Rumen: Solid[8] kp	Eat[9] time	Rum[9] time
	1	20.7	3.2	15.6	5.3	54.8	43.3		5.75	110	52.1	26.4	.059	.026		
1	2	21.9	3.3	16.5	5.6	43.1	32.1		5.88	119	65.8	21.3	.072	.037		
	3	22.8	3.7	16.4	5.6	44.2	42.9		5.73	130	59.4	25.0	.076	.041		
	4	22.3	3.7	17.4	5.9	46.3	39.0		6.07	102	62.5	21.9	.090	.045		
2	1	35.2	3.17	18.6	6.30											
	2	32.1	3.15	17.9	5.75											
3	1	33.6	3.41	26.1	8.5	71.5	55.0	110	6.23	103	68.4	18.1	.084	.052		
	2	33.1	3.22	24.4	8.0	68.8	48.6	99	6.08	88	66.9	20.0	.083	.048		
4	1	30.3	3.54	17.9	7.03			100	5.99	168	58.3	27.8	.113	.059		
	2	26.3	3.92	18.0	7.15			84	5.92	141	60.4	23.5	.097	.050		
	1	24.3	3.82	20.1	8.20	76	64	≈129	6.23	105	66	17				
5	2	24.5	3.95	20.7	8.19	78	67	≈132	6.28	108	66	17				
	3	24.9	3.92	20.3	8.41	77	67	≈133	6.24	105	67	17				
	4	25.3	3.96	19.9	8.08	78	70	≈126	6.23	105	67	17				
	1	28.6	3.58	22.0	8.89											
6	2	27.3	3.66	21.4	8.95											
	3	28.4	3.55	22.0	7.55											
	4	26.8	3.69	21.6	7.67											

Table 4 (cont.)

[1]References 1 to 4 include diets with varying sources of NDF or varying forage:concentrate ratios. References 5 to 6 include diets with the same forage source and forage:concentrate ratios but different forage fiber digestibilities.

[2]NDF content of diet DM (%).

[3]NDF content of diet DM from forage (%).

[4]NDF digestibility of diets after (T) hours of fermentation as measured by in situ analysis.

[5]units of kg/d.

[6]dig = apparent in vivo digestibility.

[7]Ac = acetate; Pr = propionate.

[8]Fractional rate of passage from the rumen (h^{-1}).

[9]Time (min/d) spent eating (Eat) or ruminating (Rum).

by-product feeds that differ substantially in NDF digestibility (Stern and Ziemer, 1993) is another approach to study fiber digestibility.

Plant Factors Affecting Fiber Digestibility

To understand why plant cell wall is not uniformly available to ruminal fermentation requires an appreciation for the diversity of molecular composition and structure within different forages. Cell wall, as isolated by the NDF procedure, consists of the general molecule types of cellulose, hemicelluloses, and lignin (Van Soest, 1982). Other chemical methods are available to isolate each of these components in a fashion more amenable to traditional plant cell wall chemists (Theander and Westerlund, 1993), however, the gravimetric NDF method has been preferred by nutritionists because of its relative speed and nutritional uniformity of neutral detergent solubles. Cellulose and hemicelluloses are part of the polysaccharide fraction of plant cell walls. Cell wall polysaccharides are generally classified according to their structure into one of five groups: glucans (which includes cellulose), rhamnogalacturonans and associated arabinans, mannans, xylans, and glucuronomannans (Aman, 1993). Polysaccharide names are based on the structure of their monosaccharide residues.

Pectic polysaccharides are common in primary cell walls but are not included in the NDF fraction because of their rapid availability to ruminal fermentation (Van Soest, 1967). Cellulose is the most abundant organic polymer on earth and consists of beta 1-4 linked glucopyranosyl units (Aman, 1993). The extended polymer forms a flat ribbon supported by intra- and intermolecular hydrogen bonds. Multiple cellulose polymers aggregate into highly ordered crystalline and noncrystalline regions. Hemicellulose is a general name for polysaccharides soluble in dilute acid or alkali and consist mainly of substituted xylans. Lignin is a general name for phenylpropanoid molecules deposited in cell wall in highly diverse, almost amorphous, polymers (core lignin) or linked to polysaccharide (Jung and Deetz, 1993). Lignin monomers include coniferyl, sinapyl, and *p*-coumaryl alcohols. During forage plant growth, lignin is deposited predominantly

into the secondary cell wall with some also found in the primary wall and middle lamella. For the plant, lignin serves to decrease water permeability and add structural strength to the maturing cell wall.

Fiber digestibility is variable across forages because of differences in the relative proportion of cell wall components and because of variation in structural linkages between these components. Lignin is the cell wall component most closely associated with indigestibility. Not only is lignin considered to be unavailable to rumen fermentation, it also complexes with cell wall polysaccharides making them less susceptible to microbial attachment and enzymatic degradation (Chesson, 1988). Lignin does not depress fiber digestibility the same across all forages. Smith et al. (1972) found a greater depression in NDF digestibility after 72 h of in vitro fermentation for grasses compared to legumes as lignin concentration in the NDF increased, but no relationship between lignin concentration of NDF and rate of NDF digestion. The lignin:NDF ratio was not highly correlated to NDF digestibility after 30 h in vitro digestion for some forage cuttings, but was for others (Allen et al., 1991). It appears that not all lignin has the same composition nor does it link to carbohydrate to the same degree in all cell walls. The diversity of lignin structure continues to make this a complex area of research (Ralph and Helm, 1993). Diversity in polysaccharide composition also creates variability in cell wall degradation. Cell wall polysaccharides interact through structural relationships associated with ionic, hydrogen, and covalent bonds (Hatfield, 1993). Linkages among different polymer types creates additional variation. Differences in structure within a given polysaccharide, such as cellulose crystallinity, also add diversity. Lack of uniformity in structural linkages and sugar composition generates a complex molecular puzzle for microbial enzymes. Not only do these enzymes need to be able to recognize the specific linkage and conformation of the fiber polymers, they also must have sufficient space to access their binding locations. A

greater understanding of the entire cell wall matrix is necessary before specific predictions can be made about cell wall digestibility.

Even though forage cell wall chemistry is complex, there are a few general trends among different types of forages and forage maturity that allow for some precision in estimating fiber digestibility. Grasses contain higher concentrations of NDF, but the maximum extent of NDF digestion in grasses is greater because of lower lignin concentrations. Because of lower cell wall content, legume DM is generally more digestible even though legume fiber is less digestible. In general, the ratio of lignin to carbohydrate in indigestible residue is 1:1.4 (Van Soest, 1982) so lignin concentrations tend to define the limit of cell wall digestion. Rate of cell wall degradation, however, is faster in legumes, perhaps because a larger portion of their lignin is present in core lignin compared to grasses (Jung, 1989). Noncore lignin has the potential to bind with noncellulosic polysaccharides; as its concentration increases, it depresses digestibility more than equivalent increases in core lignin. These factors may help explain why fiber digestibility of grasses declines faster with maturity compared to legumes (Sharma et al., 1988). Legumes demonstrate greater intake potential compared to grasses, perhaps due to lower ruminal digesta volumes, greater fragility, or faster digestion rates (Thorton and Minson, 1973). Legumes generally contain higher concentrations of pectic polysaccharides while grasses contain more hemicelluloses, although it is unknown what effect these have on fiber digestibility. An extensive study with legumes, temperate grasses, and tropical grasses has been summarized that illustrates fiber differences between forage types and their effect on ruminant performance (Reid et al., 1988). Differences between legumes and grasses have been incorporated into intake models for dairy cattle (Williams et al., 1989).

As forage plants grow, concentrations of NDF generally increase and protein decrease, suggesting a significant decline in forage quality with maturity (References in Table 3). Early cut forages had faster rates and maximum extents of DM digestion

compared to later cut mixed forages (Cleale and Bull, 1986). With perennial grass species, NDF content (40 to 63%), lignin content (2 to 5%), and in vitro indigestible fiber (6 to 26%) increased as maturity advanced by 50 d, while maximum extent of fiber digestibility decreased from 80 to 44% (Cherney et al., 1993). They suggested that maturity differences were more significant than species differences. Similar declines in fiber digestibility due to maturity were found in a more diverse set of forages (Smith et al., 1972). The significance of decreases in forage quality because of maturity were illustrated by Kawas et al. (1991), who observed that not only did intake and production of dairy cows decrease as maturity of alfalfa at cutting increased, but also that decreases in forage quality could not be compensated for by increases in concentrate feeding.

Several mechanisms exist for possible improvements in fiber digestibility. Researchers are beginning to measure fiber digestibility in forage breeding programs and are observing sufficient genetic variation to warrant selection on this trait (Buxton and Casler, 1993). Genetic improvements in certain compositional characteristics of forage quality, such as crude protein content and detergent fiber concentrations, have already been obtained. Improvements in fiber digestibility will probably be centered around changes in the lignin:NDF ratio. As previously noted, certain mutant strains of corn, as well as sorghum, millet, and sudangrass, contain lower concentrations of lignin that has been shown to improve fiber digestibility (Cherney and Cherney, 1991). Isolation of the gene(s) responsible for this mutation and its incorporation into other forage species remains a possibility. Other techniques may be available to increase fiber digestibility after the forage has already been harvested (Fahey et al., 1993). Physical alterations, including pelleting and grinding, irradiation, steam treatment, and mechanical separation of plant parts, have been investigated with limited success. Chemical treatments have included hydrolytic cleavage with alkali, such as sodium hydroxide, ammonia, or urea, and oxidation with ozone, sulfur dioxide, and other oxidizing agents. Grasses have been more easily improved with chemical treatments

because of their higher proportion of ester linkages compared to other plant lignins. Finally, biological treatments have been implemented and include the use of white-rot fungi (Agosin et al., 1985), cellulases, and bacterial inoculants in fermented silages (Pitt, 1990). Most of these treatments work best on poor quality forages with high fiber and lignin concentrations. Additional efforts are being made to improve their utility in higher quality forages more commonly fed to lactating cows.

Future Directions

If fiber digestibility is found to have an important influence on feed intake in dairy cows, it will be necessary to understand what aspect of fiber digestibility is most important. Fiber digestion has been defined in terms of rate of digestion, lag until fermentation, or extent of digestion at various times post commencement. What definition is most highly related to intake? Mertens (1973) observed that in vitro digestion after 6 h was the most highly correlated time point with intake for sheep. This may, however, only reflect the effect of fiber content on intake. Miller and Muntifering (1985) suggested that the amount of potentially digestible fiber is more important than rate of digestion, rate of passage, or digestion lag in determining in vivo digestibility. Rumen content mass in lactating cows was related more to fiber rate of digestion and passage than to total tract digestibility or maximum extent of fiber digestion (Shaver et al., 1988a). Finally, Von Keyserlingk and Mathison (1989) found that forage intake in steers was related most to 36 h in situ degradation values.

Because fiber digestion depends on such a plethora of plant and animal characteristics, it may seem impossible to ever quantify its true affect on intake. Models of fiber digestion offer researchers the opportunity to visualize how these different factors interact with one another (Allen and Mertens, 1988b). Besides suggesting what potential experiments might be crucial to more accurately describe fiber digestion, models may also enable researchers to assess the importance of fiber digestibility under numerous plant, animal, and environmental conditions.

CHAPTER 2

Continuous Computer Acquisition of Feed and Water Intakes, Chewing, Reticular Motility, and Ruminal pH of Cattle

ABSTRACT

Monitoring of feeding, chewing, and rumen activity was integrated into one data acquisition system for continuous measurement of 12 dairy cows. Feed mangers were hung from single-point load cells for measurement of feed disappearance from individual stalls. Water flow meters were inserted in supply lines for each stall and generated pulse output for electronic summation of water intake. Jaw movements were detected with a water-filled tube connected to a pressure transducer under the cow's jaw to determine chewing activity. Similar tubes were used to detect contractions in the reticulum. Rumen pH was monitored continuously with an electrode and pH transmitter. All signals were processed and recorded on a microcomputer using commercially available computer hardware and software. One file was written for each animal monitored. Data were interpreted using algorithms developed with SAS®. Two studies were conducted with 10 lactating cows to evaluate the performance of acquisition hardware, protocols, and interpretation algorithms. Interpreting behavior of many cows with one algorithm sacrificed accuracy of bout time borders for some individual cows. Nonetheless, high correlations ($r \geq .85$) between computer-interpreted and manually determined variables indicated acceptable performance of the acquisition system. With continuous measurement of many animal feeding variables, a more complete understanding of dietary effects on digestive function and animal performance is possible.

INTRODUCTION

Interactions among dietary characteristics and ingestive behavior of ruminants have received considerable research attention (Balch, 1958; Freer and Campling, 1965; Jaster and Murphy, 1983). Intake, feeding rate, salivation, rumination, and digesta passage are animal traits that may respond to changes in diet characteristics such as nutrient composition, physical properties, or palatability. Interpreting effects of dietary manipulation on digestive efficiency and animal performance requires quantitative measurement of responsive animal variables. More frequent measurement is necessary to obtain reliable information from rapidly changing variables. Continuous measurement ensures that even the most rapid fluctuations are detected. Numerous animal monitoring systems have been developed to provide such information.

Feed consumption of individually housed ruminants has been recorded throughout the day by frequently offering known quantities of feed in separate containers for each meal (Wangsness et al., 1976) or by electrical measurement of strain gauge devices placed below (Brewer et al., 1977) or suspended above (Metz and Borel, 1975; Heinrichs and Conrad, 1987) feed mangers. Loose housed animals have been monitored using computer-controlled feeders with animal identification capabilities (Mason et al., 1991). Water intake has been recorded continuously by Metz and Borel (1975). Automatic methods to detect chewing activity have been reviewed by Penning (1983) for grazing ruminants and by Beauchemin et al. (1989) for ruminants fed in stalls. All methods use jaw movement as an indication of chewing, which is detected with electronic switches (Metz and Borel, 1975; Luginbuhl et al., 1987), pneumatic transducers (Law and Sudweeks, 1975), or hydraulic transducers (Jaster and Murphy, 1983). Ruminant forestomach motility is essential for fractionation, fermentation, and passage of rumen digesta (Ruckebusch, 1988) and frequently is measured to assess factors affecting digestive function (Stevens and Sellers, 1968). Monitors for detection of motility include balloons pneumatically linked to chart pens (Balch, 1958), pressure-sensitive

radio-telemetry capsules (Riley and Cook, 1974), and catheter tubes connected to pressure transducers (Okine et al., 1989). Digesta pH in the reticulorumen was measured in vivo as early as 1941 (Smith, 1941). Since then, continuous pH measurements have been made by various groups (Johnson and Sutton, 1968; McArthur and Miltmore, 1968) for several weeks using electrodes designed to withstand the rumen environment.

Advantages of all automatic monitoring systems include reduced labor required for visual or manual determinations, improved accuracy, and measurement of some activities that are manually impossible to monitor. Multiple animal responses may result from a single dietary change due to ruminant digestion complexity. Monitoring two or more variables allows interactions among activities to be examined and may improve accuracy of measurement and interpretation for each activity because of such interdependence. Some studies have monitored more than one response variable continuously and simultaneously (Freer and Campling, 1965; Metz and Borel, 1975); these data, however, are rare.

More recent studies incorporated monitoring devices into complete data acquisition systems (Penning et al., 1984; Luginbuhl et al., 1987; Beauchemin et al., 1989). Striving for complete automation, these systems consist of activity monitors, data collectors, and interpretation programs. Unfortunately, these systems have been limited by inabilities to record activity over long periods, to measure many experimental animals simultaneously, or to monitor more than one activity. Recent advances in data acquisition software and computer technology enable flexible acquisition control, rapid data collection, and large data storage. It is now possible to expand the number and length of experimental observations and the number of activities that may be monitored automatically and continuously.

Objectives of this experiment were to develop and construct a data acquisition system that continuously and simultaneously monitors feed and water intake, chewing activity, reticular motility, and ruminal pH of cows housed in stalls. A further objective

was to evaluate monitoring equipment and interpretation algorithms against manual observation for each activity.

MATERIALS AND METHODS

Acquisition System

The complete measurement system consists of monitoring equipment for 12 cows, a computer, software, and data acquisition boards for data collection, and a computer program for data interpretation (Appendix Figure 1). Tie stalls at the Michigan State University Dairy Teaching and Research Center were modified to accommodate monitoring equipment. Equipment wiring was designed to enable detachment so cows could be milked in a parlor. All electronic equipment was purchased from commercial sources to ensure compatibility among original equipment and replacement parts.

Feed Intake. A 425-L polyethylene feed manger (Model #99075; Bastian Material Handling Corporation, Indianapolis, IN) was suspended with four cables from a single S beam load cell (Table 1) for each stall. The 225-kg capacity load cell was mounted to metal framework 2 m above the floor. The stall and frame were designed in a manner

Table 1. Monitoring equipment.

Activity	Device	Model	Output	Range	Accuracy
Feed intake	Load cell	LCCA-500[1]	Analog	0-225 kg	.25 kg
Water intake	Flow meter	FTB6105-PR[1]	Pulse	.9-94 L/min	.05 L
Chewing activity	Pressure transducer	PX236-015[1]	Analog	0-1.05 kg/cm^2	.016 kg/cm^2
Reticular motility	Pressure transducer	PX236-015[1]	Analog	0-1.05 kg/cm^2	.016 kg/cm^2
Ruminal pH	pH electrode	450CD[2]	Analog	0-14 pH units	.02 pH
	pH transmitter	PHTX-91[1]	Milliamp	0-14 pH units	.02 pH

[1]Omega Engineering, Inc., PO Box 2284, Stamford, CT.
[2]Sensorex, Inc., 11661 Seaboard Circle, Stanton, CA.

similar to that developed by Metz and Borel (1975), that minimized cow interaction with the manger except during eating. Loadcells were supplied with 10 V of power that could be switched on and off independently and generated output of 30 mV over a 0- to 225-kg range. Load signals required 200x amplification prior to input into the analog converter. Supply current and return signal for all monitored activities were transmitted with 24-gauge four-conductor shielded wire (Belden 9534; Belden Wire and Cable, Richmond, IN). An example of feed weights measured with this design for one cow during one day is presented in Figure 1.

Water Intake. Individual drinking cups and in-line water flow meters (Table 1) were provided for each cow. Cumulative water flow could be read directly from the meter register or electronically totaled. Meters calibrations indicated that 26.6 ± .35 electronic pulses/L were registered using an input of 5 V. Additional signal conditioning was required to amplify pulse signals prior to processing. Counter-timer circuits accumulated pulses for each cow over time (Figure 1).

Chewing Activity. Jaw movements were monitored and counted to estimate chewing activity. A water-filled rubber bicycle tube (31.8 cm i.d. x 30.5 cm) was fixed to a nylon halter under the cow's jaw and connected to a pressure transducer (Table 1) via a compression fitting on the valve stem (Jaster and Murphy, 1983). The tube was supported by a piece of latex to ensure contact of the tube with the jaw while maintaining elasticity for free jaw movement. A retractile cable (Belden 8415) allowed head movement and connected the halter and transducer to the power source (10 V) and analog converter. Opening of the jaw decreased the volume of the tube causing increased pressure that was read as an analog signal by the computer. Typical analog signals for eating and ruminating activity are presented in Figure 2. Analog signals were sampled at 4 Hz, enabling detection of chewing rates up to 2 Hz for cows receiving mixed forage and concentrate diets. A potential chew was identified when the derivative of the sampled analog signal exceeded a negative threshold value that was constant for all cows monitored. This

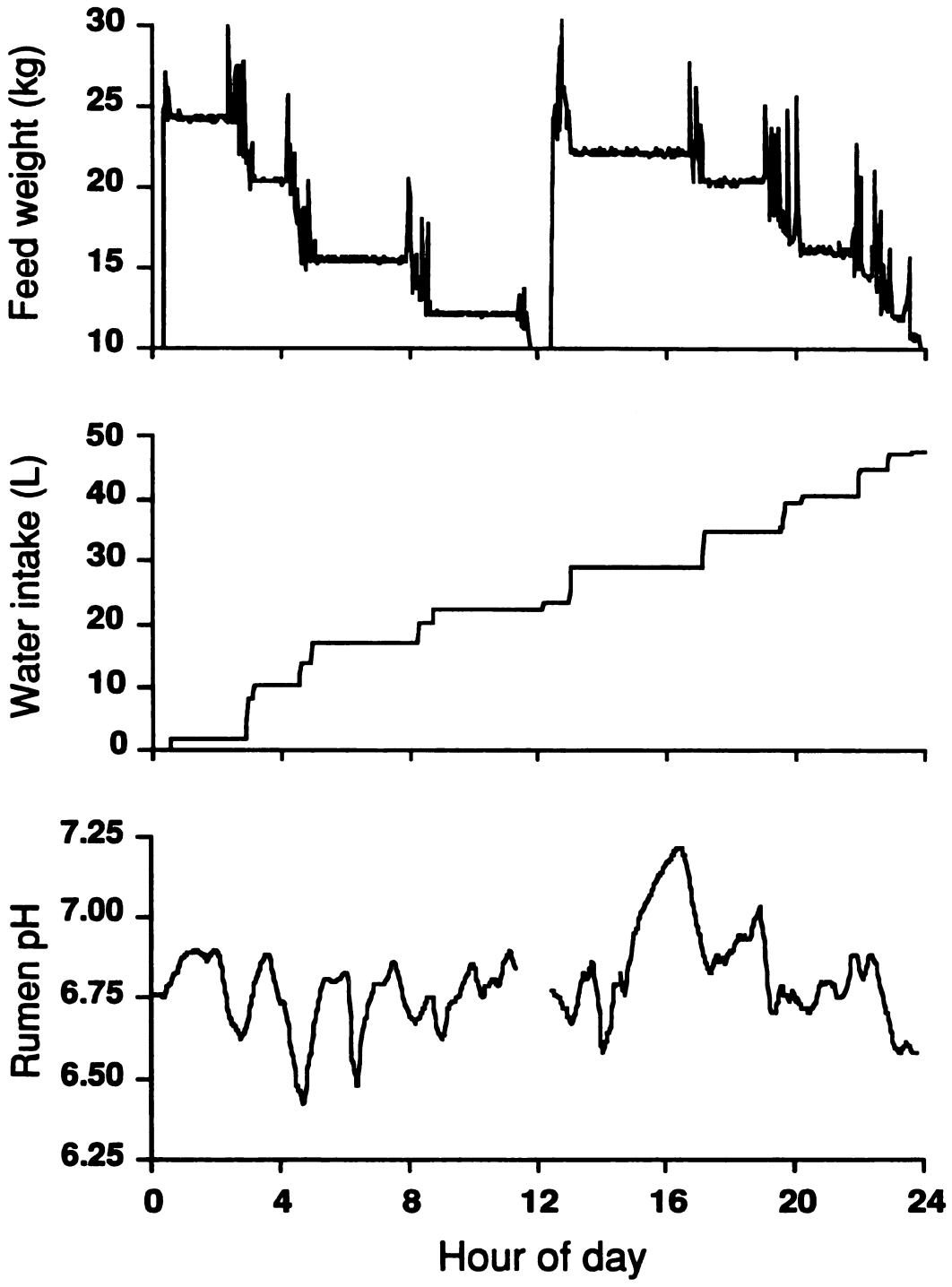


Figure 1. Scaled output of feed manger, water meter, and pH monitors throughout 1 d for a cow fed twice daily.

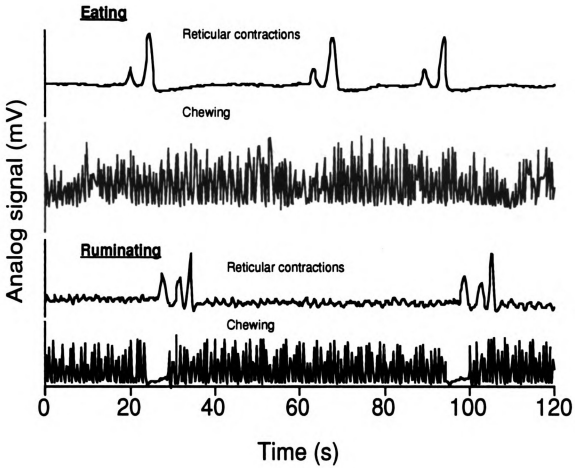


Figure 2. Analog output from chewing and reticulum motility monitors during episodes of eating and ruminating. Values presented are scaled pressure transducer output.

threshold value, determined by trial and error, depended on characteristics of the monitors, such as degree of water filling in the tube and proximity to the cow's jaw. This criterion allowed accurate peak counting, regardless of baseline location. Detection of higher chewing frequencies are possible with this system, however a rate of 4 Hz allowed more accurate peak detection when using the derivative threshold method.

Reticular Motility. A pressure transducer and water-filled rubber tube similar to that used for monitoring chewing was used to detect pressure changes from reticular contractions. Ends of the tube were tied to form a "balloon" 20 x 7.5 x 3 cm. The tube contained 1.0 kg of lead mass to keep the device within the reticulum. Electrical wires were protected from the rumen environment with plastic tubing (Tygon R-3603; 1.3 cm in diameter, American Scientific Products, McGaw Park, IL), and retractable four-conductor wire was used exterior to the rumen to allow cow movement. Monitoring devices were placed in the reticulum through a permanent rumen fistula and secured to its plug. Figure 2 illustrates typical analog signals received from a motility monitor supplied with 10 V during eating and ruminating activity. Motility signals were sampled at 4 Hz and averaged over a period of 1 s. Potential reticular contractions also were identified by the derivative of a smoothed signal, similar to that performed for chewing activity. Two or more potential contractions occurring within 15 s of each other were required for verification of a reticular contraction. This criterion helped keep reticular pressure changes due to coughing, licking, and other activities from being recorded as contractions.

Ruminal pH. Continuous pH measurement required use of an electrode and transmitter. An epoxy body, liquid-filled combination pH electrode (Table 1) with recessed bulb and sealed reference electrode provided durability necessary to withstand the rumen environment for extended periods. The wire lead and upper quarter of the electrode were protected from digesta with a 1.6-cm diameter plastic hose. A metal shroud attached to the end of the electrode allowed digesta to pass freely around the pH bulb while keeping it from resting against the ventral rumen wall. Against the wall, electrode pH was

approximately .7 pH units greater than within the ventral sac, possibly because of rapid absorption of VFA or elevated ammonia concentrations near the wall. Values within the ventral sac digesta probably are more important for characterizing ruminal fermentation than are readings near the rumen wall. The electrode was held about 8 cm off the floor of the ventral sac by attaching 1.0 kg of lead sealed in plastic to the metal shroud and securing the plastic tubing to the cannula plug through which it passed.

Outside the cow the electrode lead was plugged into a four-wire pH transmitter (Table 1). A separate transmitter was used for each cow monitored. Transmitters provided 4 to 20 mA direct current output over any two units of pH that was converted to a millivolt signal at the computer by use of a shunt resistor. In addition, pH was displayed visually on the transmitter panel where two point calibration and manual temperature compensation could be performed. Transmitters required a 110-V standard power supply. Electrode leads were suspended from elastic cord to keep wires away from cows' hooves.

During periods of pH measurement, each electrode-transmitter combination was calibrated at pH units of 4 and 7 before insertion of the electrode into the ventral sac. Rumen pH for one cow for 1 d are presented in Figure 1. Electrode calibration was difficult to maintain over several days because of static build-up, faulty solid-core electrode leads, and rumen fluid leakage. Electrodes were recalibrated once every 2 d to help to maintain accuracy. Recent changes in tubing, connectors, and electrode leads have improved electrode performance.

Data Collection. All electronic signals were received by an IBM PC-AT compatible computer (Table 2) located in a room adjacent to the cow stalls. One, eight-channel analog to digital converter and two, five-channel counter-timer boards (Table 2) fit into three half-slots of the computer. Each of four channels of the analog to digital converter was expanded to 16 channels by using an analog multiplexer (Table 2) for a total of 68 available analog inputs. Each multiplexer provided analog signal filtering and independent attenuation. Pulse output from water meters was measured via the two

Table 2. Computer, software, and data acquisition boards.

Device	Model/Title	Specifications
IBM PC-AT compatible computer	Premium/286[1]	80286 microprocessor at 10 MHz, 0 wait state, 80287 co-processor, 640 kbyte base memory, 40 Mbyte fixed hard disk, 88 Mbyte removable hard disk[2]
8 channel analog-digital converter	DAS-8[3]	Expandable to 128 channels; 12 bit, 2.4 mV resolution at ± 5 V fullscale; 2 counter-timer channels
Analog multiplexer	EXP-16[3]	16 channel with user-selectable gains
Counter-timer board	CTM-05[3]	5 independent up/down counters at 16 bit resolution
Uninterruptable power supply	PC-2400[4]	120 VAC, 800 watt; on-line output, inverter powers load continuously
Data acquisition software	Labtech Notebook[5] Version 5.0	Menu-driven program for data acquisition and process control with real-time graphic data display; fully compatible with data acquisition boards

[1]AST Research, Inc., 2121 Alton Avenue, Irvine, CA.

[2]SyQuest Technology, 47071 Bayside Parkway, Fremont, CA.

[3]Omega Engineering, Inc., PO Box 2284, Stamford, CT.

[4]Clary Corporation, 320 West Clary Avenue, San Gabriel, CA.

[5]Laboratory Technologies Corp., 400 Research Drive, Wilmington, MA.

counter-timer boards and two available counting channels on the analog to digital converter. Separate screw terminal boards were required for each counter-timer board and the converter. This hardware setup enabled each of the five activities to be measured on 12 cows simultaneously with one computer.

Collection protocols were carried out with a commercially available data acquisition software program (Table 2; Appendix Table 2). The menu-driven program provided flexibility, with easy adjustment of channels monitored, sampling rate, channel triggering, and data processing. Real-time graphical displays permitted efficient acquisition and algorithm debugging. All acquisition boards were compatible with the software and were controlled automatically once defined in a collection protocol.

To collect information for five activities from 12 cows, 145 channels were required: 1 time channel, 12 counter channels, 48 analog input channels, and 84 calculation channels. Channels were sampled at various rates depending on the activity and algorithm; however, channels written to files all were sampled at .2 Hz. One file was written for each cow monitored with all five activities contained in each file. An example of a file produced from an acquisition run for 1 cow is presented in Figure 3. Water values are total pulses since commencement of the run, load and pH values are their respective measurements at the listed time, and chews and contractions are their total within the previous 5-s interval. During collection, files were written directly to the computer's internal hard disk. The 88-Mbyte removable hard disk has adequate capacity for 14 d of continuous collection for 12 cows.

Data Interpretation. Completed data files were interpreted using data management procedures of SAS (1985) on a microcomputer (Appendix Table 4). Objectives of interpretation were to designate time as eating, ruminating, drinking, or idle and determine chews, feed consumption, water consumption, pH changes, and contractions during each period. Activities were determined with a precision of 30 s. Time definitions shorter than

"Cow 1, Expt. 91RD001"
"Feeding Behavior Validation"
"The time is 12:00:01.50"
"The date is 1-28-1991"

"Time"	"Water"	"Load"	"Chews"	"Contr."	"pH"
"sec"	".01L"	"kg"	"chews"	"counts"	"units"
5	0	24.8	6	0	6.73
10	0	24.8	4	0	6.73
15	0	24.8	5	0	6.73
20	0	25.0	1	1	6.73
25	0	24.9	4	1	6.73
30	0	24.8	5	1	6.71
35	0	24.8	7	0	6.72
40	0	24.7	6	0	6.73
45	0	24.7	7	0	6.73
50	0	24.8	5	0	6.73
55	0	24.8	1	0	6.75
60	0	25.0	2	1	6.74
65	0	24.8	5	2	6.74
•	•	•	•	•	•
•	•	•	•	•	•
•	•	•	•	•	•

Figure 3. File output of feeding behavior data from Labtech® Notebook in ASCII format.

30 s led to inconclusive evidence for the presence or absence of certain chewing activities, especially when cows changed from one activity to another slowly or erratically.

Jaw movements met three criteria to be considered as chews. No drinking could have occurred during periods of jaw movement, chewing rate must have equaled or exceeded .45 chews/s over a 180-s period, and chewing rate also must have exceeded .3 chews/s over a 30-s interval. The first chewing rate threshold permitted accurate differentiation between active chewing and idle jaw movement; the second threshold defined more accurate time borders between events. Any jaw movement not meeting requirements was considered idle activity. Frequent disturbances of the feed manger by the cow were used to differentiate ruminating and eating chews. If the standard deviation of manger weights over a 110-s range exceeded .45 kg, chews for that particular 5-s were denoted as eating chews, otherwise they were considered ruminating chews. Additional robustness was gained by comparing eating and ruminating chew totals over longer periods of time and minimizing inconsistent chewing patterns. Stable feed manger weights, averaged over 110 s that occurred in the absence of chewing, were used to determine meal size. Beginning and ending pH for each bout of activity were the average of 24 measurements recorded over 2 min. Drinking periods occurred when water flow was indicated.

Determination of the minimum interbout interval for eating, ruminating, and drinking activity was performed using procedures of Metz (1975). A minimum interbout interval is the minimum time interval between two of the same activities required to consider these two periods as separate events. For each type of activity, the frequency of all inactive intervals was determined. The smallest interval was .5 min, and the largest exceeded 300 min. Frequency was plotted as percentages of all intervals cumulatively and backwards on a log scale to produce survivorship curves (Metz, 1975) (Figures 4 and 5). Deviations from linearity indicated that probabilities of beginning new periods of activity were not random. Plateaus of the line occurred when a shortage of intervals existed and

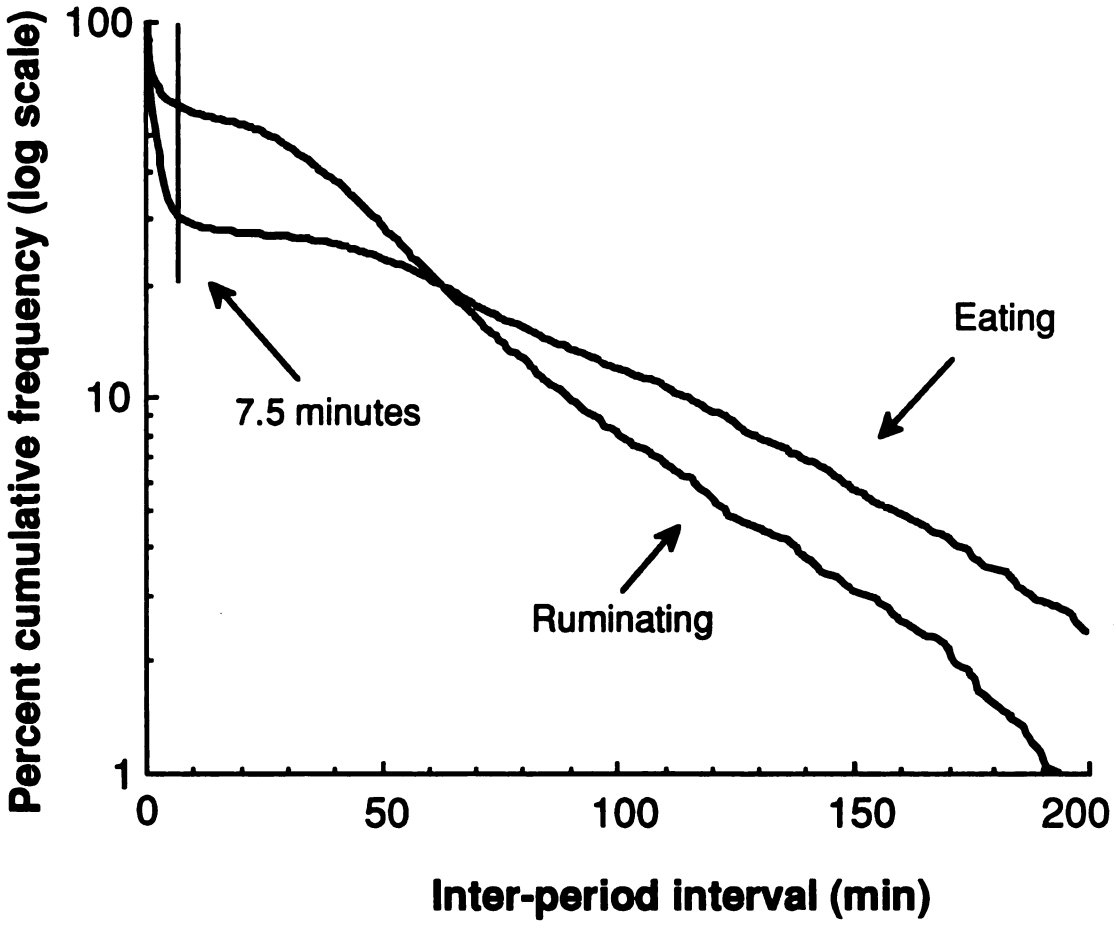


Figure 4. Frequency of inter-period intervals for eating and ruminating activity of twelve cows measured for twelve days. Data are expressed as survivorship curves with percent frequency determined cumulatively and backwards (Metz, 1975). The chosen minimum inter-bout interval of 7.5 minutes is indicated.

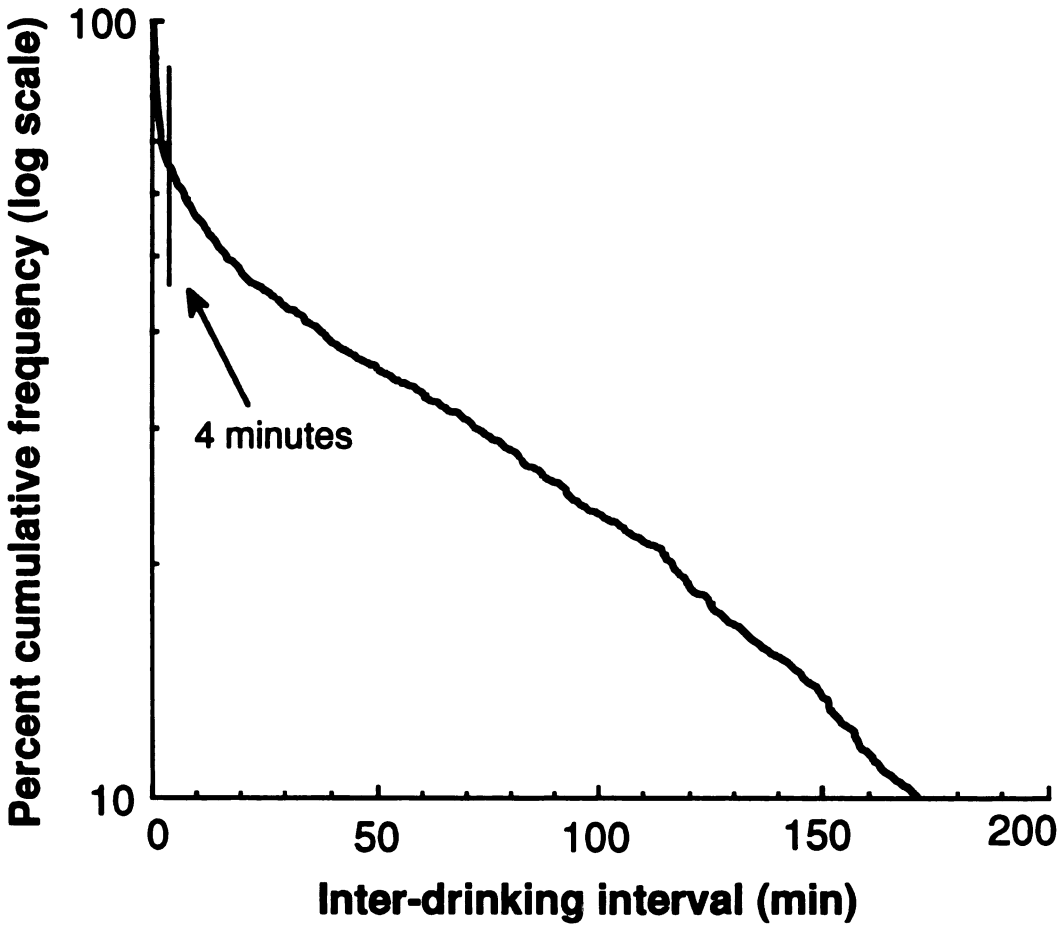


Figure 5. Frequency of inter-drinking intervals of twelve cows measured for twelve days. Data are expressed as a survivorship curve with percent frequency determined cumulatively and backwards (Metz, 1975). The chosen minimum inter-bout interval of 4 minutes is indicated.

provided a point of demarcation between those intervals that were likely to occur within the same bout of activity and those that were breaks between different bouts. Based on curves generated from data gathered on 12 lactating cows measured over 12 d, minimum interbout intervals of 7.5 min were chosen for both eating and ruminating activity (Figure 4) and 4.0 min for drinking activity (Figure 5). These criteria were included in the interpretation algorithms to aid in differentiating bouts.

Output generated after data interpretation are presented in Table 3 for one animal monitored for 1 d. Bout start and stop times are expressed as fractions of a day to aid in comparison of activities across days. Actual activity times for each bout are the sum of all 30-s intervals of the same activity within the bout. Because of presence of small breaks within activity bouts, actual time spent performing a particular activity could be equal to or less than the overall time difference between the start and stop time of a given bout. Overall and actual activity durations have been used in another study (Wangsness et al., 1976). All calculated rates involving time were determined using actual activity times. Rumination bouts less than 5 min were deleted as well as eating bouts when less than .05 kg of feed was consumed. Idle bouts were periods of time where eating, ruminating, or drinking were not occurring. Output was saved as permanent SAS data sets for subsequent statistical analysis. Run-time on the microcomputer (IBM PS/2 Model P70 386-20 MHz; International Business Machines Corporation, Armonk, NY) for data interpretation was 15 min for each cow and day combination.

Validation

Two validation studies were performed to determine the operational performance of monitoring equipment and interpretation algorithms. Feed intake, water intake, and chewing activity of 10 lactating dairy cows (4 primiparous) were measured both manually and automatically for 3 d in the first study. Cows averaged 79 DIM (SD = 11) and produced 34.4 ± 5.9 kg/d of milk. Cows were monitored electronically and adjusted to equipment and diet for 16 d prior to manual data collection. Diets were mixed once daily

Table 3. Output from the feeding behavior data interpretation program generated for eating, ruminating, and drinking bouts for one cow measured for 1 d.

Bout no.	Start	Stop	Time since last	Activity time	Feed intake	Water intake	Chews	Chew rate	pH Start	pH Stop	1 Cont
(no.)	---(d)[2]---		---(min)---		(kg)	(L)	(no.)	(no. /min)			(no. /min)
Eating bouts											
1	.017	.030	...	13.0	.36	...	768	59.1	6.72	6.76	1.77
2	.097	.135	97.5	46.0	3.94	...	3294	71.6	6.91	6.61	1.84
3	.173	.211	54.5	48.0	5.17	...	3400	70.8	6.67	6.54	1.93
4	.330	.364	171.5	44.0	3.45	...	3266	74.2	6.88	6.69	1.79
5	.472	.485	156.5	14.5	1.22	...	972	67.0	6.97	6.84	1.73
6	.520	.541	50.0	30.5	2.04	...	2209	72.4	6.75	6.70	1.71
7	.691	.712	215.5	29.5	1.90	...	2198	74.5	7.22	6.92	1.77
8	.788	.824	109.5	41.5	3.72	...	3059	73.7	7.01	6.74	1.75
9	.832	.839	11.0	9.5	.82	...	669	70.4	6.81	6.72	1.89
10	.907	.919	98.5	15.5	1.41	...	1127	72.7	6.96	6.78	1.83
11	.932	.956	17.5	31.0	2.81	...	2207	71.2	6.90	6.61	1.77
12	.970	.983	19.5	15.0	1.13	...	1011	67.4	6.58	6.58	1.78
Ruminating bouts											
1	.013	.017	...	7.0	...	...	414	59.1	6.75	6.72	1.57
2	.035	.050	26.0	20.0	...	...	923	46.2	6.73	6.87	1.67
3	.059	.070	13.5	15.0	...	...	674	44.9	6.89	6.89	1.73
4	.085	.097	22.5	17.0	...	...	819	48.2	6.89	6.91	1.71
5	.147	.165	72.0	25.0	...	...	1176	47.0	6.76	6.89	1.49
6	.222	.237	81.5	22.0	...	...	1137	51.7	6.63	6.82	1.55
7	.247	.269	14.0	31.5	...	...	1532	48.6	6.78	6.83	1.69
8	.316	.330	68.0	20.0	...	...	1355	67.8	6.77	6.88	1.50
9	.378	.407	69.5	41.0	...	...	2567	62.6	6.80	6.78	1.42
10	.424	.446	25.0	31.0	...	...	2069	66.7	6.80	6.77	1.32
11	.466	.472	29.0	9.0	...	...	496	55.1	6.77	6.97	1.56
12	.551	.579	113.5	38.5	...	...	2108	54.8	6.71	6.54	1.58
13	.590	.605	15.0	21.0	...	...	1028	49.0	6.71	7.00	1.51
14	.636	.652	45.0	16.5	...	...	857	51.9	7.03	7.09	1.70
15	.671	.691	27.0	24.5	...	...	1314	53.6	7.17	7.22	1.58
16	.724	.744	47.0	28.5	...	...	1691	59.3	6.83	6.85	1.73
17	.758	.767	20.0	7.5	...	...	323	43.1	6.88	6.99	1.52
18	.852	.880	122.0	35.0	...	...	1676	47.9	6.71	6.81	1.63
19	.893	.906	19.5	18.5	...	...	1109	59.9	6.79	6.76	1.46

Table 3. (cont.)

Bout no.	Start	Stop	Time since last	Activity time	Feed intake	Water intake	Chews	Chew rate	pH		1 Cont
									Start	Stop	
(no.)	----(d)[2]----		----(min)----		(kg)	(L)	(no.)	(no. /min)			(no. /min)
Drinking bouts											
1	.026	.026	...	.50	...	2.16	...	...	...	...	...
2	.123	.125	139.5	1.33	...	6.09	...	...	...	...	...
3	.132	.133	10.0	.42	...	2.19	...	...	...	...	...
4	.192	.194	86.0	.83	...	3.33	...	...	...	...	...
5	.208	.208	19.0	.67	...	3.29	...	...	...	...	...
6	.346	.347	198.0	.75	...	3.33	...	...	...	...	...
7	.364	.365	24.5	.50	...	2.19	...	...	...	...	...
8	.508	.509	206.5	.25	...	1.14	...	...	...	...	...
9	.541	.543	47.0	1.17	...	5.33	...	...	...	...	...
10	.712	.714	244.0	1.42	...	5.52	...	...	...	...	...
11	.811	.817	140.5	1.17	...	5.11	...	...	...	...	...
12	.840	.841	33.5	.17	...	.83	...	...	...	...	...
13	.914	.916	106.0	1.08	...	4.35	...	...	...	...	...
14	.951	.952	51.0	.50	...	2.12	...	...	...	...	...
15	.983	.983	45.0	.17	...	.46	...	...	...	...	...

[1]Cont = Contractions.

[2]Time expressed as fraction of a day.

and offered for ad libitum intake as a TMR twice daily when cows were away from stalls for parlor milking. Ration ingredients included alfalfa silage (20% CP, 40% NDF; DM basis), corn silage (6% CP, 40% NDF), high moisture shelled corn (9% CP, 9% NDF), soybean meal (55% CP, 15% NDF), a commercial protein pellet (65% CP, 4% NDF), and necessary minerals and vitamins to provide a ration with 17% CP, 31% NDF, .8% Ca, and .5% P. Manual observations of chewing activity were recorded once every 5 min for the 3-d period. Hourly and daily summaries of chewing times and bouts determined from manual observation were compared with acquisition system values for each cow. Feed and water intakes were determined manually twice daily and compared to system totals.

A second study was conducted with 10 ruminally cannulated cows to evaluate performance of automatic reticular motility and rumen pH measurements. Cows were monitored during early lactation and received a mixed ration (25 or 35% NDF; 18% CP) with the same ingredients as those of the first study. Motility and pH monitors were placed in the reticulorumen at various times during 1 wk, and computer measurements were made at .2 Hz as previously described. Reticular contractions were determined manually by visual observation of analog signals produced by each motility monitor on the graphic display of the acquisition program. Rumen liquor samples were obtained from the same location in the ventral sac as the in vivo electrode using a covered beaker and immediately measured for pH with another electrode exterior to the cow. Computer estimates and manual estimates were compared for both 30-min contraction totals and pH readings for each cow.

For both validation studies, computer and manually derived variable means were tested for equality using paired *t* tests (Snedecor and Cochran, 1980). Statistical procedures similar to those used by Beauchemin et al. (1989) were employed to examine further the relationships between the two methods of observing cow activity and to partition sources of variation among these methods.

RESULTS AND DISCUSSION

Cow adjustment to the monitoring equipment and collection stalls was minimal because of little change in variable means across time during the adaptation period. Feed removed by cows from the suspended manger but not consumed was less than .10 kg/d per cow. Equipment malfunctions were limited to short circuits in connectors for chewing, motility, and pH monitors, ruptured chewing and motility tubes, and drifts in pH calibration. Improvements have been implemented to alleviate most of these problems. Currently, greater than 90% of all attempted measurements are obtained successfully.

Daily means of intake and chewing activity for cows on the first validation study are presented in Table 4. Based on the definition of chewing bouts described earlier, mean numbers of eating and ruminating bouts were 10.6 and 14.4 /d, respectively, which are similar to other data reported for cattle (Metz, 1975; Deswysen et al., 1987a).

Table 4. Intake and chewing activity of 10 cows measured for 3 d using computer acquisition and manual observation.[1]

	Computer		Manual		Difference	
	Mean	SE	Mean	SE	Mean	SE
DMI, kg	23.5	.7	23.7	.7	-.2**	.1
Water intake, L	83.0	2.8	83.0	2.8	0	.1
Eating bouts, no.	10.6	.4	11.0	.4	-.4*	.2
Eating time, min	306	12	315	12	-9*	4
Eating chews, no.	19456	834	...	...	...	...
Ruminating bouts,[2] no.	14.4	.4	14.3	.4	.1	.2
Ruminating time,[2] min	495	9	491	9	4	4
Ruminating chews,[2] no.	31874	786	...	...	...	...
Total chewing time,[2] min	801	14	806	15	-5	6
Idle chews, no.	2729	108	...	...	...	...

[1]Data expressed as daily means of 26 observations.

[2]Does not include rumination (mean = 33 min/d) observed during milking.

*$P < .05$.

**$P < .01$.

The chosen minimum interbout interval for chewing activity of 7.5 min appears adequate for differentiating bouts and is in agreement with the 7-min criterion described by Dulphy (1971). A mean of 54,059 total chews/d were measured of which 36% were denoted as eating chews, 59% as ruminating chews, and 5% as idle chews (nonchewing jaw movements). Because cows were away from monitoring equipment about 2 h/d for milking, an average of 33 min/d of rumination (6% of all rumination), as determined by manual observation, was not recorded by the acquisition system. Stall milking has since been implemented to allow collection of all data.

No differences ($P > .25$) in means between measurements obtained with the acquisition system and manual observation occurred for daily water intake, ruminating bouts, ruminating time, and total chewing time (Table 4). Dry matter intake measured manually was .2 kg (.9% of total intake) greater ($P < .01$) than that recorded automatically due to omission of meals less than .05 kg in size for computer data. Eating bouts and eating time per day also were greater for manual measurement for similar reasons. In addition, differentiation of eating bouts for manual observations was performed with a minimum interbout interval of 5 min, compared with the 7.5-min interval used for electronic observations. Consequently, more bouts were likely to be identified with the manual method. Magnitudes of these differences were small, suggesting good performance of the acquisition equipment and interpretive algorithms.

Relative agreement between automatic and manual methods of measuring cow activity was estimated as the root mean square error (RMSE) (Beauchemin et al., 1989). This estimate of total error was further decomposed into error associated with mean bias (Table 4), regression, and random error (Table 5). Slopes between the two methods of collection indicated the direction of regression error. Hourly totals of chewing activity were correlated highly between the two methods ($r \geq .94$) with most error associated with random disturbance. Daily total RMSE as a percentage of the mean was lowest for DM and water intake (< 2.5%) and highest for eating and ruminating bouts. Eating and

Table 5. Relationship of intake and chewing activity of 10 cows measured with computer acquisition and interpretation (independent data) and manual observation (dependent data).

	RMSE[1]	Regression error	Random[2] error	Slope	r
Hourly totals					
Eating time, min	3.78	.41	3.75	1.00	.97
Ruminating time, min	3.46	.02	3.35	.97**	.97
Total chewing time, min	4.67	.36	4.50	.97	.94
Daily totals					
DMI, kg	.57	.09	.39	.99	1.00
Water intake, L	.52	.16	.49	1.01	1.00
Eating bouts, no.	.94	.26	.80	.87	.91
Eating time, min	20.3	2.45	18.2	.96	.95
Ruminating bouts, no.	.98	.25	.94	.88	.88
Ruminating time, min	21.7	6.91	20.2	.85	.89
Total chewing time, min	28.5	2.04	28.0	.97	.93

[1]RMSE = Root mean square error.

[2]Random error = Discrepancy between two procedures not associated with mean bias or regression.

**Slope significantly different from unity ($P < .01$).

ruminating time RMSE were 20.3 and 21.7 min/d, respectively. Most error was due to random error (> 68%) for all variables; however, the slope for hourly ruminating time differed significantly ($P < .01$) from unity. Correlations for daily totals were high. Lowest correlations were obtained for ruminating bouts (r = .88) and ruminating time (r = .89). Manual observations indicated the presence of several sporadic rumination bouts of short duration nested within eating bouts. From scanning of raw computer collection data, it was noted that some activities that were determined manually were incorrect. For example, eating was noted manually at times when no activity at the feed manger was detected electronically, as well as ruminating recorded during periods of feed disappearance. This suggests that trained observers may err in differentiating eating from ruminating. Less agreement between manual and automatic observations for rumination events may have occurred because of incorrect manual observations or the inability of the algorithms to handle rapid fluctuations in cow behavior.

Feed and water intake measurements by the acquisition system were most accurate among all activities measured in the first study. Chewing interpretation was more difficult because of variable chewing and feeding patterns among cows and the presence of jaw movements that were not chewing. Other workers that have developed chewing interpretation algorithms have differentiated eating and ruminating chews based on rates of chewing (slower and less variable for rumination), duration of chewing, and presence of pauses during rumination due to bolus swallowing and regurgitation (Penning et al., 1984; Luginbuhl et al., 1987; Beauchemin et al., 1989). In the present study, chewing rates for cows in early lactation were nearly identical for both eating and ruminating (61.6 and 62.9 chews/s, respectively). In addition, 1 of the 10 cows continued to have jaw movement during rumination bolus swallowing and regurgitation, consequently limiting the usefulness of this characteristic for distinguishing chew types. Use of feed disappearance to make this distinction was a viable alternative. Separating idle jaw movements has been performed using various criteria with most based on inadequate event numbers per unit

time (Penning et al., 1984; Beauchemin et al., 1989). Similar criteria were useful in this study. Regardless of algorithm specifics, the greatest challenge in algorithm development for any cow activity is establishing a compromise between robustness necessary to interpret varied behavior patterns and event accuracy. When activities change rapidly, it is difficult to achieve both correct activity identification and exact event time borders. Inevitably, accuracy is sacrificed as more diverse behavior is interpreted with the same algorithm. Requirements of individual experiments should dictate the relative position of this compromise.

Comparisons between computer- and manually derived measurements for reticular motility were made using 88 observations from the second validation study (Figure 6). Monitors successfully remained in the reticulum regardless of animal position or movement. Number of contractions in each 30-min period ranged from 22 to 58. Total error between measurement methods was 1.6 contractions/30 min with most (80%) due to random error. Mean contraction counts for computer (38.8) and manual (39.3) observations were significantly different ($P < .01$) due to missed computer counting of small peaks from lying cows. This error, however, was small and occurred infrequently. Correlation between methods was greater than .98. Previous studies of rumen motility have relied typically on manual interpretation of strip-chart recordings (Okine et al., 1989). Automation of collection and interpretation of these data could greatly expand the scope and duration of motility studies.

Each pH electrode remained in the ventral rumen for the duration of the second study. A total of 40 observations were compared between in vivo computer measured and in vitro manual measured pH (Figure 7). Total error between methods was .17 units of pH with 41% due to mean bias and 54% due to random disturbance. Correlation between methods was .85. In vivo measurements averaged 6.17 and in vitro averaged 6.28 pH units for a significant ($P < .01$) difference of .11 units. Other workers also have shown lower values for in vivo pH compared to in vitro, with a mean difference of .17 units of

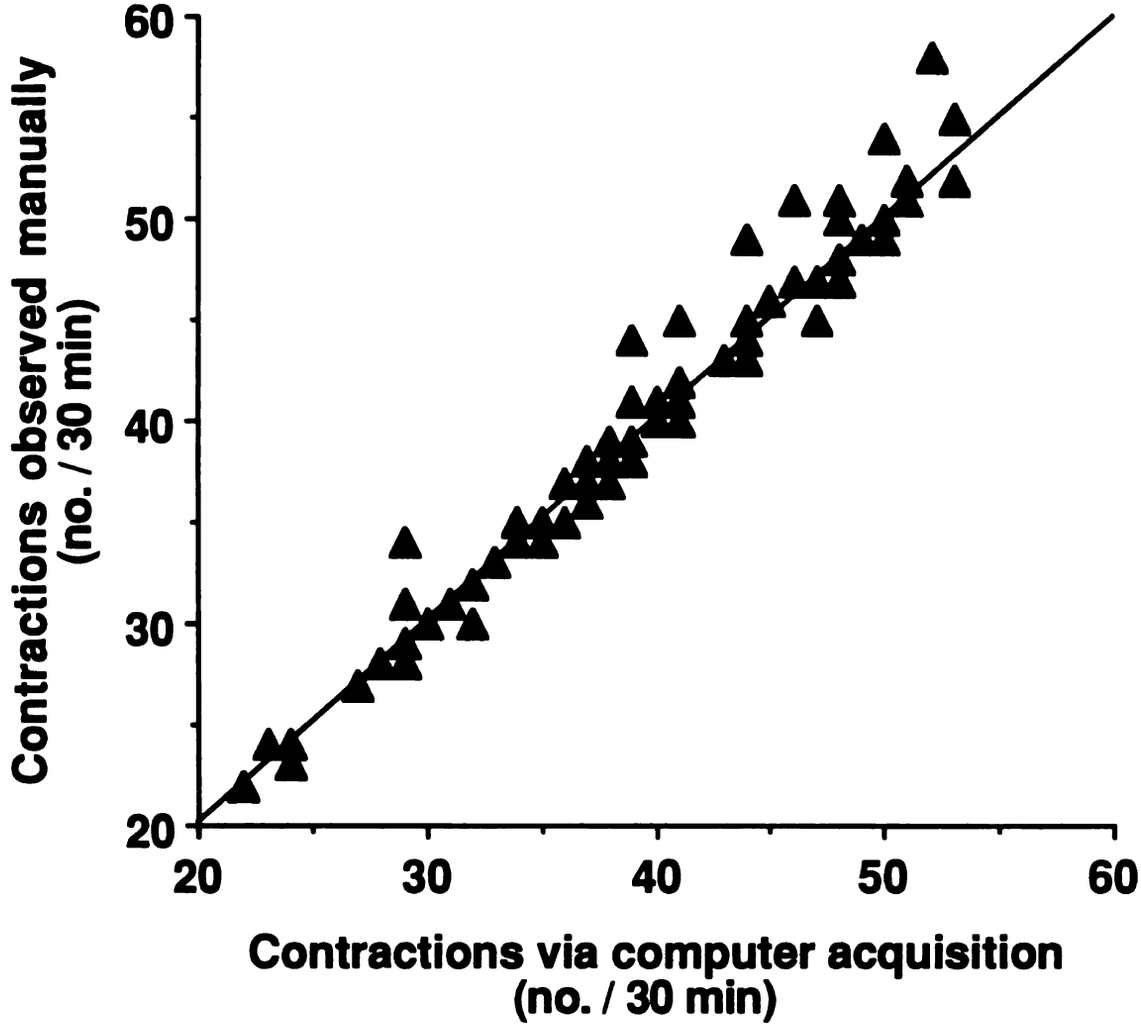


Figure 6. Relationship between reticular contractions determined by manual observation of signal waveform and computer algorithm interpretation for 88 observations. Data are expressed as total number of contractions within a 30-min period. The line represents perfect correlation.

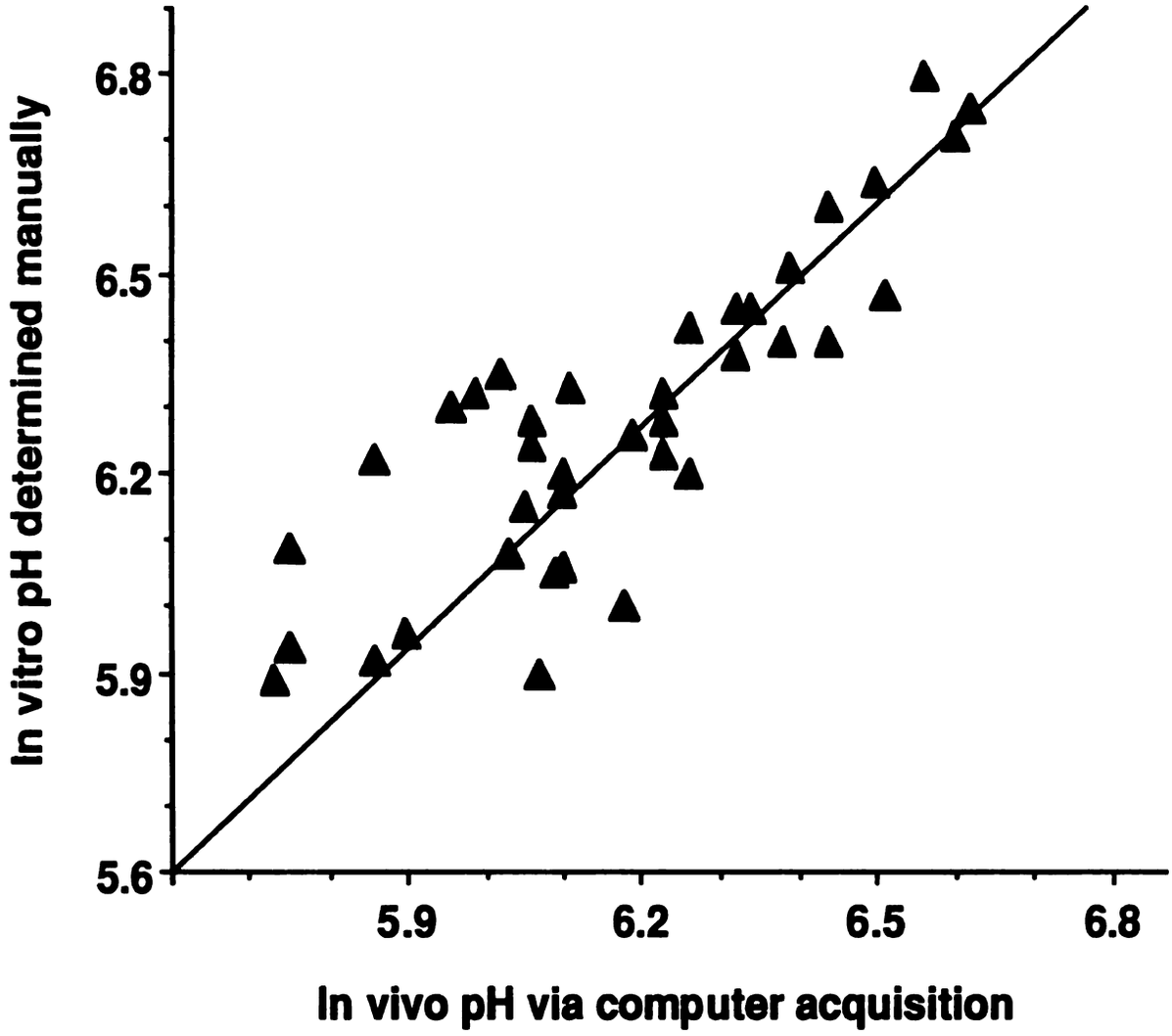


Figure 7. Relationship between ruminal pH determined in vitro by manual sampling and in vivo by computer acquisition for 40 observations. The line represents perfect correlation.

pH (McArthur and Miltmore, 1980; Smith, 1941). Smith (1941) suggested that rapid loss of CO_2 from in vitro samples may have caused their elevated pH. Additional work is needed to determine the consequences of this disparity between in vivo and in vitro pH on interpretation of past and future rumen pH studies.

CONCLUSIONS

A computer data acquisition system has been developed successfully to automatically and continuously monitor feeding behavior and rumen function of 12 cows in stalls. The system permits measurement of many events simultaneously for long periods, is fast and very flexible, and does not require extensive training in electronics or computer programming to construct or operate. Computer interpretation of collected data provides additional automation and is essential for studies involving many cow observations.

High correlations ($r \geq .85$) between computer interpreted and manually determined variables suggest that the system and interpretive algorithms were successful in accurately measuring animal behavior. Some accuracy in event interpretation was lost because of attempts to achieve greater robustness. Such sacrifice is necessary, however, regardless of the algorithm chosen in order to measure more diverse cows and to expand the population of inference. With continuous measurement of many animal feeding variables, a more complete understanding of dietary effects on digestive efficiency and cow performance is possible.

CHAPTER 3

Variation In and Relationships Among Feeding, Chewing, and Drinking Variables for Lactating Dairy Cows

ABSTRACT

Twelve Holstein cows (63 DIM; 6 primiparous) were offered a common diet and monitored for 21 d (11 d adaptation, 10 d collection) with a data acquisition system to measure continuously feed and water intakes and chewing behavior. Objectives were to examine relationships among feeding behavior variables for non-competing cows producing various quantities of milk and to determine experimental designs with adequate power to detect reasonable treatment differences in future experiments. Coefficients of variation across cows ranged from 5 to 41% for the variables studied. Milk production was correlated positively with DM and water intakes within and across parities. For multiparous cows, production was related positively to meal size (r = .78) and length of eating bouts (r = .75), and unrelated to meal number and eating rate. For primiparous cows, production tended to be related positively to meal number (r = .55) and eating rate (r = .87), and unrelated to meal size. Ruminating and total time spent chewing per unit of DMI were correlated negatively (r = -.58) with milk production both within and across parities. These correlations suggest that differences exist between cows for chewing efficiency. Reasons why high producing cows consume and chew more effectively deserves further study. Contrast differences of 10% of means for variables examined had an 80% probability of detection with a Latin square design utilizing 12 cows monitored for 5 d.

INTRODUCTION

Feed and water intakes by dairy cattle are related significantly to milk production (Freeman, 1975; Holter and Urban, 1992). Increases in intake are associated positively with both phenotypic and genotypic increases in milk production (Freeman, 1975). Intake is defined as mass consumed per unit of time, with time commonly measured in days. Shorter units of time, however, may be appropriate if they describe relationships that cannot be detected with once daily measurements.

A complete understanding of daily intake requires that its individual components be studied. Daily feed intake can be described in terms of number of meals consumed per day, the length of meals, and the rate of eating that occurs during meals. For daily intake to increase, one or more of these three variables must increase. Feeding commences when cows are in a state of hunger and stops when they are satiated. Therefore, daily intake is the sum of several meals that are controlled individually by hunger and satiety mechanisms (Savory, 1979). Within-day measures of feeding, ruminating, and drinking behavior provide a mechanism to examine these components that contribute to daily intake.

Measurement of feeding and chewing activity has become common in nutrition studies and has been reviewed by others (Beauchemin, 1991b; Campling and Morgan, 1981; DeBoever et al., 1990). Unfortunately, little is known about sources of variation in feeding behavior studies and the likelihood of detecting true differences between sample means. Estimation of sample sizes required for effective studies would be useful. Only a few studies have examined variation in feeding behavior among animals. Heifers (Deswysen et al., 1987b), dry cows (Harb and Campling, 1985), and lactating cows (Vasilatos and Wangsness, 1980) have been studied; however, limited information is available for high producing lactating cows. Identifying how high producing cows differ in behavior compared with low producing cows is also of significant value. Such information may help describe the mechanism involved with high intake and production.

Objectives of this experiment were to obtain feeding, chewing, and drinking behavior information from lactating cows varying in milk production to examine relationships among feeding variables across cows. A second objective was to estimate the number of cows required to detect differences between potential treatments using various experimental designs.

MATERIALS AND METHODS

Cow Trial

Six multiparous and 6 primiparous lactating Holstein cows averaging 63 DIM (SD = 11) were housed in stalls designed for continuous collection of feeding activity. The study was conducted in January under continuous lighting in a white-colored tie-stall barn with no windows. Cows with similar DIM were selected to obtain a large range in milk production and intake. All cows received a common diet of 29% alfalfa silage (DM basis), 29% corn silage, and concentrate for a total ration composition of 51% DM, 17% CP, 31% NDF, .8% Ca, and .5% P. The ration was mixed once daily and offered for ad libitum intake as a TMR at 0300 and 1500 h when cows were parlor-milked. Cows averaged 2 h/d away from feed and monitoring equipment during milking. Cow BW was determined for 3 consecutive d immediately prior to and following behavior measurements. Feed amounts offered and refused were recorded daily for use in comparison to computer-collected data. Samples of feed and individual orts were collected daily and composited weekly. Samples were dried in a forced-air oven at 55°C, ground with a Wiley mill (1-mm screen; Arthur H. Thomas, Philadelphia, PA), and analyzed for NDF (Goering and Van Soest, 1970) modified by addition of 4 ml of a 2% α-amylase solution (Sigma A-3051, Sigma Chemical Co., St. Louis, MO) to each sample, substitution of triethylene glycol for 2-ethoxyethanol, and omission of decahydronaphthalene and sodium sulfite. Values for NDF were expressed as a percentage of DM determined from forced-air oven drying at 105°C.

Feed intake, water intake, and chewing activity were measured continuously and simultaneously for all cows with a data acquisition system (Chapter 2). Measurements were made for 21 d with the last 10 d used for statistical comparisons. Behavior was summarized for each cow-day combination according to eating, drinking, and ruminating bouts. Minimum inter-bout intervals (**MIBI**) that define the occurrence of two separate bouts of similar activity were used as described in Chapter 2. A minimum of 7.5 min between events was required to define two eating periods or two ruminating periods as separate bouts. For drinking, 4 min was required to define two periods as separate bouts. A new meal was noted if feed disappearance ≥ .05 kg, time elapsed since the previous meal was ≥ 7.5 min, and chewing rate criteria were met. Variables for each bout included start and stop times, duration, number of chews (for eating and ruminating), meal size (for eating), drink size (for drinking), and ratios of these variables. Meal size was expressed in units of DM and NDF. Calculations were required to account for changes in feed moisture and NDF concentration during the day because of cow drooling and selectivity. Because orts samples were not obtained after every meal, estimates of amounts of DM and NDF in feed remaining after a meal were made by assuming linear changes in nutrient mass between the beginning and end of the day for each unit of intake. Computer data were screened and compared with manual data to eliminate errors that were due to equipment malfunction, cow interference, and human error. If data were incomplete for any time during a day, data for that cow-day were omitted from analysis. From the 10-d collection period, 7.3 ± 2.6 d/cow and 8.2 ± 2.4 d/cow contained acceptable data for chewing and drinking activities, respectively.

Statistical Analysis

Feeding activity was summarized for each cow-day combination to obtain either daily means or totals of bout variables. Descriptive statistics were determined for all daily variables; differences in means between parity groups were evaluated for significance using analysis of variance. Pearson product-moment correlation coefficients were

calculated among individual bout variables using procedures of SAS (1985). Variables of interest included bout duration, number of chews per bout, meal or drink size, and interbout intervals. These intervals were the periods of time between the current bout and the bout of similar activity immediately prior to or following the current bout, whether or not the interval contained bouts of different activities. Correlation coefficients were determined for variables summarized by cow to examine relationships across cows differing in production.

To examine potential sources of variation among feeding variables, variance components were estimated from mean square estimates for each behavior variable using the general linear models procedure of SAS (1985). Three linear models were examined:

$$Y_{jk} = \mu + C_j + D_{k(j)} \quad [1]$$

$$Y_{ijk} = \mu + P_i + C_{j(i)} + D_{k(j)} \quad [2]$$

$$Y_{jk} = \mu + \beta_1 x_{1jk} + C_j + D_{k(j)} \quad [3]$$

where Y was the variable of interest, assumed normally distributed with mean μ and variance σ^2, C_j = the random effect of cow (j = 1 to 12), $D_{k(j)}$ = the random effect of day nested within cow (k = 1 to 10), P_i = the fixed effect of parity (i = 1, primiparous to 2, multiparous), $C_{j(i)}$ the random effect of cow nested within parity, and β_1 = the slope of regression on a defined covariate (x_{1jk}). For each dependent variable, the covariate was the mean of the same variable over the 5-d period immediately prior to the 10-d collection period. Cows were denoted as experimental units, and effect of cow served as experimental error and effect of day as sampling error.

The minimum number of experimental units required to detect significant contrast differences between two potential treatments in future experiments was estimated for each variable for four different experimental designs using procedures of Gill (1978). Eighty percent probability (Type II error $\leq$ 20%) of detecting contrast differences of 10% of variable means with Type I error of 5% was desirable. Future experiments were assumed to have four treatments, but results should be similar if studies have three or five

treatments. Experiment sizes were determined for completely random, randomized complete block, covariate (adjustment for covariance), and Latin square crossover designs (Gill, 1978). A variable ϕ was iteratively calculated as $\phi = \sqrt{(c \cdot d / 4)(\Delta^2 / (\hat{\sigma}^2_{d/c} + d \cdot \hat{\sigma}^2_e))}$ and compared with sample size charts for the power of an *F* test (Gill, 1978), where c = suggested number of cows per treatment, d = suggested number of days in collection period, Δ = detectable contrast difference, $\hat{\sigma}^2_{d/c}$ = variance component estimate for day(cow), and $\hat{\sigma}^2_e$ = estimated experimental error. For example, the value of ϕ for milk production in a randomized design was 1.996 when c = 64, d = 5, Δ = 3.3 kg/d, $\hat{\sigma}^2_{d/c}$ = 2.58, and $\hat{\sigma}^2_e$ = 43.2. This value was sufficiently large to obtain Type II error less than 20%.

A different estimate for $\hat{\sigma}^2_e$ was used for each experimental design. For the random design, variance due to cow from model [1] was used for $\hat{\sigma}^2_e$. For the block design, in which parity was the nuisance factor, variance due to cow(parity) from model [2] was used. For the covariate design, variance due to cow|covariate from model [3] was the estimate for $\hat{\sigma}^2_e$. For the Latin square design, $\hat{\sigma}^2_e$ was assumed to be equal to zero, so only variance due to days was used. This represents the minimum error possible with Latin square designs and assumes no interaction among cows, periods, treatments, or squares.

RESULTS

A summary of daily milk production and feeding behavior variables is presented in Table 1 for primiparous, multiparous, and all cows combined. Milk production averaged 33.1 kg/d per cow. Mean milk fat and protein concentrations were 3.3 and 3.1%, respectively. Feed intake occurred during 11.0 eating bouts each day that lasted 28.8 min and averaged 2.2 kg of DM in size. Average daily DMI was 22.8 kg. Mean daily DMI does not equal the product of the mean number of eating bouts per day and meal size because all variables were determined on a daily basis before summary statistics were

Table 1. Summary statistics for milk production and feeding behavior of six primi- and six multiparous lactating Holstein cows measured for 10 d.[1]

	Primiparous		Multiparous		All cows	
Variable	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
Milk production,[a] kg/d	28.7	15.5	37.5	13.7	33.1	19.7
DMI,[a] kg/d	20.0	13.6	24.8	11.3	22.8	16.1
NDF intake,[a] kg/d	6.2	13.8	7.6	11.4	7.0	16.1
Meal size, kg						
DM	1.8	17.0	2.5	29.8	2.2	30.6
NDF	.56	17.3	.75	29.7	.67	30.5
Eating bouts, /d	11.3	17.3	10.8	25.4	11.0	22.1
Eating bout length, min	25.9	22.2	31.1	33.4	28.8	31.3
Eating time						
min/d	284	16.5	314	16.8	301	17.3
min/kg DM	15.9	23.7	13.6	14.1	14.6	21.0
min/kg NDF	51.1	22.4	44.3	14.4	47.2	20.1
Eating chews, /d	18,276	22.8	19,256	16.9	18,832	19.6
Eating chew rate, chews/min	62.7	7.4	60.8	8.7	61.6	8.3
Ruminating bouts, /d	15.4	17.5	12.9	13.3	14.0	17.8
Ruminating bout length,[a] min	29.7	15.9	36.0	19.9	33.3	20.9
Ruminating time						
min/d	453	18.3	460	14.8	457	16.3
min/kg DM	22.9	21.1	18.7	18.9	20.5	22.5
min/kg NDF	74.1	20.8	60.9	19.0	66.6	22.3
Ruminating chews, /d	29,645	21.5	28,946	17.6	29,248	19.3
Ruminating chew rate, chews/min	64.4	10.7	61.8	7.2	62.9	9.1
Total chewing time						
min/d	738	13.9	774	11.4	758	12.6
min/kg DM[a]	37.2	15.9	31.4	13.6	33.9	17.1
min/kg NDF[a]	120.7	15.6	102.0	13.8	110.1	17.0
Total chews, /d	47,921	19.1	48,201	14.3	48,080	16.4
Water intake,[a] L/d	63.2	19.5	89.5	15.0	77.6	23.8
Drinking bout size, L	5.4	33.2	7.2	43.8	6.4	43.1
Drinking bouts, /d	13.0	35.9	14.9	41.9	14.0	40.2
Drinking time, min/d	17.7	37.4	19.1	20.0	18.5	28.7
Drinking rate, L/min	3.9	31.0	4.6	11.0	4.3	22.4

[1]Statistics calculated from daily total or daily mean for each cow and day combination.
[a]Means differ between parities ($P < .05$).

calculated. The 12 h of greatest intake, compared to any other consecutive 12 h period, occurred between 1200 and 2400 h (59.2% of total DMI). Cows ruminated during 14.0 bouts/d lasting 33.3 min per bout. Rumination data do not include activity occurring when cows were away from stalls during milking.

Cows spent 301 min/d eating and 457 min/d ruminating. Distribution of chewing activity within a day is presented in Figure 1. Large meals were consumed after milking and allocation of fresh feed. When not eating, cows spent considerable time ruminating. Time spent chewing was distributed evenly throughout the day; 3 to 6% of chewing occurred within each hour of the day when not milking. Chewing rates during eating and ruminating were similar, averaging 61.6 and 62.9 chews/min, respectively (Table 1). Total time spent chewing was 758 min/d during which 48,080 chews occurred. Daily water consumption was 77.6 L/cow and required 18.5 min to drink. Cows averaged 14.0 drinking bouts/d of 6.4 L each. Parity means differed significantly ($P < .05$) for milk production, DMI, NDF intake, ruminating bout length, total time spent chewing per unit of DM and NDF, and water intake (Table 1). Coefficients of variation ranged from 8.3 to 43.1% (mean = 21.5%) across variables from combined parity data. Within parity CV tended to be slightly lower than for all data combined, although average CV across all variables were similar for both parities (primiparous = 19.9%; multiparous = 18.6%).

Meal size, eating bout length, and number of eating chews were correlated ($r \geq .90$) among individual eating bouts (Table 2). Ruminating bout length and number of chews ($r = .97$) and drinking bout length and water intake ($r = .85$) also were highly correlated when summarized by their respective bouts. Eating and drinking activities were correlated significantly with their respective pre- and post-interdrinking intervals, however, ruminating activities were not highly related to pre- and post-rumination intervals. Pre- and post-interbout intervals were not related for any activity.

Means averaged across the 10 d of measurement for each of the 12 cows were used to determine relationships among feeding behavior variables summarized by cow

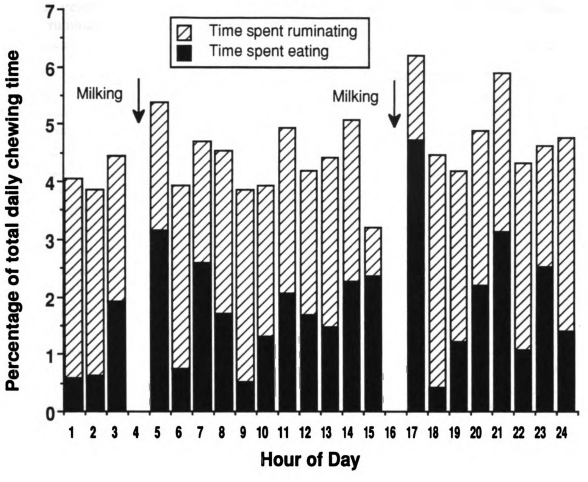


Figure 1. Distribution of chewing time within a day expressed as the mean of 12 cow means. Feed was offered when cows were away from stalls for milking.

Table 2. Pearson correlation coefficients among feeding behavior variables for individual eating, ruminating and drinking bouts.[1]

Variable	Variable number									
	1	2	3	4	6	7	8	10	11	12
1 Meal size, kg of DM										
2 Eating bout length, min	.91									
3 Eating chews, /bout	.90	.98								
4 Pre-intermeal interval,[2] min	.38	.38	.36							
5 Post-intermeal interval,[3] min	.14	.15	.14	.03						
6 Ruminating bout length, min										
7 Ruminating chews, /bout					.97					
8 Pre-interrumination interval,[2] min					.12	.10				
9 Post-interrumination interval,[3] min					.05	.06	.005			
10 Drinking bout size, L										
11 Drinking bout length, min								.85		
12 Pre-interdrinking interval,[2] min								.48	.41	
13 Post-interdrinking interval,[3] min								.34	.31	.03

[1]Total number of bouts: eating, 969; ruminating, 1232; and drinking, 1385. Significant correlation ($P < .01$) for $r > .07$.

[2]The time interval between the beginning of a bout and the end of its preceding bout.

[3]The time interval between the end of a bout and the beginning of its succeeding bout.

(Table 3). Milk production, BW, daily DMI, and daily water intake were highly correlated with one another ($r \geq .89$, 95% confidence interval: $.65 \leq r \leq .97$) and were correlated to other variables in a similar manner. Production was correlated positively with meal size and ruminating bout length; negatively with eating, ruminating, and total time spent chewing per unit of DM consumed; and uncorrelated ($r < .10$) with daily number of eating bouts. As length of eating bouts increased, meal sizes tended to increase ($r = .72$), and number of bouts per day decreased ($r = -.72$). Similarly, as ruminating bout lengths increased, the number of ruminating bouts per day decreased ($r = -.80$). Consequently, daily eating and ruminating durations were not related significantly to meal size, daily intake, or milk production, although their sum, total chewing duration, was related positively to intake and production. Drinking bout size and number of drinking bouts were not related to daily water consumption but were correlated negatively to each other ($r = -.80$).

Correlations within parity were calculated to examine relationships among milk production and eating variables unconfounded by the effect of parity (Table 4). Relationships among milk production, BW, DMI, and water intake were similar to combined data correlations. For primiparous cows, production was not related to meal size but was related negatively ($r = -.78$) to length of eating bouts and time spent eating per unit of DMI. For multiparous cows, production was related positively to meal size ($r = .78$) and length of eating bouts ($r = .75$) but unrelated to time spent eating per unit of DMI. Relationships within parity among other variables (e.g., rumination, data not shown) were similar to relationships described for combined data (Table 3).

Sources of variation in feeding variables are presented as variance component estimates in Table 5. Variation across cows without considering parity was greater than variation across days for 19 of the 28 variables. Including effect of parity in the model decreased variance due to cow for 19 variables; however, effect of cow(parity) was still significantly greater than zero. The other 9 variables had increased variance due to

Table 3. Pearson correlation coefficients among feeding behavior variables for 12 cow means averaged across 10 d of measurement.[1]

Variable[2]	Variable number																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 Milk production																			
2 BW	.93																		
3 DMI	.91	.89																	
4 Meal size	.76	.54	.58																
5 Eating bouts	.04	.24	.35	-.55															
6 Eating bout length	.26	-.01	.06	.72	-.72														
7 Eating time	.35	.25	.42	.31	.11	.58													
8 Eating time (DM)	-.64	-.70	-.67	-.41	-.14	.30	.33												
9 Eating chews	.13	.09	.30	.04	.29	.36	.90	.42											
10 Ruminating bouts	-.50	-.39	-.57	-.40	-.19	-.42	-.79	-.11	-.74										
11 Ruminating bout length	.73	.60	.72	.68	.02	.46	.63	-.28	.42	-.80									
12 Ruminating time	.46	.45	.36	.48	-.20	.10	-.09	-.62	-.33	.10	.51								
13 Ruminating time (DM)	-.68	-.68	-.83	-.32	-.47	.02	-.44	.36	-.47	.65	-.46	.21							
14 Ruminating chews	.38	.48	.41	.06	.33	-.20	.15	-.39	.11	-.22	.51	.61	-.12						
15 Total chew time	.59	.51	.57	.58	-.06	.52	.71	-.19	.47	-.55	.84	.64	-.20	.55					
16 Total chew time (DM)	-.77	-.81	-.89	-.36	-.47	.24	-.10	.72	-.09	.40	-.42	-.11	.89	-.26	-.15				
17 Total chews	.33	.36	.46	.06	.41	.15	.76	.08	.81	-.67	.62	.12	-.42	.68	.67	-.22			
18 Water intake	.94	.86	.96	.71	.17	.21	.42	-.67	.25	-.58	.80	.46	-.72	.41	.65	-.80	.43		
19 Drinking bout size	.31	.25	.45	.14	.26	.21	.59	-.05	.60	-.48	.31	-.16	-.48	.09	.34	-.29	.50	.47	
20 Drinking bouts	.11	.17	.11	.14	-.01	-.24	-.41	-.36	-.49	.17	-.07	.33	.01	.01	-.08	-.23	-.35	.04	-.80

[1]Significant correlation: ($P < .05$) for $r \geq |.58|$; ($P < .01$) for $r \geq |.71|$; ($P < .001$) for $r \geq |.83|$.

[2]Units for each variable: (1) kg/d, (2) kg, (3) kg/d, (4) kg of DM, (5) /d, (6) min, (7) min/d, (8) min/kg of DM, (9) /d, (10) /d, (11) min, (12) min/d, (13) min/kg of DM, (14) /d, (15) min/d, (16) min/kg of DM, (17) /d, (18) L/d, (19) L, (20) /d.

Table 4. Pearson correlation coefficients among feeding behavior variables for six primiparous and six multiparous cow means averaged across 10 d of measurement.[1]

	Variable number								
Variable	1	2	3	4	5	6	7	8	9
1 Milk production, kg/d		.97	.96	.16	.55	-.78	-.55	-.87	.97
2 BW, kg	.81		.99	.13	.59	-.77	-.43	-.87	.95
3 DMI, kg/d	.68	.58		.03	.67	-.78	-.33	-.78	.92
4 Meal size, kg of DM	.78	.33	.32		-.72	.40	-.25	-.37	.11
5 Eating bouts, /d	-.36	-.03	.34	-.78		-.86	-.08	-.28	.58
6 Eating bout length, min	.75	.30	.27	.89	-.69		.56	.69	-.79
7 Eating time, min/d	.56	.41	.63	.23	.20	.54		.76	-.52
8 Eating time, min/kg of DM	.16	.17	-.03	-.07	.08	.35	.71		-.87
9 Water intake, L/d	.81	.49	.89	.64	-.04	.65	.73	.09	

[1]Primiparous cow data above diagonal; multiparous cow data below diagonal. Significant correlation: ($P < .10$) for $r \geq |.73|$; ($P < .05$) for $r \geq |.81|$; ($P < .01$) for $r \geq |.92|$.

Table 5. Variance component estimates for feeding variables using three linear models.[1]

	Model			
	[1]	[2]	[3]	[1,2,3]
Variable	Cow	Cow(parity)	Cowlcovariate	Day(cow)
Milk production, kg/d	43.2**	24.3**	2.01**	2.58
DMI, kg/d	10.2**	4.4**	.56	3.98
NDF intake, kg/d	.94**	.40**	.059*	.41
Meal size, kg				
DM	.25**	.16**	-.023	.21
NDF	.024**	.015**	-.002	.02
Eating bouts, /d	2.86**	3.16**	.058	3.32
Eating bout length, min	48.5**	46.4**	22.4**	36.7
Eating time				
min/d	2133**	2123**	372.5**	770.2
min/kg DM	5.53**	4.69**	2.17**	4.28
min/kg NDF	58.0**	51.0**	20.1**	36.8
Eating chews (x 10^{-5}), /d	83.2**	90.4**	26.0**	59.4
Eating chew rate, chews/min	12.1**	12.5**	3.50*	14.7
Ruminating bouts, /d	3.85**	2.51**	1.83**	2.70
Ruminating bout length, min	24.2**	15.2**	11.9**	26.1
Ruminating time				
min/d	495	608	161	5079
min/kg DM	10.3**	6.49**	1.28	11.8
min/kg NDF	101.3**	61.7**	11.5	127.0
Ruminating chews (x 10^{-5}), /d	-9.28	-7.2	-10.1	327.4
Ruminating chew rate, chews/min	18.8**	19.1**	3.03*	15.6
Total chewing time				
min/d	2176**	2129**	1198*	7198
min/kg DM	20.7**	12.9*	4.13**	14.8
min/kg NDF	207.3**	128**	37.7*	159
Total chews (x 10^{-5}), /d	81.4*	98.0*	81.8*	549
Water intake, L/d	304.6**	129**	8.92*	60.0
Drinking bout size, L	7.02**	6.89**	.44**	1.13
Drinking bouts, /d	27.2**	29.11**	3.26**	6.60
Drinking time, min/d	24.5**	26.7**	5.07**	5.54
Drinking rate, L/min	.82**	.77**	.104**	.16

[1]Model [1]: Y = cow + day(cow); Model [2]: Y = parity + cow(parity) + day(cow); Model [3]: Y = covariate + cowlcovariate + day(cow).

* Variance component significantly > 0 ($P < .05$).

** Variance component significantly > 0 ($P < .01$).

cow(parity) because degrees of freedom were used for parity. Compared with model [1], including the covariate effect decreased the residual effect of cow for all 28 variables; for 6 variables cow|covariate was not significantly greater that zero ($P > .05$).

Contrast differences (10% of variable mean) between two potential treatments and the total number of cows required to detect these differences under four experimental designs are listed in Tables 6 and 7. Cow numbers declined as variables were measured for additional days. Greater declines were achieved for variables with large day(cow) variance compared with cow variance (e.g., ruminating duration). For random designs, differences in eating chew rate (chews/min) required the fewest animal units (28 cows), and drinking bout size required the most (1132 cows) when measured for 5 d (data not shown). Cow number decreased for some variables when cows were blocked by parity. Nonetheless, requirements still exceeded 32 cows for all variables (Table 6). A minimum of 232 cows was required to detect differences for all variables when covariate effects were included in the model (Table 7). When measured in a Latin square design, all variable differences were detectable using 52 cows measured for 1 d or 12 cows measured for 5 d.

DISCUSSION

Feeding and drinking behavior means obtained in this experiment were similar to those observed by others for lactating cows receiving similar diets (Andersson et al., 1984; Beauchemin and Buchanan-Smith, 1989; Colenbrander et al., 1991). Some variation in results among studies may be because of different production levels, variation in definitions used to describe behavior, chemical composition and physical form of the diet, and differences in management and environment. Beauchemin and Buchanan-Smith (1989) offered three levels of NDF in alfalfa silage-based diets to multiparous, mid-lactation cows. Cows receiving the 30% NDF diet spent 237 min/d eating and 413 min/d ruminating compared with 314 and 460 min for eating and ruminating, respectively, for multiparous cows in our study. Milk production (20 kg/d) and DMI (18 kg/d) also were

Table 6. Estimated cow numbers required for 80% probability of detecting significant contrast differences between two treatment means for feeding variables for random and complete block designs.[1]

	Contrast[2] difference	Days measured					
		CRD[3]			RCB[4]		
		1 d	3 d	5 d	1 d	3 d	5 d
		(no. of cows required)					
Milk production, kg/d	3.3	268	260	256	160	148	148
DMI, kg/d	2.3	176	144	140	104	76	68
Meal size, kg of DM	.22	628	440	400	504	312	276
Eating bouts, /d	1.1	328	212	188	344	228	204
Eating time, min/d	30	208	172	164	208	168	164
Ruminating bouts, /d	1.4	216	156	144	172	112	100
Ruminating time, min/d	46	172	68	52	176	76	56
Total chewing time, min/d	76	108	56	44	104	56	44
Water intake, L/d	7.8	388	348	340	204	160	152
Drinking bouts, /d	1.4	1104	960	932	1168	1024	996

[1]Assumes probability of Type I error = .05; treatment number = 4.

[2]Selected contrast difference equals 10% of variable mean.

[3]CRD = Completely random design; estimated $\hat{\sigma}_e^2$ = Variation due to cow (Model [1]).

[4]RCB = Randomized complete block design with parity as blocking factor; estimated $\hat{\sigma}_e^2$ = Variation due to cow(parity) (Model [2]).

Table 7. Estimated cow numbers required for 80% probability of detecting significant contrast differences between two treatment means for feeding variables for covariate and Latin square designs.[1]

	Contrast[2] difference	Days measured: COV[3] 1 d	COV 3 d	COV 5 d	LS[4] 1 d	LS 3 d	LS 5 d
		(no. of cows required)					
Milk production, kg/d	3.3	32	20	20	8	4	4
DMI, kg/d	2.3	60	28	20	12	8	4
Meal size, kg of DM	.22	256	64	28	52	20	12
Eating bouts, /d	1.1	180	64	40	32	12	8
Eating bout length, min	2.9	456	268	232	52	20	12
Eating time							
min/d	30	84	48	40	12	8	4
min/kg of DM	1.5	196	112	92	24	12	8
Eating chews, /d	1880	156	84	72	24	8	8
Ruminating bouts, /d	1.4	148	92	80	20	8	8
Ruminating bout length, min	3.3	220	120	100	28	12	8
Ruminating time							
min/d	46	164	60	40	32	12	8
min/kg of DM	2.1	200	80	60	36	12	8
Ruminating chews, /d	2920	240	76	44	44	16	12
Total chewing time							
min/d	76	96	44	32	16	8	8
min/kg of DM	3.4	108	56	44	16	8	8
Total chews, /d	4800	176	76	56	28	12	8
Water intake, L/d	7.8	76	36	28	16	8	8
Drinking bouts, /d	1.4	324	180	152	40	16	12
Drinking rate, L/min	.43	96	60	52	12	8	4

[1]Assumes probability of Type I error = .05; treatment number = 4.

[2]Selected contrast difference equals 10% of variable mean.

[3]COV = Covariate design; estimated $\hat{\sigma}_e^2$ = Variation due to cow|covariate (Model [3]).

[4]LS = Latin square crossover design with four cows and periods per square; estimated $\hat{\sigma}_e^2$ = Variation due to day(cow); day(cow) represents the smallest estimate of LS $\hat{\sigma}_e^2$.

lower for cows in their study. After adjusting for differences in intake, time spent chewing was more similar between these two studies.

Daily number and length of eating, drinking, and ruminating bouts depend greatly on the chosen size of their MIBI, which is the minimum time interval between two similar activities required for considering them separate events (Metz, 1975). In studies measuring drinking (Andersson et al., 1984, MIBI = 30 s) and chewing activity (Beauchemin and Buchanan-Smith, 1989, MIBI = 4 min; Harb and Campling, 1985, MIBI = 2 min), shorter MIBI resulted in more daily bouts of shorter duration, compared with those in our study. Many studies have been conducted to investigate diet and management factors that affect feeding and chewing behavior. Dietary fiber concentrations (Beauchemin and Buchanan-Smith, 1989; McLeod and Smith, 1989), forage particle size (Colenbrander et al., 1991; Norgaard, 1989), feeding time (Gordon, 1958), and housing type (Colenbrander et al., 1991; Harb et al., 1985) have been examined.

Certain feeding variables assume many values within a day (e.g., meal size) that may vary greatly. Consequently, daily means of these variables may be of little utility. Experimental treatments may not affect the mean values of these variables but rather alter their temporal distribution within a day. To detect distributional differences due to treatments, distributions must be similar across cows receiving the same treatment. In the present study, intake occurred throughout the entire day, however, periods of greater and lesser intake occurred that were consistent across cows (Figure 2). Distributional consistency should allow detection of differences in future experiments when treatments are applied.

Correlations within eating bouts between eating bout length and number of chews, and within ruminating bouts between ruminating bout length and number of chews were high and positive ($r = .97$, Table 2), indicating that either bout duration or number of chews could be used to describe chewing activity. Correlations between bout duration and number of chews may be smaller, however, when various treatments are applied. Eating

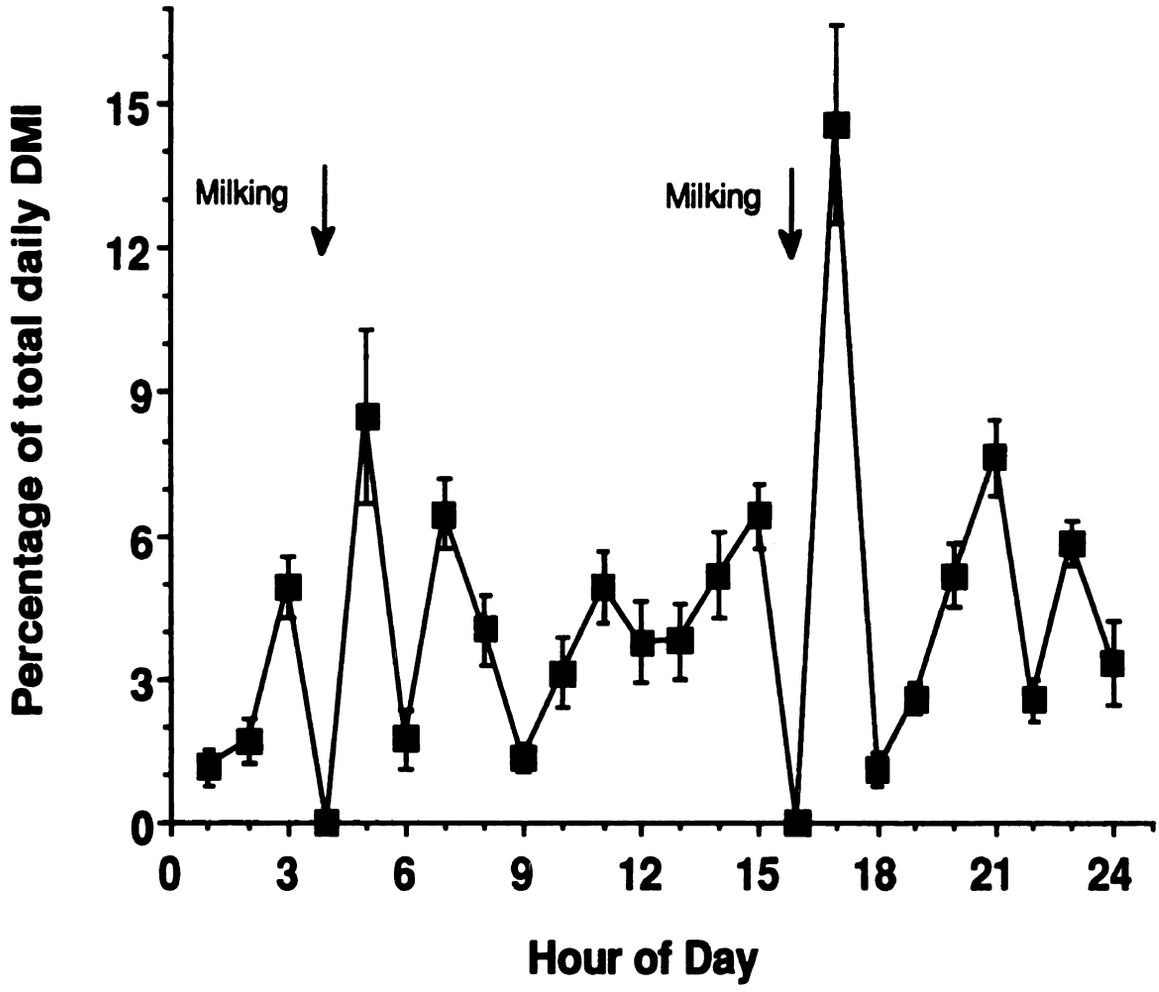


Figure 2. Distribution of DMI within a day expressed as the mean of 12 cow means. Bars represent the standard error of each mean. Feed was offered when cows were away from stalls for milking.

activities were correlated more positively ($P < .01$) with the time interval between bout and previous bout (r = .37) than with the time interval between bout and succeeding bout (r = .14). For example, as time between meals increased, size and length of the meal that followed this interval tended to increase. The higher correlation between meal size and length of its pre-intermeal interval agrees with data of Metz (1975). These correlations may exhibit diurnal variation (Metz, 1975) and vary among physiological states. Savory (1979) stated that under these conditions a satiety mechanism is controlling intake, in contrast to a hunger mechanism initiating intake when meal size is correlated highly with post-intermeal intervals. Such relationships suggest that cows in this study stopped eating once a certain level of repletion was reached and may indicate that rumen fill was determining meal size (Metz, 1975).

Ranges in mean daily milk production (23 to 44 kg, SD = 6.6) and DMI (15 to 27 kg, SD = 3.9) across the 12 cows were sufficiently large to compare cows varying in production. Cows were at similar DIM, so production differences among cows were not due to stage of lactation. Multiparous cows produced 8.8 kg/d of milk more than primiparous cows and had greater DMI and water intakes. Not all of the multiparous cows, however, produced and consumed more than the primiparous cows. High milk production was accompanied by high DM and water intakes both within and across parities. Smaller correlations among these variables were noted by others (Holter and Urban, 1992; Murphy et al., 1983) perhaps because of less variation across cows or their use of more diverse experimental conditions. Increases in daily DMI may occur because of increases in number of meals consumed per day or increases in average meal size. Correlations in Table 3 indicate that across all cows, meal size was related more to DMI (r = .58) than was meal number (r = .35), a result also found by others (Metz, 1975; Vasilatos and Wangsness, 1980).

Within parity (Table 4), DMI was related equally to meal size and number of meals for multiparous cows and more related to number of meals than meal size for primiparous

cows. Multiparous cows ate larger meals by eating longer during each meal (r = .89). High producing primiparous cows spent less time eating per unit of DMI (r = -.87) than other primiparous cows, however, eating bout lengths were shorter so meal size was unrelated to production and intake. Because rumen capacity tends to be smaller for primiparous cows (Bines, 1976), their meal size may have been limited by rumen fill and is supported by cow behavior results. These results suggest that different mechanisms may be controlling individual meals and total daily DMI between cows of different parity, or, perhaps, for cows differing in rumen capacity, BW, or growth requirements. Only six observations within parity group were used so these relationships must be viewed with caution. Other workers have reported that heifers with greater intake spent less time eating per unit of intake (Deswysen et al., 1987b), and dry cows exhibited no relationship between eating rate and daily intake (Harb and Campling, 1985), which agrees with results found in our study. Results of Bae et al. (1983) indicated that time spent eating per unit intake of cell wall constituent was correlated negatively with BW in nonlactating cows and steers. Because BW and milk production were correlated highly in our study, it cannot be determined whether increased production across uniform BW cows would result in decreased eating duration per unit of intake.

Relationships for rumination and total chewing were similar within parity groups; therefore, only results of combined data will be discussed. Higher producing cows tended to have fewer ruminating bouts per day, but each bout was significantly longer (Table 3), resulting in only a tendency (r = .46) for these cows to ruminate longer each day. Total time spent chewing per day was associated positively with milk production (r = .59). Increases in chewing duration, however, were not proportional to increases in DMI because ruminating and total chewing durations per unit of intake decreased as production and intake increased. This is in agreement with reports by some workers (Deswysen et al., 1987b; Harb and Campling, 1985) but in disagreement with others (Bae et al., 1981; Beauchemin and Buchanan-Smith, 1989), who found similar chewing durations per unit

of fiber intake. The latter studies may differ in behavior because of restricted feeding conditions. The amount of time spent chewing per unit of intake has been implicated as a measure of mastication efficiency (Deswysen et al., 1987b; Welch, 1982). Increased efficiency may be due to a shorter interboli time, a greater number of chews per unit time, a lower proportion of pseudo-rumination, or more efficient regurgitation of long particles (DeBoever et al., 1990). Efficiency also may be increased because of larger mouths, larger tooth surfaces, stronger jaw muscles, or improved articulation of the jaw. Elucidating why high producing cows process more feed during a given length of chewing time should remain an active area of nutrition research. Whether similar relationships exist at all stages of lactation remains in question and deserves study.

Variance component estimates were calculated to examine the relative importance of independent sources of variation. Feeding behavior measurement is difficult and expensive; therefore, knowledge about potential variation is useful for planning experiments that minimize experimental error and replication. Differences between cows were the greatest source of variation for most variables (Table 5), suggesting that reducing experimental unit heterogeneity would be effective. Coefficients of variation across cows ranged from 5 to 41%, and most variables ranged between 15 and 20%. Norgaard (1989) and Harb and Campling (1985) observed similar variation across cows, but Vasilatos and Wangsness (1980) detected larger variation (e.g., 30 to 40%), perhaps because of their use of cows earlier in lactation. Blocking cows by parity in the present study did little to reduce replicate heterogeneity. An alternative blocking factor, such as pretrial milk production or intake, may be more effective. A pretrial covariate period reduced across-cow variation more significantly. However, this period was extensive (5 d) and immediately preceded the experimental collection period. The effect of a covariate period probably is maximal under these conditions and likely will be smaller with a shorter, earlier, or later period of measurement.

Days were considered as random samples within the main effect of cow; therefore, the effect of day could not be tested for significance. Variation across days within cow was substantial, especially for traits associated with rumination. Measuring behavior for more than 1 d will decrease experimental error because a more accurate measure of the replicate's true value is obtained. Only a limited decrease in error is possible by increased sampling, and greatest gains occur with initial increases in sampling (Berndtson, 1991). Variables with large across day variance compared with across cow variance have the most to gain from more days of measurement.

Estimates of experimental error facilitate calculation of replicates required for adequate power and sensitivity in future studies measuring feeding behavior. A maximum Type II error rate of 20% commonly is used for replicate estimation (Berndtson, 1991; Gill, 1969). Biological significance of a 10% difference from a control mean probably depends on the variable of interest. Variables with the largest variance components used as error estimates required the most replicates to achieve desired power (Tables 6 and 7). Gill (1969) determined sample sizes required for detection of differences in milk production for various designs using more than 25,000 cow records. Replicates per treatment were slightly greater than those calculated for milk production in the current study because of different assumptions used in calculating experimental errors. Similarity between the two studies suggests that our replicates were sufficiently diverse to represent a more general cow population.

Many studies have monitored feeding behavior for only a single day (Colenbrander et al., 1991; McLeod and Smith, 1989). Based on our data, 1-d studies require a minimum of 52 cows to detect 10% treatment differences for all feeding variables using a Latin square design. Because experiments rarely utilize this many replicates, they will have substantially less than 80% power. If differences are at least 20%, number of cows required decreases to 20. At contrast differences of 40% of mean values, 8 cows are required in Latin squares. Consequently, only when treatment differences are large will

statistical detection likely be achieved with 1-d studies. Partial day measurements extrapolated to complete day means (Norgaard, 1989) will require even larger differences if small numbers of cows are used.

Replication required for completely random, block, and covariate designs exceeded that typically available to researchers. Only with Latin square designs was sufficient cow variation removed to obtain 80% power and 10% sensitivity while using a reasonable number of cows. Twelve cows measured for 5 d in a Latin square design was the most effective design for this feeding behavior study where mid-lactation cows received medium quality diets.

CONCLUSIONS

Milk production was correlated positively with DM and water intakes both within and across parities. For multiparous cows, production was related positively to meal size and length of eating bouts, and unrelated to meal number and eating rate. For primiparous cows, production tended to be related positively to meal number and eating rate, and unrelated to meal size. These results suggest that different mechanisms may be controlling individual meals and total daily DMI between cows of different parity, rumen capacity, or BW. Milk production was correlated negatively with ruminating and total time spent chewing per unit of intake, suggesting that differences may exist among cows for chewing efficiency. Future experiments that involve feeding behavior measurements with lactating cows may attain sufficient statistical power and sensitivity when they use 12 cows measured for 5 d in a Latin square design.

CHAPTER 4

Intake Limitations, Feeding Behavior, and Rumen Function of Cows Challenged with Rumen Fill from Dietary Fiber or Inert Bulk

ABSTRACT

Twelve multiparous, rumen cannulated cows (17 DIM) were fed 25 or 35% NDF rations with or without added rumen inert bulk as water-filled plastic containers (500 ml each) within 3, 4 x 4 Latin squares (21 d periods). Added bulk equaled 25% of pretrial rumen volume. Objectives were to challenge early lactation cows with rumen fill in the form of dietary NDF and rumen inert bulk to determine if intake limitations from ruminal fill vary with NDF content of the diet, or if within-day feeding behavior changes allow cows to adapt to higher fill. Inert bulk had no effect on DMI for cows fed 25% NDF but decreased DMI for cows fed 35% NDF (18.7 vs. 16.6 kg/d). Production and rumen fermentation results support the statement that fiber and inert bulk addition created an energy deficit compared to the basal treatment. Volume of rumen digesta plus inert bulk was similar for 35% NDF treatments regardless of inert bulk (mean = 102 L), and suggests that cows receiving high fiber diets have intakes limited by the physical capacity of the reticulorumen. Changes in feeding behavior were insufficient to maintain intake under conditions of high rumen fill, however, added fiber and bulk altered rumination and reticular motility in a similar fashion, demonstrating that NDF may have rumen-filling properties. Increased passage and rumination may help alleviate fill. Future study is required to determine the effect of fiber digestibility and animal characteristics on fill-limited intake.

INTRODUCTION

Maximum feed intake in early lactation cows establishes a foundation for high milk production throughout the entire lactation. Cows do not consume adequate amounts of energy during initial stages of lactation to support their energy requirements, which supports the hypothesis that intake by cows during this period is not limited by physiological control, but rather, by the physical limitation of insufficient reticulorumen capacity. Minimizing rumen fill becomes more critical with larger energy deficits to avoid excess loss of body energy reserves and metabolic disease. Once cows have reached positive energy balance, physical fill may not be as important a control mechanism for intake.

Several previous studies have added artificial forms of inert bulk to the rumen of ruminants, including dairy cows, to examine the effect of reticuloruminal fill on intake (Campling and Balch, 1961; Carr and Jacobson, 1967; Johnson and Combs, 1991, 1992). It is a common misconception that if intake is limited by rumen capacity, intake should decline in proportion to the amount of artificial fill added. Responses to fill, however, have been variable. Campling and Balch (1961) observed linear decreases in intake (52 g of hay/L of fill) with non-lactating cows after additions of 23 and 34 L of inert bulk. Johnson and Combs (1991) fed mixed diets to early lactation cows and detected decreases in intake of 99 and 130 g/L of inert bulk, however these same workers found no depression in intake with larger cows filled with similar levels of artificial bulk (Johnson and Combs, 1992). Failure to achieve intake depression may be due to submaximal volume in the reticulorumen prior to bulk addition because of other dominating control mechanisms, or increased digesta disappearance from the rumen after bulk addition (Waybright and Varga, 1991). Because intake is not likely controlled by only one satiety factor at all times (Forbes, 1988), dilution of physical effects by other control mechanisms may obscure detection of depressions due to fill.

Not all diets produce the same level of rumen fill. Blaxter et al. (1956) calculated "ballast", or indigestible DM in the rumen using meal patterns, digestibility, and passage data and found more digestible feeds resulted in less ballast. Feeds that ferment and pass more quickly through the rumen are believed to be less filling because they occupy space within the rumen for a shorter period of time (Aitchison et al., 1986). The more slowly fermented, fibrous fraction of feedstuffs, as measured by NDF, has been implicated as the component responsible for rumen fill (Mertens, 1987). Diets with high NDF concentrations have been shown to promote greater rumen fill and less DMI compared to lower fiber controls (Aitchison et al., 1986; Llamas-lamas and Combs, 1991). Cows receiving higher fiber diets may also be more susceptible to depressions in intake upon addition of inert bulk to the rumen, illustrating that these diets may be under greater control by physical regulation of intake.

Under constraints of high rumen fill, cows may adjust their feeding behavior or rumen activity to compensate for such fill with no decline in daily feed intake. For example, they may increase the rate of passage of digesta from the rumen by increasing extent or efficiency of rumination, allow larger particles to leave the rumen, increase frequency or strength of reticular contractions (Okine et al., 1989), or eat smaller meals with greater frequency (Baumont et al., 1990) in an attempt to keep the rumen at maximum capacity as much as possible. Only by measuring within-day activity is it possible to evaluate the effects of rumen fill on meal characteristics, rumination, and rumen function. Use of high producing early lactation cows consuming high fiber diets with large amounts of added inert bulk should increase the likelihood that capacity effects will be observed.

Objectives of this study are to 1) challenge early lactation cows with rumen fill in the form of dietary NDF and rumen inert bulk to determine if limitations to intake from ruminal fill vary with NDF content; 2) measure feeding behavior and rumen activity to determine if within-day behavior changes allow cows to adapt to higher fill conditions

and maintain normal daily intakes; and 3) compare fiber and bulk additions to determine if dietary NDF has rumen filling characteristics.

MATERIALS AND METHODS

Experimental Design and Data Collection

Twelve multiparous Holstein cows in early lactation (17 ± 6 DIM; mean ± SD) were blocked by calving date and assigned to one of three, 4 x 4 Latin squares balanced for carry-over effects. Cows were ruminally cannulated 30 d prior to calving, were at least 10 DIM when treatments commenced, and were not bred until treatments concluded. Treatment periods were 21 d in length, with the last 7 d used for data and sample collection. A 2 x 2 factorial arrangement of treatments was applied in each square. Factors tested were concentration of dietary NDF and addition of rumen inert bulk (**RIB**). Levels of NDF were 25% (**LF**) and 35% (**HF**) of diet DM; levels of RIB were 0% (**+0**) and 25% (**+B**) of pretrial rumen volume. Inert bulk consisted of 500 ml polyethylene containers filled with water and sealed with locking screw caps. Number per cow ranged from 36 to 51 containers.

Diet ingredients were alfalfa and corn silages, ground shelled corn, soybean meal, animal protein, minerals, and vitamins (Table 1). Values represent average ingredient and nutrient compositions from across the entire experiment. Rations were formulated to contain either 25 or 35% NDF, 18.5% CP, and provide at least .4 kg/cow per d of rumen undegraded protein supplement. Alfalfa silage and corn silage were offered in equal DM amounts within each diet. Differences in NDF content between diets were achieved by altering forage:concentrate ratio. All concentrate ingredients contained greater than 87% DM and were combined for each diet prior to the experiment. Except for mineral concentrations, nutrient composition of the diets was determined from chemical analysis of individual feed ingredients. Nutrient composition of forages and concentrates is presented in Table 2. Rations were mixed once daily and offered for ad libitum intake (10% refusal rate) as a TMR at 0700 and 1900 h when cows

Table 1. Ingredient and nutrient composition of 25% NDF, low fiber diet (LF) and 35% NDF, high fiber diet (HF) offered to 12 cows during the first 14 wk of lactation.

	LF		HF	
Ingredient Composition	------(% of diet DM)-------			
Alfalfa silage	22.6		40.1	
Corn silage	22.7		40.7	
Ground shelled corn	34.1		2.6	
44% Soybean meal	16.4		12.9	
Protein supplement[1]	1.6		1.8	
Dicalcium phosphate	.8		.9	
Calcium carbonate	1.0		.2	
Trace mineral supplement	.6		.6	
Vitamin supplement[2]	.2		.2	
Nutrient Composition	LF	SD[3]	HF	SD
DM, %				
52°C oven	57.1	.9	44.9	1.1
Toluene	56.6	.9	44.2	1.0
NE_L,[4] Mcal/kg of DM	1.76		1.61	
	----------(% of diet DM)----------			
OM	92.0	.6	91.0	.2
NDF	25.7	.5	35.2	.9
ADF	14.0	.4	21.3	.6
Lignin	2.4	.2	3.7	.2
Indigestible NDF[5]	8.3	.3	13.8	.4
CP	18.2	.4	18.9	.3
RUP,[4,6] % of diet CP	36.6	ND[7]	32.1	ND
Ca	1.3	ND	1.4	ND
P	.47	ND	.54	ND
Mg	.24	ND	.25	ND

[1]Contains 55% meat and bone meal, 25% blood meal, 10% fish meal, and 10% feather meal.

[2]Contains 1733, 512, and 7.3 kIU/kg of DM of vitamins A, D, and E, respectively.

[3]Represents variation in chemical composition of samples composited weekly.

[4]Calculated from NRC (1989).

[5]Neutral detergent fiber residue after 120 h in vitro fermentation with buffered rumen fluid.

[6]RUP = rumen undegraded protein.

[7]ND = not determined.

Table 2. Nutrient composition of forages and concentrates used to formulate low fiber (LF) and high fiber (HF) diets.

	Alfalfa silage	Corn silage	Concentrate LF	Concentrate HF
DM, %				
52°C oven	46.6	35.5	88.1	89.6
Toluene	44.9	35.3	...	...
	----------(% of DM)----------			
OM	89.4	96.1	91.7	83.2
NDF	37.4	41.6	14.0	16.9
ADF	27.4	21.8	5.1	7.4
Lignin	6.3	2.3	.8	1.1
Indigestible NDF[1]	18.9	14.1	1.5	2.8
CP	20.4	7.3	21.8	40.5

[1]Neutral detergent fiber residue after 120 h in vitro fermentation.

were parlor-milked. Feed amounts offered and refused were recorded daily. Feed ingredients and diets were sampled daily (.5 kg), frozen, and composited weekly. Feed refused was sampled daily (12.5% of orts) during collection weeks and composited by cow. Milk yield was recorded daily. Milk samples were obtained on d 16 and 17 of each period for both milkings and individually analyzed for components. Cow BW was determined at 2100 h (d 19) and 1700 h (d 21) each period and averaged. Cows were visually scored for body condition (d 19) each period.

Fecal samples were obtained and frozen every 15 h from d 14 to 19 of each period to represent defecation every 3 h throughout a 24 h day. Sampling commenced at 2000 h on d 14 and continued at 1100 h (d 15), 0200 h and 1700 h (d 16), 0800 h and 2300 h (d 17), 1400 h (d 18), and 0500 h (d 19). Cows were not disturbed to obtain samples but were allowed to defecate naturally to prevent interruption of natural feeding behavior that was being monitored concurrently. The eight samples for each cow were composited on an equivalent wet basis. Fecal composites were split and analyzed for nutrient composition and particle size.

Rumen digesta was manually removed from each cow via the cannula at 2100 h on d 19 (2 h postfeeding) and 1700 h on d 21 (2 h prefeeding). Inert bulk, if present, was removed with digesta and quantified to assure complete recovery. A 10% aliquot of the digesta was separated during evacuation for sampling. Two digesta samples were obtained. A 600 g sample of the complete digesta was taken for determination of DM and nutrient composition. A second sample was strained through four layers of cheesecloth to obtain 50 ml of fluid and combined with 10 ml of 10% (v/v) H_2SO_4 for VFA analysis. Both digesta and fluid samples were frozen immediately (-20°C) following collection. Total digesta weight and volume were determined. Following the d 21 evacuation, RIB and rumen digesta were switched among cows to assist in adaptation to the next treatment. Immediately prior to digesta removal, head space (gas) volume within the dorsal rumen was estimated at both evacuation times by filling the space with empty polyethylene containers and quantifying their number.

Feed disappearance, water intake, jaw movements, reticular contractions, and ruminal pH were measured continuously from d 14 to 19 each period with monitors and a computer data acquisition system described in Chapter 2. Data were written to files every 5 s for each cow and variable. Monitors were calibrated each period, placed on the cows 1 d prior to collection to allow for animal adaptation, and removed during the first rumen digesta evacuation. Monitors were disconnected twice daily to permit cows to leave the tie stalls for milking and exercise. Cows averaged 1.8 h/d away from feed and monitoring equipment during which no behavior was recorded.

Sample and Statistical Analysis

Diets, dietary ingredients, orts, feces, and rumen digesta were analyzed for nutrient concentrations. Samples were dried in a forced-air oven at 52°C for 72 h, ground with a Wiley mill (1-mm screen), and analyzed in duplicate for ash, NDF, ADF, lignin, and indigestible NDF. Ash was determined following sample ignition at 500°C for 6 h. Analysis of NDF (Goering and Van Soest, 1970) was modified by addition of 4

ml of a 5% α-amylase solution (Termamyl 120L, Novo Nordisk Bioindustrials, Inc., Danbury, CT) to each sample, substitution of triethylene glycol for 2-ethoxyethanol, and omission of decahydronaphthalene and sodium sulfite. Neutral detergent residues were sequentially analyzed for ADF and acid detergent sulfuric acid lignin (Goering and Van Soest, 1970). Indigestible NDF was estimated as the NDF content of samples following in vitro fermentation in buffered rumen media (Goering and Van Soest, 1970) for 120 h without addition of pepsin. Cellulose content was calculated as ADF minus lignin content; hemicellulose content was calculated as NDF minus ADF content. Diets, dietary ingredients, orts, and feces were analyzed for CP (N x 6.25) using a modified Kjeldahl (Hach) procedure (Watkins et al., 1987). Mineral analysis of diets was performed using inductively coupled plasma emission spectroscopy (Northeast DHIA, Ithaca, NY). Sample DM was determined by oven drying (52°C) for all samples and by toluene distillation (AOAC, 1990) for forages, diets, and rumen digesta. Oven DM was used in calculations for intake and nutrient digestibility. Concentrations of all nutrients, except DM, were expressed as a percentage of DM determined from forced-air oven drying at 105°C.

Milk samples were analyzed for lactose, fat, and protein content with infrared spectroscopy by Michigan DHIA. Particle size of fecal NDF (oven dried at 105°C) was determined by wet-sieving 40 g of feces following boiling (1 h) in 300 ml of neutral detergent with .6 ml of 100% termamyl 120L. Sieve sizes used were 600, 1200, and 2400 μm. Data generated were percentage of total fecal NDF retained on each sieve and percent < 600 μm calculated by difference. Acidified rumen fluid was centrifuged at 13,000 x *g* for 30 min, decanted, and the supernatent centrifuged at 26,000 x *g* for an additional 30 min. Concentration of VFA in the supernatent was determined using the procedure of Siegfried et al. (1984) with HPLC. The column used was Aminex HPX-87H, catalog number 125-0140, 300 x 7.8 mm (Bio-Rad Laboratories, Richmond, CA). Column temperature was 50°C and solvent was .005 N H_2SO_4. Detection was by

refractive index (Waters 410, Millipore Corp., Milford, MA). Concentration of major rumen VFA and their molar proportions were calculated.

Fecal output and apparent total tract digestibility of dietary nutrients were calculated using indigestible NDF as an internal marker (Cochran et al., 1986). Fractional rate of NDF passage from the rumen (k_p) was calculated by dividing the rumen pool size of indigestible NDF into the hourly intake of indigestible NDF, based on the two-pool, first-order model of rumen fiber digestion of Waldo et al. (1972). This model divides the total rumen fiber pool into a digestible pool and indigestible pool. Fractional rate of digestible NDF digestion in the rumen (k_d) was calculated as the difference between total rate of escape of digestible NDF from the rumen and its rate of passage (Allen and Mertens, 1988b):

$$kd = \frac{(\text{hourly digestible NDF intake})}{(\text{rumen pool size of digestible NDF})} - kp$$

Finally, apparent rumen digestibility of NDF as a percent of NDF intake was calculated as:

$$\text{Fraction of feed NDF that was digestible} \times \left[\frac{kd}{(kd + kp)}\right]$$

These calculations assume that rumen NDF pool sizes and fluxes are at steady state and that the k_p of digestible and indigestible NDF are equal. Apparent rumen digestibility of NDF was also expressed as a percent of total tract NDF digestibility.

Eating, ruminating, and drinking activities, in addition to reticular motility, and ruminal pH were determined from collected behavior data with previously developed algorithms (Chapter 2). An IBM 3090 mainframe computer was used for data interpretation (International Business Machines Corporation, Armonk, NY). Feeding behavior was summarized into variables each day as performed in Chapter 3, and averaged by cow and period. Variables included number and length of eating bouts, eating time, meal size, number and length of ruminating bouts, ruminating time, number

and size of drinking bouts, frequency of reticular contractions, and summary of rumen pH, among others. Variables were screened to remove data when noted to be incorrect as determined by manual observation of graphical displays during data collection. Across the five activities monitored, 91% of the collected computer data were considered acceptable.

All data were statistically analyzed using the general linear models procedure of SAS (1985). The model used was consistent with replicated Latin squares:

$$Y_{ijkl} = \mu + S_i + C_{j(i)} + P_{k(i)} + T_l + ST_{il} + E_{ijkl}$$

where μ = overall mean,
S_i = random effect of square (i = 1 to 3),
$C_{j(i)}$ = random effect of cow within square (j = 1 to 4),
$P_{k(i)}$ = random effect of period within square (k = 1 to 4),
T_l = fixed effect of treatment (l = 1 to 4),
ST_{il} = interaction of square and treatment,
and
E_{ijkl} = residual, assumed normally distributed.

A reduced model without square x treatment was used when this effect was not significant ($P > .10$). Type III sums of squares were used to determine significance of treatment effects. Separation of treatment means was performed using protected least significant differences (Snedecor and Cochran, 1980). Preplanned orthogonal contrasts were used to determine significance of the main treatment effects of fiber level and bulk level, and their interaction. Model effects were declared significant when $P < .05$, unless otherwise specified.

RESULTS

Production and Nutrient Digestibility

The addition of RIB appeared to have little adverse affect on general rumen function or cow comfort during collection weeks. Some of the containers were temporarily removed from five cows during various adjustment periods because of

difficulties in adaptation to newly added bulk. Within 4 d, 100% of the RIB was returned to their rumens without further complications. All cows contained all their added RIB for each collection period.

Milk production and nutrient intake data are presented in Table 3. Cows averaged 33 kg/d of milk and 20 kg/d of DMI across the experiment. Milk, 4% FCM, protein, and lactose production were significantly greater for LF compared to HF treatments ($P < .01$). Low fiber treatments exceeded HF by 5.7, 3.8, .21, and .31 kg/d for milk, 4% FCM, protein, and lactose production, respectively. Milk protein and lactose concentrations were higher ($P < .01$) for LF compared to HF treatments, however milk fat concentration was not different among any of the treatments. Cows receiving LF consumed 5.1 kg/d more DM and 10.7 L/d more free water ($P < .01$) than those receiving HF. Addition of RIB tended to decrease milk, 4% FCM, and lactose production within both fiber levels and significantly decreased milk protein production and concentration ($P < .01$). Average milk production was 34.2 kg/d for +0 treatments compared to 32.1 kg/d for +B treatments. Interactions among levels of fiber and RIB were present for intake data. Inert bulk had no effect on DM, NDF, or indigestible NDF intakes for cows fed LF but decreased intakes for cows fed HF by 2.1, .73, and .29 kg/d, respectively. Cow BW and body condition scores were not different among treatments, however empty BW (BW - rumen digesta mass) was significantly lower for HF and +B treatments ($P < .01$).

Apparent total tract digestibilities of DM, OM, NDF, and lignin were significantly higher ($P < .01$) for LF compared to HF treatments (Table 4). Average DM and NDF digestibilities were 71.0 and 47.9% for LF treatments and 65.4 and 44.6% for HF treatments, respectively. Digestibility of OM was slightly less for cows receiving RIB compared to no bulk addition. No differences among treatments were detected for ADF, hemicellulose, cellulose, or CP digestibilities. Cows fed LF produced less fecal NDF and indigestible NDF compared to cows fed HF. Addition of RIB lowered fecal

Table 3. Milk production and feed intake for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Production, kg/d								
Milk	37.0^{a}	35.0^{a}	31.4^{b}	29.2^{b}	1.2	**	†	NS
4% FCM	33.5^{a}	31.8^{ab}	29.9^{bc}	27.9^{c}	1.1	**	NS	NS
Fat	1.25	1.19	1.15	1.08	.06	†	NS	NS
Protein	1.07^{a}	0.96^{b}	0.85^{c}	0.77^{c}	.03	**	**	NS
Lactose	1.76^{a}	1.64^{a}	1.45^{b}	1.33^{b}	.06	**	†	NS
Milk composition, %								
Fat	3.43	3.44	3.68	3.69	.16	NS	NS	NS
Protein	2.92^{a}	2.75^{b}	2.73^{b}	2.66^{b}	.04	**	**	NS
Lactose	4.77^{a}	4.70^{a}	4.62^{b}	4.57^{b}	.03	**	*	NS
Intake, kg/d								
DM	22.8^{a}	22.7^{a}	18.7^{b}	16.6^{c}	.4	**	*	*
NDF	5.79^{b}	5.75^{b}	6.52^{a}	5.79^{b}	.15	*	*	*
Indigestible NDF[2]	1.88^{c}	1.85^{c}	2.56^{a}	2.27^{b}	.06	**	*	*
CP	4.14^{a}	4.13^{a}	3.58^{b}	3.18^{c}	.08	**	*	*
Water intake, L/d								
Free water	82.2^{a}	78.7^{ab}	74.4^{b}	65.1^{c}	2.7	**	*	NS
Total water[3]	99.0^{a}	95.4^{a}	96.9^{a}	84.8^{b}	2.8	*	*	NS
BW, kg	593	598	595	587	3	NS	NS	†
Empty BW,[4] kg	518^{a}	511^{ab}	508^{b}	493^{c}	3	**	**	NS
Body condition score[5]	2.21	2.21	2.29	2.08	.06	NS	NS	NS

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

[1]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $\dagger P < .10$.

[2]Neutral detergent fiber residue after 120 h in vitro fermentation.

[3]Total water intake = Free water intake + water from feed intake.

[4]Empty BW = BW - rumen digesta mass.

[5]Scale of 1 to 5; 1 = thin, 5 = obese.

Table 4. Apparent total tract digestibility of nutrients, fecal output, fecal composition, and fecal fiber particle size from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.[1]

	Treatment					Main effect[2] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Nutrient digestibility, %								
DM	71.5[a]	70.6[a]	65.7[b]	65.2[b]	.4	**	†	NS
OM	72.9[a]	71.6[b]	66.9[c]	66.5[c]	.4	**	*	NS
NDF	48.0[a]	47.8[a]	45.3[b]	43.9[b]	.8	**	NS	NS
ADF	45.9	45.4	46.2	46.7	1.6	NS	NS	NS
Lignin	12.3[a]	12.2[a]	-.6[b]	4.7[ab]	3.1	**	NS	NS
Hemicellulose	46.4	44.7	45.1	43.6	1.2	NS	NS	NS
Cellulose	52.6	52.4	55.3	55.0	1.6	NS	NS	NS
CP	70.2	69.8	70.3	69.1	.6	NS	NS	NS
Fecal output, kg/d								
DM	6.50[a]	6.69[a]	6.44[a]	5.80[b]	.18	*	NS	*
NDF	3.01[b]	3.00[b]	3.57[a]	3.25[b]	.10	**	NS	NS
Indigestible NDF[3]	1.88[c]	1.85[c]	2.56[a]	2.27[b]	.06	**	*	*
Fecal composition								
DM, %	16.0[a]	16.2[a]	14.1[b]	13.8[b]	.2	**	NS	NS
NDF, % of DM	46.4[b]	45.1[b]	55.4[a]	56.0[a]	.6	**	NS	NS
Indigestible NDF, % of DM	29.0[b]	27.9[b]	39.7[a]	39.1[a]	.4	**	*	NS
Fecal NDF particle size	-------(% of total fecal NDF)-------							
<600 µm	46.8[bc]	45.6[c]	49.3[ab]	51.4[a]	1.2	**	NS	NS
600-1200 µm	18.9[ab]	19.6[a]	18.4[bc]	18.0[c]	.3	**	NS	NS
1200-2400 µm	13.8[a]	14.3[a]	12.1[b]	11.8[b]	.3	**	NS	NS
>2400 µm	20.5	20.4	20.2	18.8	1.4	NS	NS	NS

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

[1]Calculated using indigestible NDF as an internal marker.

[2]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $\dagger P < .10$.

[3]Neutral detergent fiber residue after 120 h in vitro fermentation.

output of DM and indigestible NDF, but only for cows fed HF. As a percentage of total fecal NDF, fecal NDF particle size was smaller ($P < .01$) for HF treatments compared to LF, however no differences were observed between treatments for fecal particles greater than 2400 μm. A greater percentage of fecal NDF was retained on both 600 and 1200 μm screens for LF treatments while more fecal NDF was smaller than 600 μm for HF treatments. Added RIB did not alter particle size of fecal NDF.

Rumen Characteristics

Pre and postfeeding rumen digesta evacuation data, including VFA analyses, were averaged to obtain values presented in Tables 5 and 6. Digesta volume (Table 5) was largest with treatment HF+0 (98.8 L) and declined with lower dietary NDF content and addition of RIB. Volume of digesta plus RIB was similar for both HF treatments and LF+B (mean = 101.6 L) but was significantly less for treatment LF+0. Total rumen volume, as measured by the sum of digesta, RIB, and head space volume, was not different between LF and HF treatments but was significantly greater ($P < .01$) for treatments with added RIB (110 L vs. 120 L). Low fiber treatments resulted in digesta with higher DM and lower NDF contents ($P < .01$) compared with HF treatments. Added RIB decreased digesta DM content ($P < .01$) but did not affect NDF content.

Rumen mass of wet digesta followed a similar pattern to rumen volume, with the exception that treatment HF+B resulted in greater rumen wet mass compared to its volume because of its higher moisture content (Table 5). Total rumen mass (wet digesta + RIB) was highest for HF+B (94.1 kg), similar for LF+B and HF+0 (86.9 kg), and lowest for LF+0 (75.7 kg). Rumen DM mass decreased significantly ($P < .01$) upon addition of RIB, however no difference was detected between levels of dietary fiber. Masses of various components of rumen fiber all followed similar trends. Without RIB, HF increased rumen NDF mass compared to LF (6.0 vs. 7.0 kg). Addition of RIB decreased ($P < .01$) rumen NDF to the same mass (4.6 kg) for both LF and HF treatments. The greater decline in rumen fiber mass upon addition of RIB for HF

Table 5. Rumen digesta characteristics for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Rumen volume, L								
Digesta	89.8[b]	78.9[c]	98.8[a]	82.7[c]	2.4	*	**	NS
Digesta + inert bulk	89.8[b]	101.1[a]	98.8[a]	104.9[a]	2.4	*	**	NS
Digesta + inert bulk + head space[2]	108.0[b]	117.9[a]	111.5[b]	121.1[a]	2.0	NS	**	NS
Digesta composition								
DM, %								
52°C oven	14.3[a]	12.8[b]	13.0[b]	10.6[c]	.2	**	**	*
Toluene	12.7[a]	11.3[a]	11.6[a]	8.7[b]	.5	**	**	NS
NDF, % of DM	55.5[b]	54.4[b]	61.7[a]	61.4[a]	.8	**	NS	NS
Rumen mass, kg								
Wet digesta	75.7[b]	65.3[c]	86.4[a]	71.9[b]	2.0	**	**	NS
Wet digesta + inert bulk	75.7[c]	87.4[b]	86.4[b]	94.1[a]	2.0	**	**	NS
DM	10.8[a]	8.3[b]	11.3[a]	7.7[b]	.4	NS	**	NS
OM	9.5[a]	7.2[b]	10.0[a]	6.7[b]	.3	NS	**	NS
NDF	6.0[b]	4.5[c]	7.0[a]	4.7[c]	.2	*	**	NS
ADF	3.5[b]	2.6[c]	4.1[a]	2.8[c]	.1	**	**	NS
Lignin	.80[b]	.60[c]	1.01[a]	.69[c]	.03	**	**	†
Hemicellulose	2.6[b]	1.9[c]	2.9[a]	1.9[c]	.1	NS	**	†
Cellulose	2.6[b]	1.9[c]	3.1[a]	2.1[c]	.1	**	**	†
Indigestible NDF[3]	3.3[b]	2.5[c]	4.2[a]	2.8[c]	.1	**	**	†
Density, kg/L	.84[b]	.83[b]	.88[a]	.87[a]	.01	**	†	NS

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

[1]Main effect levels differ, $**P < .01$, $*P < .05$, $\dagger P < .10$.

[2]Head space = Volume of gas between digesta and top of the rumen.

[3]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 6. Concentration and molar proportion of VFA in rumen fluid from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
VFA concentrations	----------(mmol/L)----------							
Acetate	77.6[a]	73.8[a]	77.7[a]	68.6[b]	1.4	†	**	†
Propionate	30.9[a]	26.4[b]	24.2[b]	19.5[c]	1.1	**	**	NS
Butyrate	13.0[a]	12.5[a]	12.9[a]	11.0[b]	.3	**	**	*
Valerate	2.9[a]	2.5[bc]	2.7[ab]	2.3[c]	.1	†	**	NS
Branched-chain[2]	5.8[a]	5.2[b]	5.4[b]	5.2[b]	.1	NS	**	†
Total	130.2[a]	120.5[b]	122.9[b]	106.6[c]	2.2	**	**	NS
VFA molar proportions	----------(% of total VFA)----------							
Acetate	59.8[c]	61.5[b]	63.2[ab]	64.4[a]	.6	**	*	NS
Propionate	23.5[a]	21.6[b]	19.7[bc]	18.2[c]	.6	**	*	NS
Butyrate	10.0	10.5	10.5	10.3	.2	NS	NS	NS
Valerate	2.2	2.1	2.2	2.1	.1	NS	NS	NS
Branched-chain	4.5[b]	4.3[b]	4.4[b]	5.0[a]	.1	*	†	**
Acetate:propionate ratio	2.6[c]	3.0[b]	3.2[b]	3.6[a]	.1	**	**	NS

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

[1]Main effect levels differ, **$P < .01$, *$P < .05$, †$P < .10$.

[2]isobutyrate + isovalerate.

compared to LF tended to result in an interaction among levels of fiber and RIB (P = .10). Density of rumen digesta was significantly higher (P < .01) for HF compared to LF treatments.

Rumen fluid concentrations of all measured VFA were significantly lower (P < .01) upon addition of RIB (Table 6). Total VFA concentrations averaged 126.6 mmol/L and 113.6 mmol/L for +0 and +B treatments, respectively. Rumen propionate, butyrate, and total VFA concentrations were higher for LF compared to HF treatments (P < .01). Molar proportions of rumen VFA were also calculated (Table 6). Proportion of acetate increased and propionate decreased upon addition of RIB or fiber in the diet, with fiber level having a slightly greater effect than RIB. Consequently, acetate:propionate ratio increased significantly (P < .01) as additional fiber or RIB was included in the treatment.

Rumen digestibility and digestion kinetics of NDF were calculated from pre- and postfeeding rumen digesta evacuations and are presented in Table 7. Fractional passage rates of rumen NDF were similar between pre- and postfeeding estimates and were highest for treatment HF+B (.035 h^{-1}) and lowest for treatment LF+0 (.024 h^{-1}). Additional dietary fiber and RIB both significantly (P < .01) increased passage of NDF by .002 and .008 h^{-1}, respectively. Fractional digestion rate of digestible NDF tended to differ more between pre- and postfeeding estimates than did passage estimates. Digestion rates 2 h prefeeding were not different between LF and HF treatments but were greater for LF 2 h postfeeding (.046 vs. .038 h^{-1}). Conversely, digestion rates were greater (P < .01) for treatments with added RIB 2 h prefeeding (.037 vs. .049 h^{-1}) but were not greater 2 h postfeeding. Apparent digestibility of NDF in the rumen was significantly higher (P < .01) for LF compared to HF treatments. Rumen digestibility averaged 41.2 and 34% for LF and HF treatments, respectively, when expressed as a percent of NDF intake, and 86.0 and 76.2% when expressed as a percent of total tract NDF digestibility. Addition of RIB did not affect rumen digestibility of NDF.

Table 7. Rumen digestion kinetics of NDF and rumen apparent digestibility of NDF from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.[1]

	Treatment					Main effect[2] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Digestion kinetics	----------(h^{-1})----------							
Fractional passage rate								
2 h prefeeding	.024^{d}	.033^{b}	.027^{c}	.037^{a}	.001	**	**	NS
2 h postfeeding	.025^{b}	.032^{a}	.026^{b}	.034^{a}	.001	†	**	NS
Average	.024^{c}	.032^{b}	.026^{c}	.035^{a}	.001	**	**	NS
Fractional digestion rate								
2 h prefeeding	.038^{b}	.052^{a}	.036^{b}	.046^{a}	.003	NS	**	NS
2 h postfeeding	.046^{a}	.047^{a}	.034^{b}	.042^{ab}	.004	*	NS	NS
Average	.041^{bc}	.049^{a}	.034^{c}	.044^{ab}	.003	*	**	NS
Rumen apparent digestibility								
	----------(% of NDF intake)----------							
2 h prefeeding	40.7^{a}	41.1^{a}	34.6^{b}	33.9^{b}	1.0	**	NS	NS
2 h postfeeding	42.7^{a}	40.3^{a}	34.1^{b}	33.1^{b}	.9	**	†	NS
Average	41.6^{a}	40.7^{a}	34.4^{b}	33.6^{b}	.8	**	NS	NS
	----(% of total tract digestibility)----							
2 h prefeeding	85.1^{a}	86.1^{a}	76.3^{b}	77.5^{b}	2.2	**	NS	NS
2 h postfeeding	89.0^{a}	84.4^{b}	75.5^{c}	75.4^{c}	1.4	**	NS	NS
Average	86.9^{a}	85.2^{a}	75.9^{b}	76.5^{b}	1.5	**	NS	NS

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

[1]Calculated using indigestible NDF as an internal marker and rumen pool size estimates.

[2]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, †$P < .10$.

Feeding Behavior

Daily eating, ruminating, and drinking activities of cows were summarized for each treatment (Table 8). Number of eating bouts were not different across treatments and averaged 11.6 bouts/d. Mean eating bout lengths were significantly shorter ($P <$ .01) for LF treatments (27.2 min) compared to HF treatments (32.6 min) that resulted in shorter daily durations of eating for LF (301 vs. 352 min/d). Because number of eating bouts were similar across treatments, treatment differences in mean meal size were similar to differences for daily DMI (Table 3), including the presence of interaction among levels of fiber and RIB. Treatment HF+B resulted in the largest number of ruminating bouts (14.7 bouts/d) and bout number decreased ($P < .01$) as fiber or RIB were removed. Ruminating bout lengths were shorter ($P < .01$) for LF treatments but longer for +0 treatments. Consequently, time spent ruminating was less ($P < .01$) for LF (395 min/d) compared to HF treatments (500 min/d), but no effect of RIB was detected.

Time spent eating, ruminating, or chewing per unit of DM or NDF intake increased significantly upon inclusion of additional dietary NDF or RIB. Eating, ruminating, and total number of chews per day were fewer for LF compared to HF treatments ($P < .01$) and reflected time spent chewing for each activity. High fiber treatments resulted in faster chewing rates during eating compared to LF treatments (62.3 vs. 65.0 chews/min), while addition of RIB resulted in slower chewing rates during ruminating (61.8 vs. 58.2 chews/min). Number of drinking bouts and daily time spent drinking were greater for LF treatments (15.8 bouts/d; 16.6 min/d) compared to HF treatments (12.8 bouts/d; 15.1 min/d).

Reticular contractions were expressed as total per day and frequency per min during eating, ruminating, and idle periods (Table 9). No differences were detected between treatments during eating for number of contractions, however, frequency of contractions decreased as fiber was added ($P < .01$). During rumination, additional fiber or RIB increased ($P < .01$) both the total number and frequency of contractions. An

Table 8. Eating, ruminating, and drinking activities for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Eating bouts, /d	11.9	11.4	11.1	11.8	.4	NS	NS	NS
Meal size								
Mean								
kg of DM	1.9^{ab}	2.0^{a}	1.8^{b}	1.5^{c}	.2	**	NS	*
kg of NDF	.48^{b}	.50^{b}	.61^{a}	.50^{b}	.04	*	NS	*
SD, kg of DM	2.1	2.1	1.9	1.6	...	...	...	...
Maximum, kg of DM	6.2	5.9	5.6	5.1	.4	NS	NS	NS
Eating bout length, min	25.9^{c}	28.5^{bc}	33.5^{a}	31.6^{ab}	1.5	**	NS	NS
Eating time								
min/d	294^{b}	308^{b}	349^{a}	355^{a}	10	**	NS	NS
min/kg of DM	13.5^{c}	14.9^{c}	19.0^{b}	21.9^{a}	.4	**	**	NS
min/kg of NDF	53.9^{c}	59.4^{b}	55.7^{bc}	64.9^{a}	1.2	†	**	NS
Eating chews, /d	18,618^{b}	19,912^{b}	22,783^{a}	23,430^{a}	660	**	NS	NS
Eating chew rate, chews/min	61.5^{b}	63.1^{ab}	64.8^{a}	65.1^{a}	1.0	*	NS	NS
Water intake during meals, L/d	50.4^{a}	47.6^{a}	44.6^{ab}	40.5^{b}	2.5	*	NS	NS
Ruminating bouts, /d	12.1^{c}	13.4^{b}	13.5^{b}	14.7^{a}	.4	**	**	NS
Ruminating bout length, min	32.1^{c}	31.1^{c}	37.2^{a}	34.8^{b}	.8	**	*	NS
Ruminating time								
min/d	383^{b}	407^{b}	496^{a}	503^{a}	14	**	NS	NS
min/kg of DM	17.7^{d}	19.7^{c}	27.0^{b}	30.8^{a}	.4	**	**	NS
min/kg of NDF	70.8^{c}	78.2^{b}	79.0^{b}	91.1^{a}	1.5	**	**	NS
Ruminating chews, /d	23,867^{b}	24,363^{b}	31,232^{a}	29,933^{a}	917	**	NS	NS
Ruminating chew rate, chews/min	60.8^{a}	58.4^{b}	62.7^{a}	58.1^{b}	.8	NS	**	NS
Total chewing time								
min/d	677^{b}	716^{b}	846^{a}	858^{a}	20	**	NS	NS
min/kg of DM	31.3^{d}	34.6^{c}	45.9^{b}	52.7^{a}	.6	**	**	†
min/kg of NDF	125^{c}	138^{b}	135^{bc}	156^{a}	2	**	**	NS
Total chews, /d	42,485^{b}	44,275^{b}	54,015^{a}	53,363^{a}	1370	**	NS	NS
Drinking bouts, /d	16.1^{a}	15.4^{a}	13.6^{ab}	12.0^{b}	.9	**	NS	NS
Drinking bout size, L	5.6	5.4	6.0	5.7	.3	NS	NS	NS
Drinking time, min/d	16.7^{a}	16.4^{a}	15.9^{ab}	14.3^{b}	.6	*	NS	NS
Drinking rate, L/min	4.9	4.7	4.8	4.5	.2	NS	NS	NS

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

[1]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $^{\dagger}P < .10$.

Table 9. Reticular contractions and ruminal pH for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Reticular contractions								
Daily total, no./d								
Eating	564	552	607	611	20	NS	NS	NS
Ruminating	427^{c}	532^{b}	578^{b}	730^{a}	17	**	**	NS
Idle	850^{a}	764^{ab}	661^{bc}	607^{c}	35	**	†	NS
Total	1841^{b}	1848^{b}	1846^{b}	1948^{a}	22	*	*	*
Frequency, no./min								
Eating	1.93^{a}	1.80^{ab}	1.75^{b}	1.72^{b}	.05	**	†	NS
Ruminating	1.13^{c}	1.32^{b}	1.17^{c}	1.47^{a}	.02	**	**	*
Idle	1.11	1.05	1.09	1.04	.03	NS	NS	NS
Ruminal pH								
Daily pH								
Mean	6.23^{c}	6.48^{b}	6.54^{ab}	6.69^{a}	.06	**	**	NS
Variance	.24	.24	.21	.18	...	...	...	...
Minimum	5.52^{b}	5.84^{a}	5.95^{a}	6.14^{a}	.11	**	*	NS
Maximum	6.73^{b}	7.02^{a}	7.00^{a}	7.07^{a}	.05	**	**	*
Range	1.21^{a}	1.18^{a}	1.06^{ab}	.92^{b}	.09	*	NS	NS
Hours below pH:								
5.5	1.7^{a}	.2^{b}	.1^{b}	.0^{b}	.5	†	†	NS
6.0	7.0^{a}	2.8^{b}	1.6^{b}	.8^{b}	1.2	**	*	NS
6.5	15.4^{a}	11.1^{ab}	9.3^{bc}	5.3^{c}	1.7	**	*	NS
7.0	23.9^{a}	22.7^{a}	23.2^{a}	20.6^{b}	.7	†	*	NS
Start of eating	6.30^{c}	6.53^{b}	6.60^{ab}	6.77^{a}	.06	**	**	NS
End of eating	6.20^{c}	6.40^{b}	6.50^{ab}	6.62^{a}	.06	**	*	NS
Start of rumination	6.19^{c}	6.42^{b}	6.50^{ab}	6.64^{a}	.06	**	**	NS
End of rumination	6.25^{c}	6.50^{b}	6.57^{ab}	6.71^{a}	.07	**	*	NS

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

[1]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $\dagger P < .10$.

average difference of .10 contractions/min occurred between LF and HF treatments and .24 contractions/min between +0 and +B treatments, with the addition of fiber having a larger effect when RIB was present.

Ruminal pH was measured continuously each period across 5 d with an electrode placed through the rumen cannula and into the ventral sac. Ruminal pH was consistently lower for LF compared to HF treatments and +0 compared to +B treatments, regardless of summary variable used (Table 9). Mean pH was 6.23, 6.48, 6.54, and 6.69 for LF+0, LF+B, HF+0, and HF+B treatments, respectively. Both daily minimum and maximum pH values were lowest for LF+0 and highest for HF+B. The number of hours during the day in which pH was below 5.5, 6.0, 6.5, and 7.0 were all highest for LF+0 and lowest for HF+B. Hours below pH 6.5 demonstrated the most sensitivity to treatment differences compared to other pH values chosen. Declines in pH between the start and end of eating and increases in pH between the start and end of rumination averaged .12 and .07 units, respectively, and were consistent across treatments.

DISCUSSION

The primary objective of this study was to determine if depressions in intake because of RIB addition varied with NDF content of the diet. Addition of RIB decreased intake with HF but not with LF, resulting in an interaction which supports our general hypothesis that intake by cows receiving higher fiber diets is under greater control by physical constraints of the rumen. Johnson and Combs (1992) conducted a study with similar objectives using 4 cows at 53 DIM and 4 cows at 185 DIM at the start of the experiment, fed 27 and 33% NDF diets with or without RIB (25% of rumen volume). Milk and DMI responses to fiber were similar to our study, however, they observed no depression in milk production or intake from RIB at either fiber level. They suggested that their cows adapted to treatments over the 2 wk adjustment period.

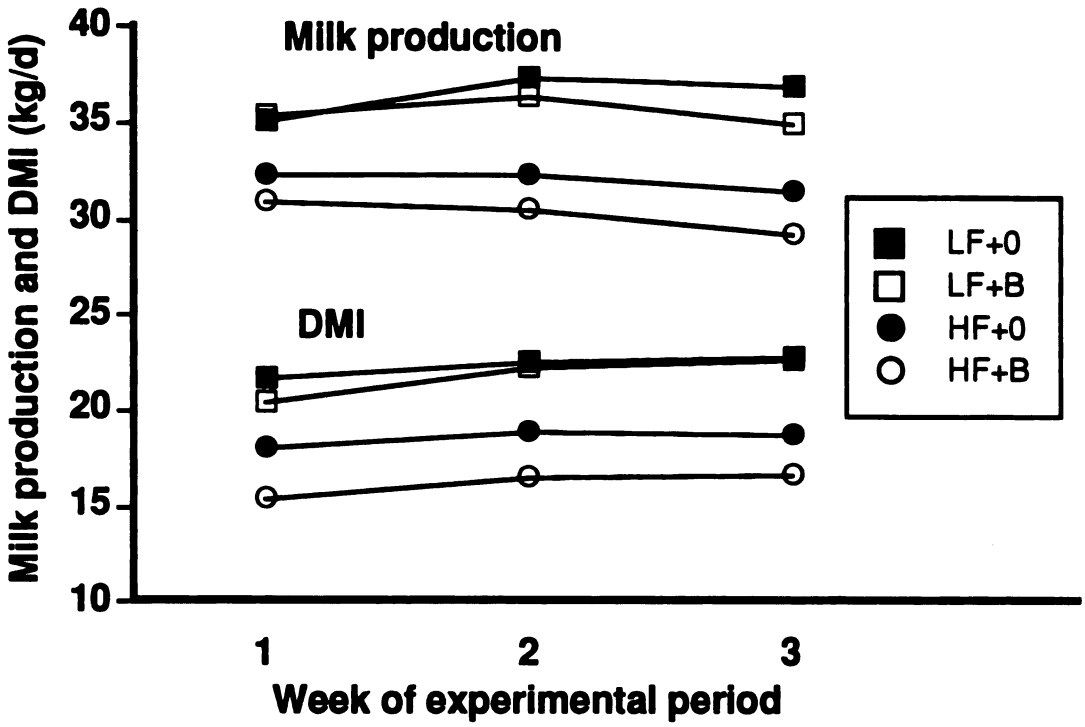


Figure 1. Mean milk production and DMI by week of experimental period for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

Figure 1 illustrates a lack of adaptation over time for cows on our study. In a review of literature (Chapter 1), depressions in DMI due to RIB addition were regressed against several factors; intake of DM was reduced to a greater degree for animals in higher states of production and for animals with smaller within species BW. Johnson and Combs (1992) may not have detected intake depressions because cows were not in early lactation throughout the duration of their study and were relatively large in size (BW = 705 kg).

The majority of the results support the general statement that fiber and RIB addition created an energy deficit compared to the basal treatment (LF+0). Milk and milk protein production and protein content decreased with both added fiber and bulk, and milk fat content tended to be higher with added fiber. These results are consistent with increases in dietary fiber concentration (Sutton, 1989). Dietary NDF concentrations

of 25 and 35% were selected for this study because they are considered to be below and above optimal NDF concentrations for milk production (Allen and Mertens, 1988a; NRC, 1989) and are near practical extremes for diets with these ingredients. No differences were observed in BW or body condition between treatments, however, lower empty BW for treatments with added fiber and RIB were indicative of energy deficit. Cow BW was similar because of higher rumen digesta mass with fiber and RIB addition. Three week experimental periods may have been too short to observe changes in external condition. When RIB was added to early lactation cows in another study (Johnson and Combs, 1991), milk production, milk composition, and BW were affected in a similar manner.

Addition of RIB resulted in no difference in ruminal or total tract digestibility of nutrients (except for OM) and is consistent with another study with cows (Johnson and Combs, 1991) but not with one with sheep (Waybright and Varga, 1991). Waybright and Varga (1991) inserted large quantities of RIB (up to 66% of rumen volume) that depressed DM, OM, ADF, and starch digestibilities. In our study, treatments with higher NDF content resulted in lower DM, OM, and NDF apparent total tract digestibilities and a shift in NDF digestion from the rumen to the hind-gut. Higher NDF concentrations with the same NDF source typically lower DM digestibility and increase NDF digestibility (Woodford et al., 1986; Cameron et al., 1991) because of improved conditions for fiber digesting microorganisms in the rumen. Changes in rumen fermentation as measured by VFA concentrations and ruminal pH were almost identical with fiber and RIB addition. Both produced lower total VFA, increased percent of VFA as acetate, decreased percent of VFA as propionate, and increased rumen pH as measured by numerous variables (Table 9). These changes are consistent with the milk production and composition data from the current study and agree with results from other studies (Johnson and Combs, 1991; Johnson and Combs, 1992). Bulk addition may alter VFA production because of decreased rumen digesta volume and increased

dilution rate of rumen liquid (Peters et al., 1990), or because of the increased extent of chewing per unit of DMI (Beauchemin, 1991a).

Insertion of inert bulk into the rumen to study physical aspects of intake control is not a novel approach, however, the type of RIB used in this study may be. Previous studies have inserted polyethylene cubes (Carr and Jacobson, 1967), expanded polystyrene (Baumont et al., 1990), air-filled balloons (Mowat, 1963), water-filled trash bags (Waybright and Varga, 1991), and water-filled balloons or tubes (Campling and Balch, 1961; Grovum, 1979; Johnson and Combs, 1992). Smaller water-filled cartons may be advantageous over large tubes because of their ability to flow among the digesta and allow a more natural movement of the digesta within the reticulorumen. Cartons were visually observed to be distributed throughout the entire reticulorumen digesta and resulted in no deleterious health effects to the cows. Amount of RIB added in this study (25% of rumen volume) was similar to that used in other studies with dairy cows (Mowat, 1963; Johnson and Combs, 1991). Added bulk may have made rumination boli more difficult to form, resulting in smaller boli and more frequent regurgitation; however, fiber also increased reticular motility during rumination so perhaps not all the increase in regurgitation frequency was because of RIB's non-physiological presence.

Changes in rumen volume upon fiber and RIB addition support the concept that daily intake was limited by rumen fill. Digesta volume declined to a greater extent with RIB on HF compared to LF treatments (16 vs. 11 L). Rumen volume expanded to compensate for added RIB, but to a lesser degree for HF. Digesta plus bulk volume was not significantly different for either bulk treatments and HF+0, suggesting that HF+0 was already limited by rumen capacity prior to bulk addition. Johnson and Combs (1992) measured digesta volume decreases of only 5 L for both fiber levels and more substantial expansion of the rumen to compensate for bulk addition. Total rumen volume includes digesta, bulk, and gaseous head space volumes. Head space volume, which may be a function of rate of fermentation and gas production, was significantly

smaller for treatment HF+0 such that no difference in total volume between fiber diets was observed. Changes in head space volume may compensate for rumen fill.

Digesta plus bulk volume was compared between measurements taken 2 h prefeeding and 2 h postfeeding (Figure 2) to examine possible control mechanisms for the main meal following the PM feeding. Main meal size averaged 2.6, 3.1, 3.3, and 2.9 kg of DM for LF+0, LF+B, HF+0, and HF+B, respectively. Volumes were similar for both determinations for treatment LF+0 but were larger postfeeding for the other three treatments. These data suggest that different mechanisms dominated satiety for LF+0 compared to the other treatments. We propose that quickly responding physiological controls had greater influence over meal size for LF+0 and that more slowly responding physical controls had greater influence over meal size for the other treatments.

Rumen NDF has been considered the component most closely associated with the space-occupying properties of rumen digesta (Mertens, 1987) because it represents the structural cell wall, and implies that neutral detergent solubles occupy no volume. Rumen digesta volume was regressed against rumen pool size of NDF using each cow-period mean (Figure 3). Every kilogram of rumen NDF was equivalent to 7.5 L of rumen digesta volume, which is similar to the bulk volume of alfalfa cell wall (Van Soest, 1982). Regression intercept was 45.9 L that represents the liquid pool in the rumen not associated with fiber particles (model $R^2 = .56$). Regression of volume on other digesta components resulted in slightly improved model fit (DM: $R^2 = .63$; OM: $R^2 = .59$; indigestible NDF: $R^2 = .57$), suggesting that NDF may not completely represent the fill properties of rumen digesta. Average RIB addition of 22.2 L to the HF diet was equivalent to a 2.3 kg decline in rumen NDF (9.6 L/kg), a .73 kg/d decrease in NDF intake, and a 2.1 kg/d decrease in DMI (94.6 g/d per L). Other studies have shown DMI depressions from RIB addition ranging from no decline with cows (Johnson and Combs, 1992) to 300 g/L with sheep (Egan, 1972); average depression in DMI from RIB addition was 94 g/L (Chapter 1).

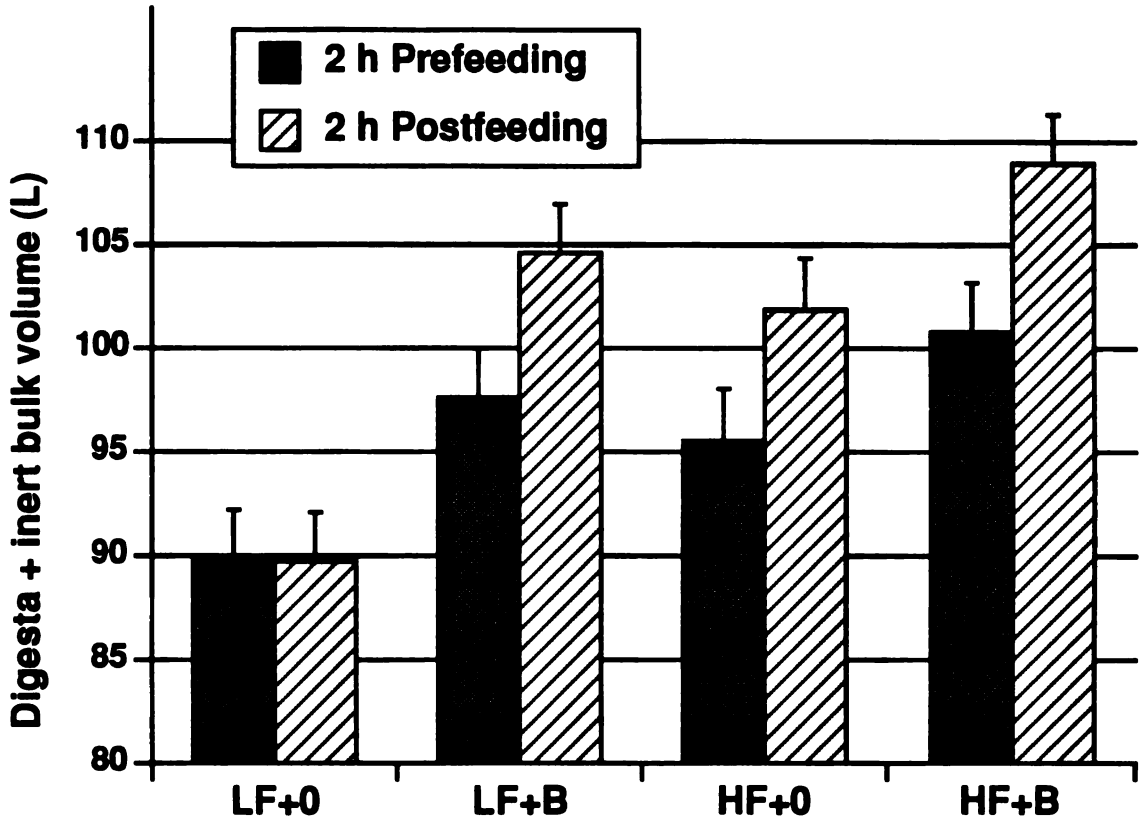


Figure 2. Rumen digesta plus inert bulk volume 2 h prefeeding and 2 h postfeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

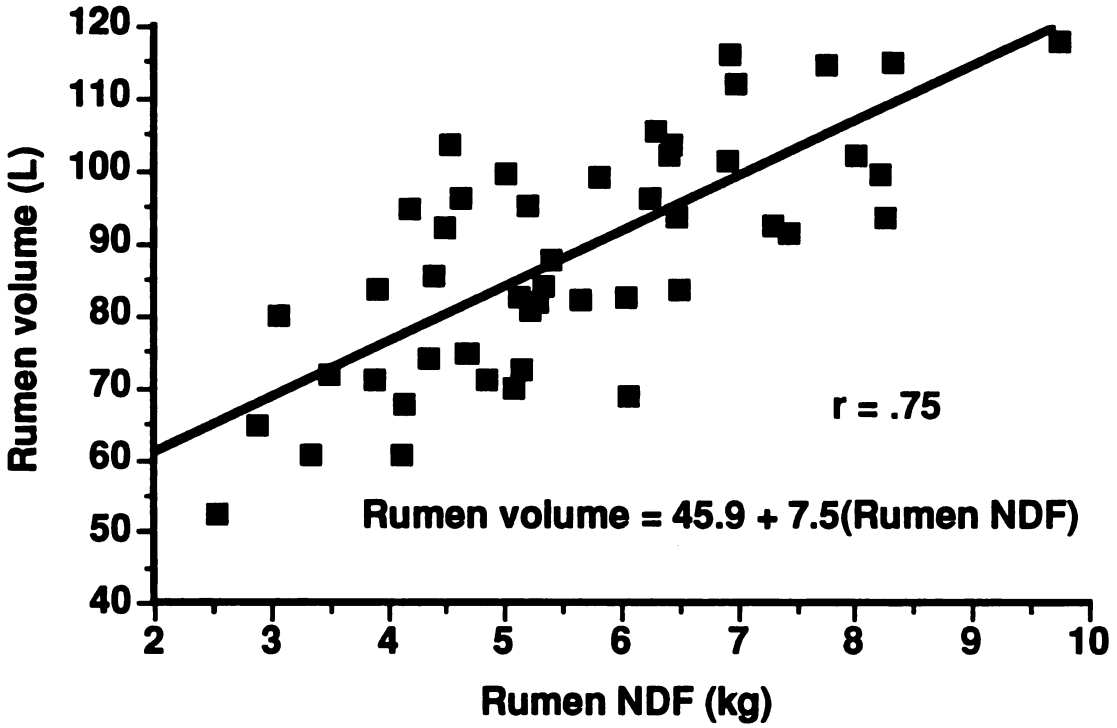


Figure 3. Rumen digesta volume as a function of rumen NDF pool size for 12 cows receiving low or high fiber diets without or with added rumen inert bulk.

Both fiber and RIB addition increased fractional passage rate of NDF from the rumen which has been previously observed (Woodford et al., 1986; Johnson and Combs, 1992). Cows may be increasing passage from the rumen in an attempt to minimize the effects of rumen fill on intake to maintain consumption of digestible energy. Fecal fiber particle size was measured to determine if increased passage from the rumen forced excretion of larger particles from the rumen and digestive tract. No increase in size was observed with added RIB, and added fiber resulted in a decrease in fiber particle size, not an increase. This fiber response may be due to the greater extent of rumination and chewing per unit of DMI for higher fiber diets (Welch, 1982; Shaver et al., 1988b). Changes in fractional digestion rates of digestible NDF because of fiber or RIB addition were in opposite directions and depended on whether they were measured 2 h pre or 2 h postfeeding. Fiber addition decreased digestion rate 2 h postfeeding and was somewhat

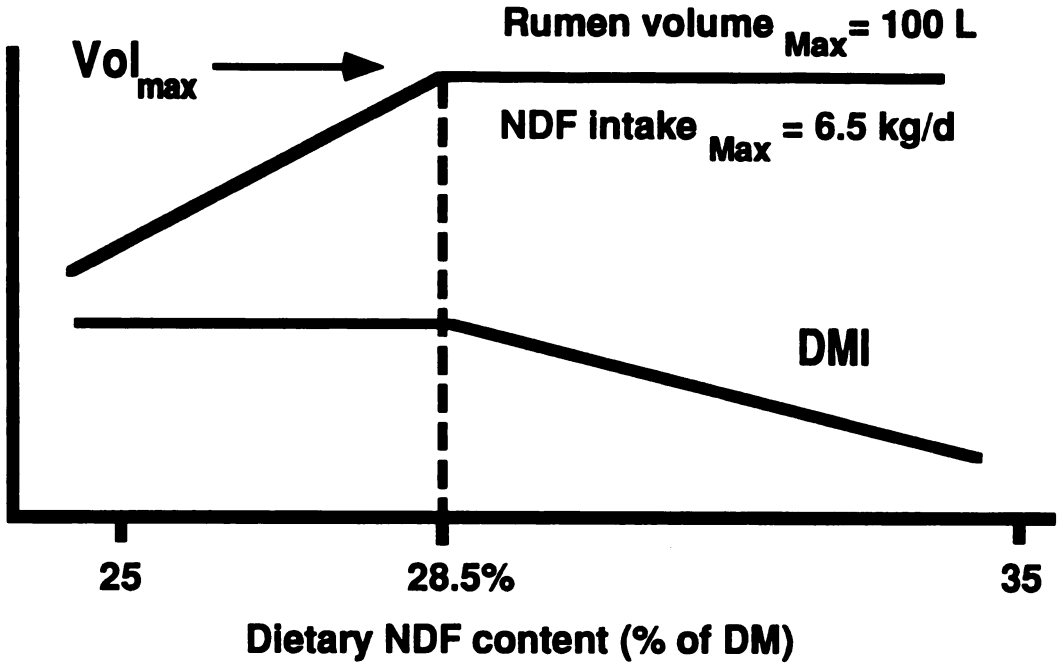


Figure 4. Model of NDF and DM intake response to increases in dietary NDF content. Intake of NDF increases until maximum rumen volume, at which point DMI decreases. Based on a maximum rumen volume of 100 L, maximum NDF intake of 6.5 kg/d, and baseline DMI of 22.8 kg/d, the threshold for intake limitation is 28.5% NDF.

expected because of a larger meal of fiber for HF and the likelihood of non-steady state conditions during measurements; addition of RIB increased digestion rate 2 h prefeeding, perhaps as a function of decreased rumen pool size of NDF.

Based on intake and rumen parameters associated with this study, a conceptual model of NDF and DM intake is proposed for diets of varying NDF concentration (Figure 4). This model is similar to others proposed by Conrad et al. (1966) and Mertens (1987). Intake of diets with low NDF content is not limited by rumen capacity. As NDF content increases, intake of NDF and rumen volume increase until a maximum rumen volume is reached. Assuming maximum NDF intake and rumen volume were obtained with treatment HF+0, maximum rumen digesta volume, digesta NDF, and NDF intake, are 100 L, 7.0 kg, and 6.5 kg/d, respectively. Using LF treatments as base DMI, the threshold for intake limitations due to rumen capacity is 28.5% NDF in the diet. At

NDF concentrations less than 28.5%, rumen volume and digesta removal rates can increase to adequately compensate for additions of dietary fiber. Above NDF concentrations of 28.5%, volume and removal rates are maximal and can no longer compensate, resulting in decreased DMI with increases in NDF content. Such values are specific for cows at physiological states receiving diets of composition similar to this study. Larger, lower producing cows likely have intake thresholds at higher NDF concentrations. Under such a model, physical limits to intake may be reduced by increasing maximum rumen volume, or by increasing rates of fiber removal from the rumen via increases in the proportion of fiber that is digestible or increases in fractional rates of digestion and passage. Further research is required to determine whether these factors influence intake in such a manner.

Cows did not increase frequency of eating to maintain intakes during fiber and RIB challenge. Changes in mean meal sizes were similar to differences in daily DMI because of no differences in the number of eating bouts. Baumont et al. (1990) reported that the number of eating and ruminating bouts increased when bulk was added to the rumen of sheep and may have helped maintain a full rumen for as much of the day as possible. Added fiber and RIB increased the percentage of small meals and decreased the percentage of larger meals (Figure 5). Distribution of DMI within a day is illustrated in Figure 6. Greater DMI occurred immediately following the fresh allocation of feed. It was hypothesized that fiber and RIB addition would promote a more even distribution of eating throughout the day, however, the opposite was observed, which is consistent with the rumen volume data depicted in Figure 2. Satiety mechanisms for individual meals may be more variable when rumen capacity is limiting daily intake. Number of ruminating bouts increased with fiber and RIB addition and may reflect the necessity to more frequently process rumen digesta to maximize digestive efficiency. Distribution of rumination activity within a day was similar for all treatments (Figure 7). Eating, ruminating, and total time spent chewing per unit of DM and NDF intake were higher

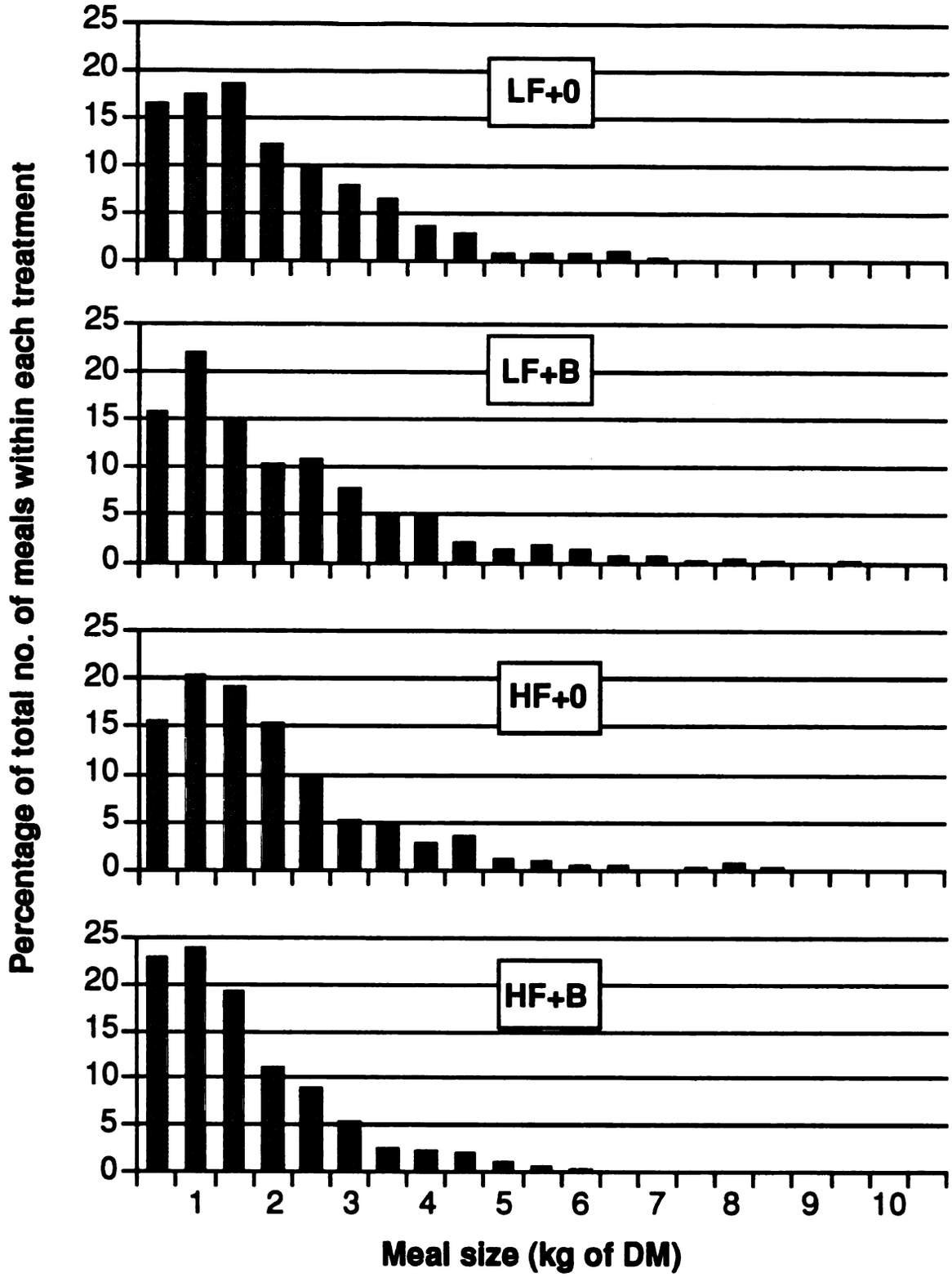


Figure 5. Distribution of individual meal sizes expressed as a percentage of the total number of meals within each treatment for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

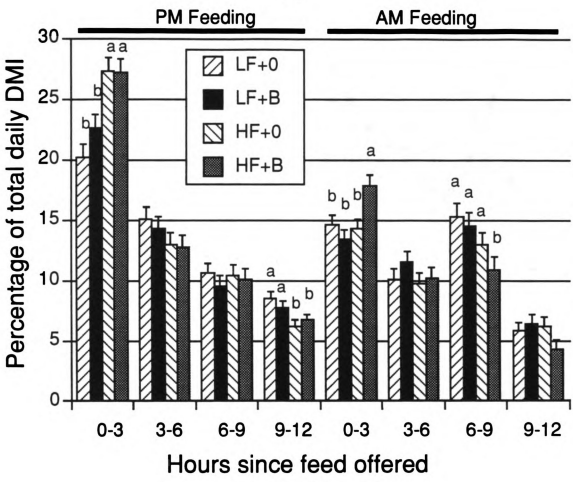


Figure 6. Distribution of DMI within a day expressed as a percentage of total daily DMI for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk. Bars within a time period with different letters differ ($P < .05$).

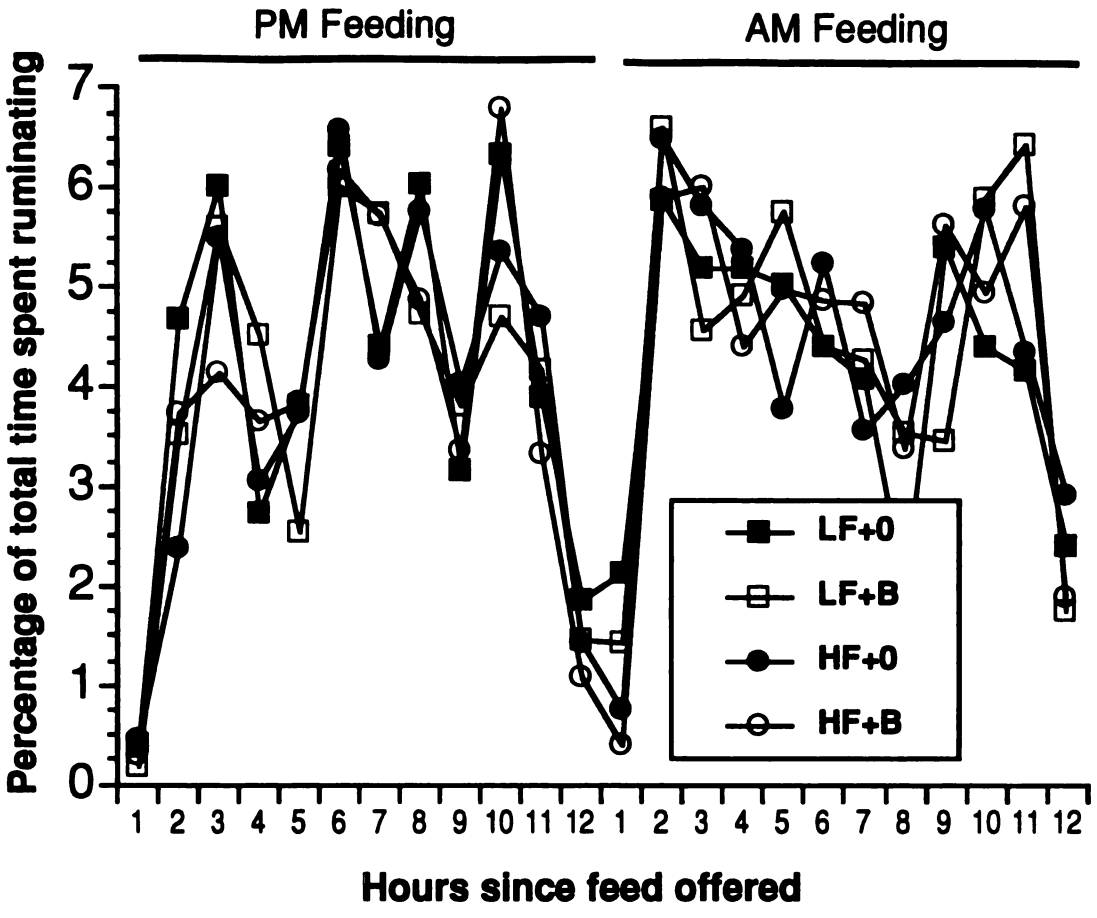


Figure 7. Distribution of rumination within a day expressed as a percentage of total time spent ruminating for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

with both fiber and RIB addition. These variables may more accurately reflect the chewing stimulation of both effects compared to examination of differences based only on time spent chewing. Increased chewing activity may have promoted greater rates of ruminal digestion and passage. Similar results have been reported (Woodford et al., 1986; Baumont et al., 1990).

Johnson and Combs (1992) monitored reticular motility and observed no differences in the frequency of contractions due to level of fiber or RIB. Frequency of contractions during eating may have decreased in our study because of slower rates of DM consumption during eating. Eating is generally considered to increase the frequency of reticular contractions (Ruckebusch, 1988). Increased frequency of contractions during rumination may have resulted from increased rumen volume, which is believed to increase frequency of contractions following feeding (Okine et al., 1989).

CONCLUSIONS

Addition of RIB decreased DMI for high producing early lactation cows receiving 35% NDF diets but not for cows receiving 25% NDF diets. Volume of rumen digesta plus RIB was similar for HF treatments whether or not RIB was present. Fiber and RIB addition increased NDF passage from the rumen in a similar manner. These data support the hypothesis that cows receiving high fiber diets have intakes limited by the physical capacity of the reticulorumen. Changes in feeding behavior or rumen function were insufficient to maintain intake under conditions of high rumen fill. Added fiber and RIB altered aspects of rumination, rumen fermentation, and reticular motility in a similar fashion, demonstrating that NDF has rumen-filling characteristics. A proposed intake model suggests that expansion of rumen volume and increases in digesta passage can compensate for increases in dietary fiber concentrations to maintain intake up to 28.5% total diet NDF for cows under conditions of this experiment. Further research is required to determine the effect of fiber digestibility and animal characteristics on fill-limited intake.

CHAPTER 5

Harvesting Alfalfa Forages with Similar Fiber Contents but Different Fiber Digestibilities from Production-Scale Fields

ABSTRACT

Five alfalfa harvests were obtained during the 1992 growing season from two adjacent 8 ha fields and ensiled in bags. Objectives were to produce silages with similar fiber concentrations but different fiber digestibilities in sufficient quantities for animal studies, and examine the consistency of production-sized fields for these variables. Four of the five silages were equal in NDF content ($P > .25$), averaging 41.2% NDF. Metabolic losses of OM during silage fermentation indicated loss of both non-NDF OM and potentially digestible NDF such that NDF content did not change between pre- and post-ensiled samples. Rate of NDF digestion, as estimated by in vitro rumen fluid digestion, was not different across silages. Extent of NDF digestion, however, was different between silages after 10, 24, and 120 h of fermentation. Two of the forages differed consistently in NDF digestibility by 5% units, resulting in a 4% difference in estimated NE_L concentration. Higher forage digestibility may significantly improve animal performance because of increased ration energy density or increased forage intake. An experiment using these two forages with early lactation dairy cows would be useful to assess the importance of fiber digestibility to ruminants with high energy requirements.

INTRODUCTION

Evaluation of forage quality and its importance to ruminant performance has been of interest for many years (Crampton et al., 1960; Waldo and Jorgensen, 1981). It is

generally agreed that the goal of forage feeding is to maximize daily intake of digestible nutrients. Such a goal requires either high forage intake, high forage digestibility, or both. The non-cell wall portion of forages is rapidly solubilized in the rumen and almost 100% digestible (Van Soest, 1965), consequently having little affect on forage intake when limited by rumen fill and little affect on digestibility at constant dietary concentrations. Conversely, concentration and availability of forage cell wall, or NDF, are the primary determinants of the digestible energy content of forages (Goering and Van Soest, 1970) and may promote differences in forage intake (Van Soest et al., 1978).

Concentration of forage NDF is negatively correlated to intake and digestibility (Van Soest et al., 1978). In dairy cattle, dietary NDF content was related negatively to both milk yield and intake (Briceno et al., 1987; Mertens, 1983), and positively to rumen fill (Shaver et al., 1988a). Fiber content alone may not describe completely the affect of fiber on intake and digestibility. Of increasing interest is NDF digestibility. Ruminants are unique among food animals because of their ability to extract large amounts of energy from forage NDF. The efficiency of rumen microbial fiber digestion depends, among other things, on the intrinsic characteristics of the plant fiber that render it more or less available to rumen fermentation. Greater fiber digestion has been suggested to improve forage energy content and intake potential (Allen, 1991).

Studies that have examined fiber digestibility on animal performance are limited. Diets similar in NDF content but different in rate and extent of NDF digestion were compared and demonstrated advantages to faster and more completely digestible NDF (Varga et al., 1984). However, this study used different sources of NDF, including NDF from by-product feeds, that confounded interpretation of results for fiber digestibility. A preferred approach is to examine ruminant performance in response to a single forage specie harvested from different environments. Environmental growing conditions can significantly alter fiber composition and digestibility (Van Soest et al., 1978). An ideal comparison would include two harvests of the same forage type with similar fiber

contents, similar protein contents, but different fiber digestibilities. Such a study would isolate the effect of NDF digestibility to allow its evaluation independent of NDF content and source. In vitro NDF digestibility has been shown to differ significantly between small plots of alfalfa with similar fiber contents grown under varying conditions (Allen et al., 1991).

Finally, analyses of forage composition useful for ration formulation require that samples not only reflect the true mean of the forage but also that the range of forage quality represented by the samples is relatively small. For example, rations formulated using an average forage NDF content of 40% vary widely in quality if the material from which the sample was taken ranges from 30 to 50% NDF. Even relatively pure stands of a forage specie may fluctuate greatly in large fields with diverse soil types and fertilization. Little is known about the consistency of forage fiber digestibility within the same harvest, especially for material from a large stand. Consistency needs to be demonstrated before this characteristic of forage quality can be implemented in ration formulation.

Objectives of this study were to harvest production-sized fields of alfalfa at similar fiber concentrations during the diverse conditions of a single growing season and in sufficient quantities to permit their use in animal studies. Consistency of differences for in vitro fiber digestibility of the resulting silages was to be examined. If significant differences were obtained, forages would be reserved to evaluate the effect of fiber digestibility on intake and in vivo digestibility in lactating dairy cows.

MATERIALS AND METHODS

One 16.2 ha field of pure-stand alfalfa (Big 10 cultivar) in its 2nd year of production on the campus of Michigan State University, East Lansing was used for this study. Two 8.1 ha plots (A and B) were generated by dividing the field in half (Figure 1). Plot A forage was cut and removed on May 19, 1992. This harvest was not included in the study and was removed to stagger regrowth and harvesting between plots A and B. After May 19, samples from each stand were taken approximately every 3 d at 4 locations

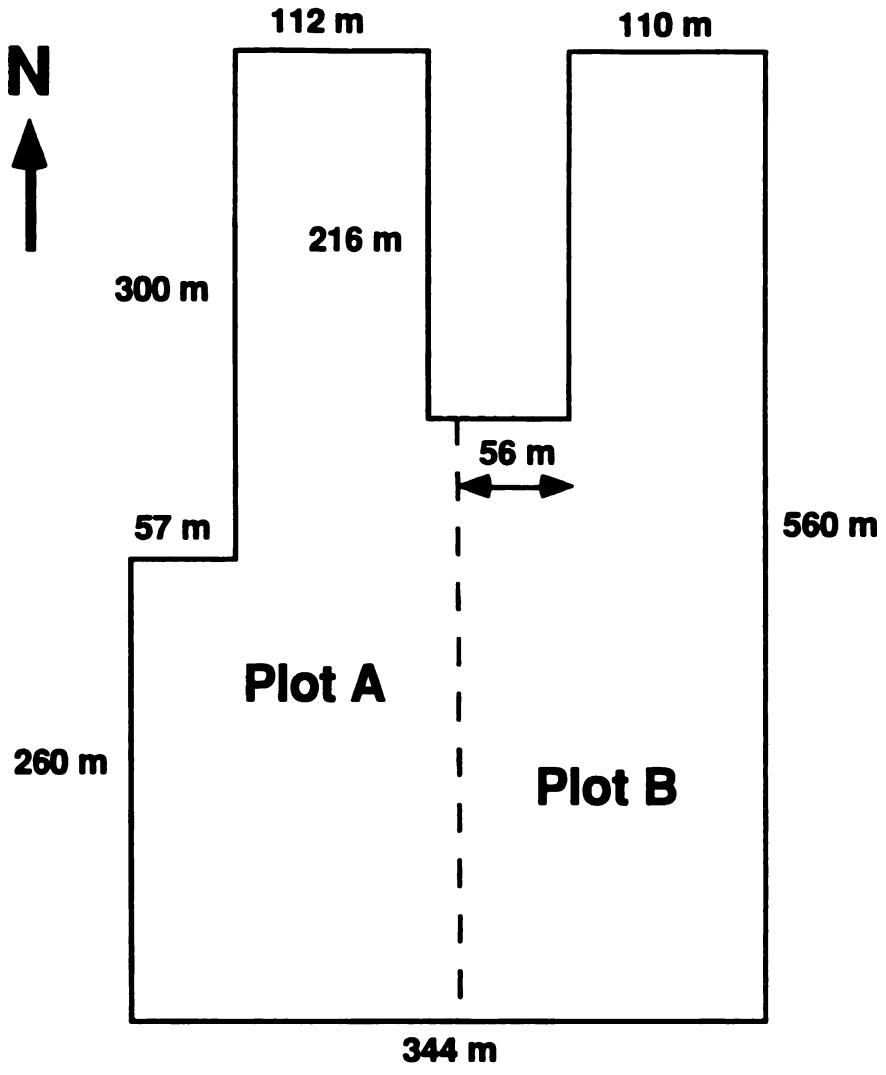


Figure 1. Dimensions of plots from which alfalfa forage was sampled and harvested.

within each plot. Samples were cut with a scissors at a height approximating that of mechanical cutting (10 cm stubble), dried at 52°C, and ground through a Wiley mill (1-mm screen). Samples were individually analyzed for NDF concentration using a procedure previously described (Chapter 2).

The decision of when to cut and harvest each plot was made when projections indicated harvested forage would contain 40% NDF. Standing forage was cut between 0800 and 1200 h with a conventional sickle bar mower-conditioner. A total of six cuttings were made (3 for each plot) throughout the summer following the initial clip of plot A. Intervals between all cuttings averaged 19 d (range = 14 to 22 d). Four samples taken on the day of cutting were separated to estimate leaf:stem DM ratios and evaluated for stage of maturity (mean stage by weight) according to procedures of Kalu and Fick (1981). Forages were field wilted for 1 to 2 d to achieve target DM concentrations of 30 to 35% and chopped between 1200 and 1700 h with a 12-knife forage harvester to achieve medium fineness of chop. Every load of forage was sampled during packing into a 2.5 m diameter silage bag (Ag-Bag Corporation, Blair, NE). A separate bag was used for each harvest. Ensiling was completed in 1 d for each forage.

Pre-ensiled samples were dried immediately at 52°C in a forced-air oven. Two months after the final harvest, post-ensiled samples were taken from four locations within each bag and dried. Following grinding to 1 mm with a Wiley mill, both pre- and post-ensiled forage samples were analyzed for ash, NDF, and NDF digestibility as estimated by in vitro fermentation with buffered rumen fluid (Goering and Van Soest, 1970). Samples were analyzed for NDF immediately following 0, 4, 10, 24, and 120 h of fermentation. Rate of NDF digestion was estimated for each sample as the negative slope of the regression between the natural logarithm of digestible NDF remaining vs. time at 4, 10, and 24 h. This model assumes first order digestion with respect to digestible NDF concentration. Indigestible NDF was defined as NDF remaining after 120 h of fermentation and was subtracted from the total NDF remaining at each time point to obtain

concentrations of digestible NDF. Post-ensiled samples were analyzed additionally for CP content using the Hach procedure (Watkins et al., 1987). Statistical differences in forage composition were determined with analysis of variance (SAS, 1985).

RESULTS AND DISCUSSION

Sampling of alfalfa plots began at least 8 d prior to the actual day of cutting (Figure 2). Concentrations of NDF ranged from 25 to 33% at first sampling and 38 to 42% at cutting. Rate of NDF increase for all forages averaged .74% units/d and ranged from .52 to 1.02% units/d. The largest NDF increase between any two sampling days was 2.2% units/d while the smallest was zero; variation in NDF accumulation appeared to be related to daily temperature and light availability, although these variables were not measured.

Out of six cuttings, five forages were successfully ensiled (Table 1). Forage C was destroyed by 6 d of continuous rain following cutting and was chopped onto the field as fertilizer to allow continued plant regrowth. Average amount of forage ensiled for the five successful harvests was 22 tonne of DM. Small but statistically significant differences were present for stage of maturity (2 = late vegetative, 3 = early bud, 4 = late bud) and leaf:stem ratio. Prior to ensiling, forage DM was similar for A and E, and B and F. Whole plant NDF content within forage was consistent such that mean differences as small as 1.4% units were different ($P < .05$) across forages. Digestibility of NDF differed significantly after 10 and 120 h of fermentation, but rate of NDF digestion was similar.

After ensiling, visual appraisal indicated that each forage silage was of excellent quality (Table 1). Our objective was to obtain forages with similar NDF concentrations after ensiling, which was achieved for forages B, D, E, and F (mean = 41.2% NDF; $P >$ .25). It should be noted that more differences were likely if more replication had been performed. Forage A will not be included in subsequent results and discussion. Several challenges were encountered in the attempt to produce silages with equal NDF contents. First, four spot samples taken immediately prior to cutting may not have represented the average composition of the cut material. A main cause of this may have been the inability

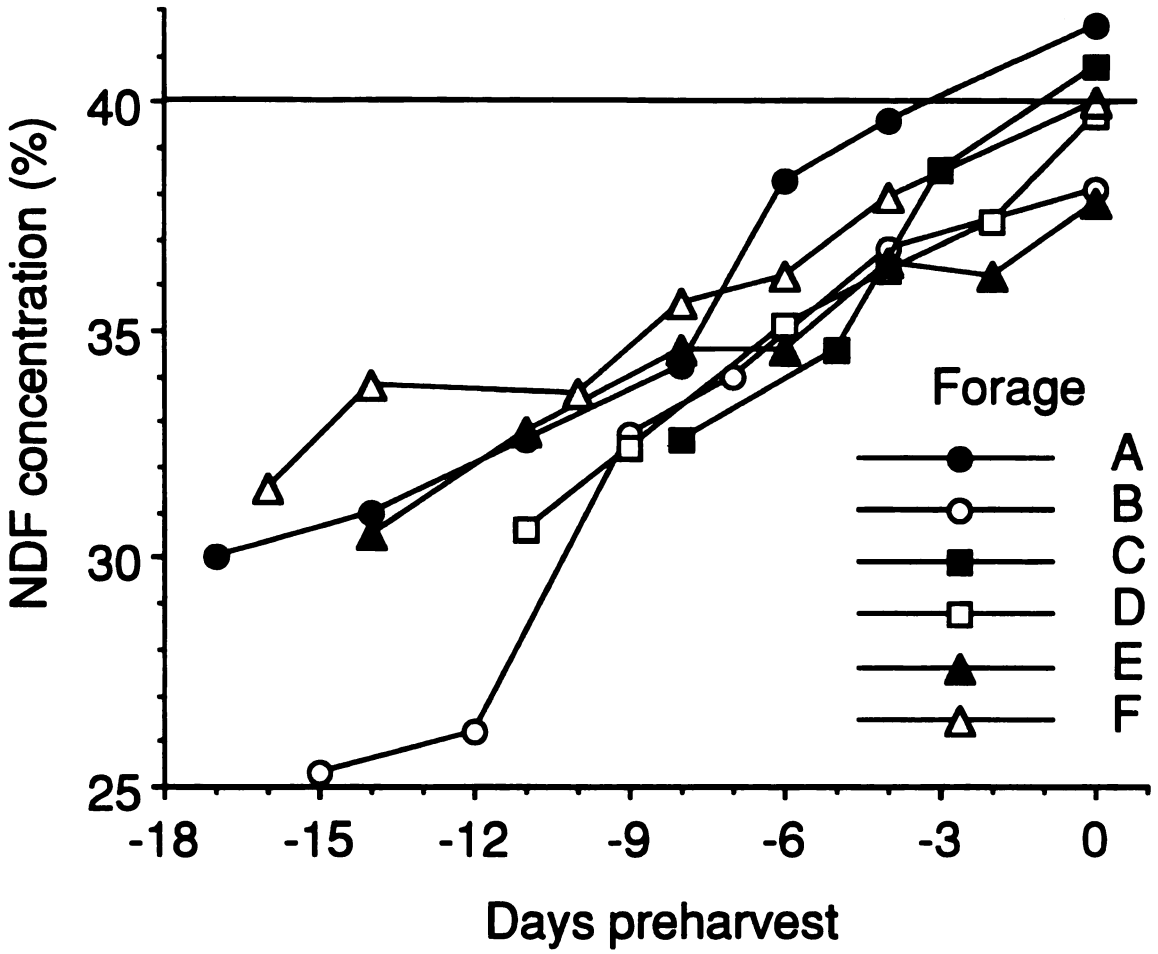


Figure 2. Concentration of NDF in alfalfa forages sampled at various days prior to harvest. Objectives were to obtain forage with 40% NDF at day 0.

Table 1. Characteristics of alfalfa forage harvested during the 1992 growing season from two adjacent 8 ha fields.

	Forage					
	A	B	C	D	E	F
Field	B	A	B	A	B	A
Cutting number	1	1	2	2	3	3
Cutting date	6/8	6/27	7/11	7/27	8/17	9/8
Yield, tonne of DM	21.6	21.7	Lost due to rain	20.7	23.6	20.8
Stage of maturity[1]	3.12^{ab}	2.72^{d}		3.02^{bc}	2.88^{cd}	3.23^{a}
Leaf:stem ratio[1]	.57^{c}	.88^{b}		.98^{ab}	1.14^{a}	.96^{ab}
	----------Pre-ensiled----------					
n	12	10		9	11	10
DM, %	33.6^{c}	40.9^{a}		35.9^{b}	33.0^{c}	39.7^{a}
Ash, % of DM	9.8^{bc}	9.6^{c}		10.2^{a}	9.9^{ab}	9.6^{bc}
NDF, % of DM						
Whole plant	44.4^{a}	40.8^{c}		40.3^{c}	38.9^{d}	42.8^{b}
Leaf[2]	23.4	22.2		24.0	23.2	25.6
Stem[2]	55.0	54.5		58.5	56.8	56.2
NDF digestibility[1,3], %						
10 h	27.2^{b}	27.7^{b}		27.6^{b}	30.1^{ab}	32.0^{a}
24 h	44.2	43.8		43.9	45.5	45.4
120 h	50.5^{ab}	50.8^{ab}		49.0^{b}	51.7^{a}	50.7^{ab}
Rate of NDF digestion, h^{-1}	.098	.092		.105	.099	.102
	----------Post-ensiled----------					
n	4	4		4	4	4
DM, %	30.0^{b}	39.6^{a}		33.3^{b}	32.5^{b}	38.0^{a}
Ash, % of DM	10.5^{c}	11.1^{b}		11.1^{b}	10.7^{bc}	12.2^{a}
CP, % of DM	21.8^{c}	24.2^{b}		26.2^{a}	24.5^{b}	24.6^{b}
NDF, % of DM	45.8^{a}	41.9^{b}		40.4^{b}	40.1^{b}	42.4^{b}
NDF digestibility, %						
10 h	17.0^{a}	19.5^{ab}		18.3^{a}	23.1^{c}	22.0^{bc}
24 h	41.3^{a}	41.2^{a}		39.6^{a}	44.8^{b}	41.4^{a}
120 h	47.7^{ab}	48.2^{ab}		45.5^{a}	51.0^{b}	47.1^{a}
Rate of NDF digestion, h^{-1}	.100	.095		.101	.104	.103

[1]n = 4.

[2]n = 1.

[3]Determined from in vitro fermentation with buffered rumen fluid for length of time indicated.

[a,b,c,d]Values in same row with different superscripts differ ($P < .05$).

to predict cutting difficulties faced with lodged plants and the extent of remaining plant stubble following cutting. Second, extent of leaf loss may have varied across harvests depending on windrow density and width, leaf density, and drying conditions. Third, harvested forages may have differed in their fermentation characteristics during ensiling, resulting in variable losses of NDF and non-NDF substrate; the correlation between pre- and post-ensiled NDF contents (r = .94) suggests that this problem was minimal. Finally, the challenges presented by the occurrence of rain and the schedule of hired labor were probably of greatest concern.

Silage DM was similar for B and F, and D and E (Table 1), with DM increasing 2 to 3% units from the first to last sample for each forage. In vitro digestion of NDF was most rapid during initial periods of fermentation, which supports the concept of first-order digestion kinetics. Nevertheless, none of the forages differed in fractional rate of digestion (mean = .101 h^{-1}). Digestibility of NDF was consistent within each ensiled forage to produce significant differences across B, D, E, and F after 10, 24, and 120 h. Figure 3 illustrates consistency of NDF content and NDF digestibility for forages D and E. Across all forages, the average coefficient of variation for NDF content within forage was 4.0%, and that for NDF digestibility was 5.2%, indicating that fiber concentration may be slightly less variable within fields of alfalfa than digestibility. Allen et al. (1991) detected a large range (25 to 55%) in alfalfa NDF digestibility after 30 h fermentations across samples taken from numerous small plots. It was not known, however, whether differences would be consistent across a field of a size typically found on farms. This study suggests that differences in NDF digestibility are repeatable within an entire field of alfalfa and may be useful in evaluating forage quality.

Forage analyses were compared between samples taken pre- and post-ensiling (Table 2), averaged across all five forages harvested. Changes in composition reflect metabolic processes associated with silage fermentation. Fermentation requires the conversion of some silage OM to organic acids and heat. A reduction in forage DM

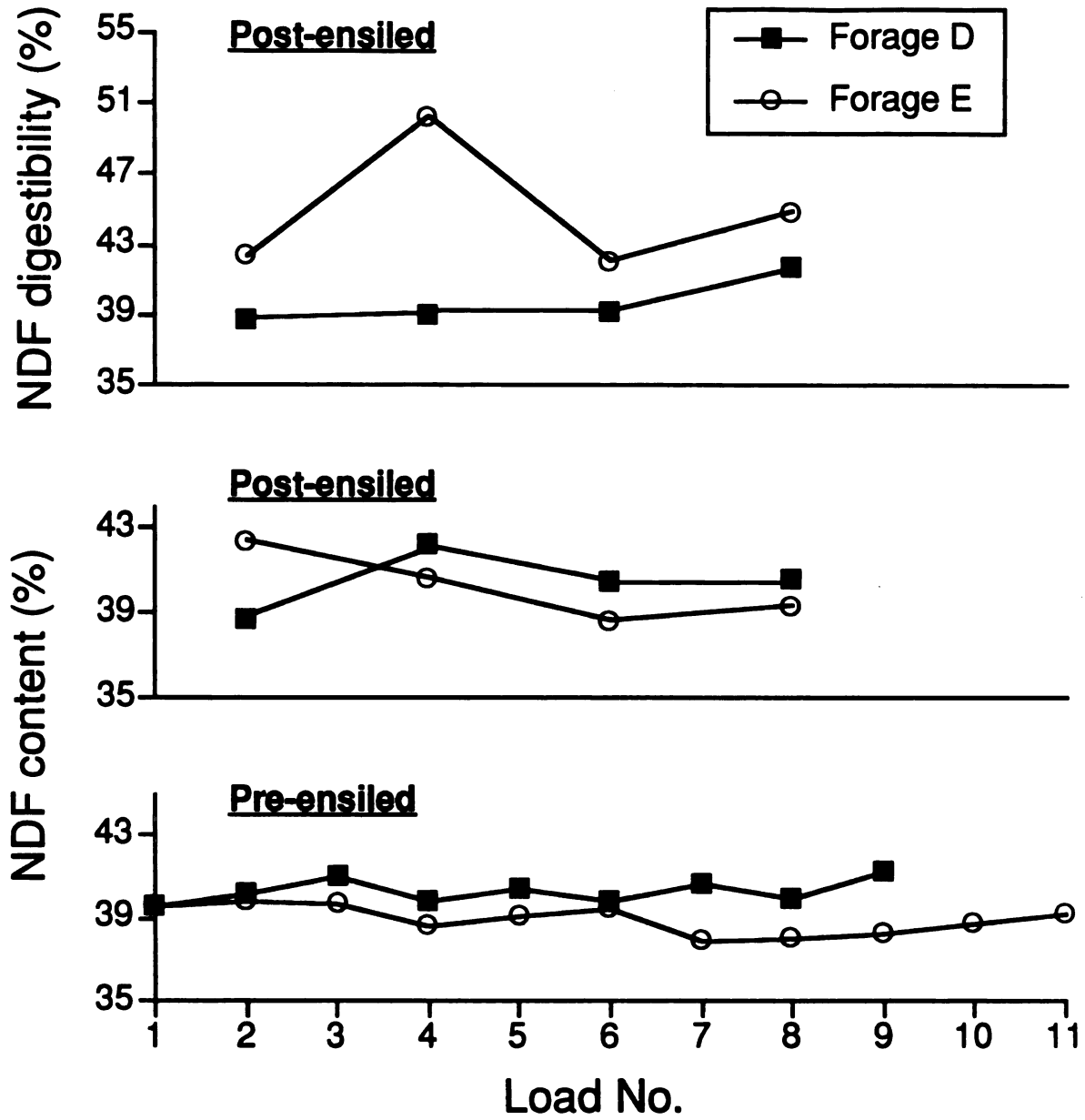


Figure 3. Neutral detergent fiber concentrations and NDF digestibility for loads of chopped alfalfa obtained pre- and post-ensiling from harvests D and E. Digestibility of NDF was determined from 24 h in vitro fermentation with buffered rumen fluid.

Table 2. Composition of alfalfa forages before and after ensiling.[1]

	Pre-ensiled	Post-ensiled	Significance
DM, %	37.1	34.7	.01
Ash, % of DM	9.8	11.1	.02
NDF, % of DM	41.3	42.1	NS[2]
NDF digestibility,[3] %			
10 h	28.9	20.0	.01
24 h	44.6	41.7	.02
120 h	50.5	47.9	.01
Rate of NDF digestion, h^{-1}	.099	.101	NS

[1]Average across all forages harvested.

[2]NS = $P > .10$.

[3]Determined from in vitro fermentation with buffered rumen fluid for length of time indicated.

content and an increase in ash is characteristic of such a process (Table 2). Concentration of NDF did not change significantly; however, NDF digestibility decreased substantially, especially with earlier lengths of in vitro fermentation. These changes suggest that both digestible NDF and non-NDF OM were consumed by microorganisms during silage fermentation such that total NDF concentration did not change. Other work also has detected fermentation of cell wall components during ensiling (Morrison, 1988). Studies that seek to improve silage fermentation should not strive solely to reduce forage NDF, but rather, strive to decrease indigestible NDF or increase the rate of NDF digestion in the rumen.

Correlations among the various descriptors of forage quality across the five harvested silages are listed in Table 3. Ratio of leaves:stems was related negatively to NDF content and tended to be positively related to CP content and 10 h NDF digestibility. Except for this tendency, differences in NDF digestibility were not related to differences in maturity, leaf:stem ratio, or NDF content, a result similar to that reported by Allen et al.

Table 3. Correlation matrix among descriptors of forage quality for all five forage silages.[1]

	Maturity	L:S[2]	CP%	NDF%	10 h[3]	24 h[3]	120 h[3]
L:S	-.28						
CP%	-.15	.79					
NDF%	.43	-.95	-.89				
10 h	-.08	.81	.35	-.59			
24 h	-.26	.44	-.20	-.24	.73		
120 h	-.44	.33	-.29	-.17	.62	.97	
Rate[4]	.59	.44	.19	-.25	.54	.45	.22

[1]Values > |.87| are significant ($P < .05$).

[2]L:S = Leaf:stem.

[3]NDF digestibility (%) following indicated time of in vitro fermentation.

[4]Rate = Fractional rate of NDF digestion (h^{-1}).

(1991). It is speculated that differences in NDF digestibility between cuttings were due to the interaction of light, temperature, and moisture during the vegetative growth period of each forage. Vough and Marten (1971), as well as others, have demonstrated the effects of these environmental factors on alfalfa yield and nutrient concentrations but have not examined their effects on fiber digestibility. Van Soest et al. (1978) summarized previous studies and found that temperature and water availability increased, and light decreased, forage cell wall content. Opposite relationships were found with DM digestibility. They suggested that increased lignification of the cell wall because of more rapid plant growth decreases the digestibility of the cell wall. Digestibility of cell wall also may vary depending on the physical structure of individual fiber molecules and their interaction with rumen microorganisms (Hatfield, 1993; Dehority, 1993).

Currently fiber digestibility is not measured routinely in forage analyses nor is it accounted for when estimating the energy content of forages. A common method for calculating forage energy is to determine its fiber concentration and then assume a direct relationship between fiber and energy (Harlan et al., 1991). For example, if two alfalfa

silages have the same NDF and ADF concentration, they are assumed to contain equal energy, regardless of their actual fiber digestibilities.

Forages D and E provide a unique opportunity to examine the potential error involved by not considering fiber digestibility when determining energy content. Except for crude protein content, D and E are identical in all respects other than NDF digestibility. In addition, they are the only two forages that differ in NDF digestibility at every time of fermentation. Based on energy:fiber relationships, both forages would be assigned an energy value of 1.34 Mcal of NE_L/kg of DM, using equation [14] from Harlan et al. (1991). Based on NDF digestibility at 24 h, forage E contains 2.1% units of TDN more than forage D ([44.8 - 39.6] * 40.25% NDF), or .05 Mcal of NE_L/kg of DM (1% TDN = .0245 Mcal NE_L/kg of DM; NRC, 1989). Increased NDF digestibility may also increase forage intake for early lactation cows, whose intakes may be limited by rumen fill (Chapter 4). If undigested NDF is the nutrient responsible for rumen fill, a limit in ruminal capacity suggests that forages are consumed to a constant undigested NDF load. For every kilogram of forage intake, forage D contributes an additional 21 g of unfermented NDF to the rumen compared to forage E. Consequently, greater quantities of forage E can be consumed prior to reaching maximum rumen load.

The potential impact of fiber digestibility on animal performance can be examined by incorporating the energy and intake differences between forages D and E into theoretical diets for early lactation cows (Table 4). When formulated to 27% NDF, the diet of forage E contains .02 Mcal NE_L/kg of DM more than diet D and an intake advantage of 1.6 kg/d of DM. The combined effect of energy density and intake potential results in an NE_L intake advantage of 3.1 Mcal/d for diet E, which is equivalent to 4.5 kg/d of milk production. Actual response to increased fiber digestibility will probably be equal to or less than this maximal estimate; increases in forage intake may increase passage of digesta from the rumen that results in decreased rumen digestibility. Robinson and McQueen (1992) examined the response of midlactation cows to differences in timothy

Table 4. Potential improvement in intake and milk production in early lactation cows because of an increase in NDF digestibility between forages D and E.[1]

	NDF digestibility	
	Low	High
Theoretical diet composition	----------% of DM----------	
Forage D	54.7	...
Forage E	...	54.7
Concentrate[2]	45.3	45.3
NDF[3]	27.0	27.0
Indigestible NDF[4]	14.9	13.8
NE_L, Mcal/kg DM	1.58	1.60
Theoretical cow performance		
Indigestible NDF intake, kg/d	3.0	3.0
NDF intake, kg/d	5.4	5.9
DMI, kg/d	20.1	21.7
NE_L intake, Mcal/d	31.7	34.8
Milk production (3.5% fat), kg/d	31.9	36.4

[1]Assumes maximal indigestible NDF intake of 3.0 kg/d because of rumen fill.

[2]Assumes concentrate composition of: NDF = 11% of DM, NDF digestibility = 67%.

[3]Diets formulated to contain 27% NDF.

[4]Calculated using NDF digestibility after 24 h in vitro fermentation.

grass NDF digestibility and found increases in milk yield and in vivo NDF digestibility but no increase in intake. Rumen fill for these cows may not have limited intake, resulting in no improvement in intake with higher fiber digestibility.

Obtaining sufficient quantities of forages like D and E to examine the effect of fiber digestibility on early lactation performance was an important objective of this work. These forages were reserved for such an experiment. The experiment was conducted during the spring of 1993 and results are reported in Chapter 6. Future work in this area should strive to obtain large quantities of forage with greater differences in NDF digestibility. Comparisons within various NDF concentrations, across different extents of NDF digestion, and across different rates of NDF digestion would also be valuable. The ultimate goal of this work is to improve estimation of forage quality as it relates to animal performance and to formulate more accurate rations for ruminant animals.

CONCLUSIONS

Interactions between heat, light, and moisture during a growing season may alter fiber formation in alfalfa throughout an entire field and make its digestibility distinctly different from that of another cutting, variety, or location. Because fiber concentration and fiber digestibility may be consistent for an entire field, average quality characteristics of the alfalfa field are useful. Forage analyses differ between pre- and post-ensiled samples, especially for fiber digestibility. Use of post-ensiled analyses are most relevant for comparing fiber digestibilities of alfalfa silage. Differences in fiber digestibility may affect currently used estimates of energy values for alfalfa and other forages. Higher forage digestibility may significantly improve animal performance because of increased energy density or increased forage intake.

CHAPTER 6

Enhanced Intake and Production of Cows Offered Ensiled Alfalfa with Higher Neutral Detergent Fiber Digestibility

ABSTRACT

Two alfalfa silages with similar NDF concentrations (40%) but different NDF digestibilities (40 vs. 45% after 24 h in vitro fermentation) were offered to 12 multiparous cows (13 DIM) in a 2 period balanced crossover experiment. Silages were mixed with a shelled corn-based concentrate to achieve diet NDF concentrations of 35%. Objectives were to determine the effect of forage fiber digestibility on intake and production of cows with intakes limited by rumen fill using treatments unconfounded by differences in fiber source, concentrate, or forage:concentrate ratio. Milk production (36.3 vs. 38.2 kg/d) and DMI (19.4 vs. 20.4 kg/d) were significantly greater with higher NDF digestibility. Apparent in vivo DM and NDF digestibilities, total rumen VFA after feeding, and molar proportion of propionate also tended to increase with higher NDF digestibility. During the trial, diets differed not only in NDF digestibility (3% units) but also in NDF content (1.8% units) because of loss of digestible NDF in the higher quality forage; consequently, interpretation of results is difficult. If increases in NDF digestibility prior to ensiling promote decreases in NDF content after ensiling, benefits to harvesting forages with higher NDF digestibility may be substantial. Further experimentation with forages with larger differences in fiber digestibility at the time of feeding is required to more closely examine this effect.

INTRODUCTION

Formulation of diets for dairy cows based on NDF concentrations of the ingredients has been advocated because of positive relationships between NDF content and rumen fill and negative relationships between NDF content and energy concentration (Mertens, 1985; 1987). Mertens (1987) indicated that cows consume approximately 1.1% of their BW as NDF per day when intake is limited by rumen capacity and suggested that this relationship was sufficiently consistent to predict DMI. Comparing data across several experiments, Briceno et al. (1987) observed curvilinear relationships between DMI and NDF content of the diet that differed by forage species, indicating that not all forage NDF results in the same intake response. Indeed, intake of NDF as a percent of BW has been shown to vary with DIM, FCM production, and NDF content of the diet (Rayburn and Fox, 1993). A recent attempt to improve intake predictions using NDF found that additional information is needed on the effect of fiber digestibility and rumen capacity on intake (Williams et al., 1989). When intake is limited by rumen fill, increases in the fraction of NDF that is digested or increases in rates of NDF digestion and passage may enhance clearance of fill from the rumen and improve DMI (Chapter 4).

Rumen digestion of fiber is a dynamic process that involves microbial attachment and fermentation of cell wall polysaccharides. The extent of fiber digestion (i.e., fiber digestibility) at any time is a function of the proportion of fiber that is potentially digestible, the rate of fiber digestion in the rumen, and the rate of fiber passage from the rumen (Allen and Mertens, 1988b). Measurement of digestion rate, digestion lag, potential extent of digestion, and passage rate is required to completely describe fiber digestion quantitatively (Mertens, 1977). Several studies have provided evidence that rate and potential extent of NDF digestion varies both across and within fiber sources (Smith et al., 1972; Varga and Hoover, 1983; Robinson and McQueen, 1992). Smith et al. (1972) observed variation in rate and extent of digestion between numerous forage

species and within forages differing in maturity. Varga and Hoover (1983) detected differences between forages and a number of concentrate and by-product feeds. More recent studies have shown differences in digestibility within forage species (Llamas-lamas and Combs, 1990; Allen et al., 1991; Allen et al., 1992; Robinson and McQueen, 1992). Interest in cell wall digestibility by ruminants has stimulated a recent international symposium (USDA-ARS, 1993) that reviewed current knowledge of forage fiber digestion.

Improvements in forage fiber digestibility may not only increase the energy value of a particular forage, but also stimulate additional DMI (Gill et al., 1969). Crampton and co-workers (Crampton et al., 1960; Donefer et al., 1960) developed a nutritive value index for forages and found that relative forage intake with sheep was highly correlated ($r > .83$) with cellulose digestibility after 12 h of in vitro incubation. Muller et al. (1972) fed sheep corn silage stover from a normal and brown mid-rib mutant variety that contained similar NDF concentrations but different in vitro NDF digestibilities. In vivo DM digestibility increased 11% and DMI increased 29% with improved fiber digestibility. Intake by steers fed straw was related to rate and extent of DM, and likely NDF, digestion (Orskov et al., 1988). Recent studies with lactating dairy cows have shown variable responses to fiber digestibility (Keith et al., 1979; Varga et al., 1984; Miller et al., 1990; Llamas-lamas and Combs, 1990; Robinson and McQueen, 1992; Feng et al., 1993). In only one study (Llamas-lamas and Combs, 1990) was DMI significantly greater with higher fiber digestibility. Studies of Varga et al. (1984), Miller et al. (1990), and Feng et al. (1993) were based on rumen fill characteristics of numerous feeds (Varga and Hoover, 1983) but are difficult to interpret because of the wide variety of fiber and starch sources utilized. Studies of Keith et al. (1979) and Robinson and McQueen (1992) were not confounded by differences in fiber source and forage:concentrate ratio. Both studies showed improved milk production with greater fiber digestibility but no difference in DMI, perhaps because cows were not in early

lactation and did not have intakes limited by rumen capacity. If changes in intake are shown to be related to fiber digestibility, it may be possible to more accurately predict the intake potential of forages.

Perhaps a more appropriate experimental design would involve use of early lactation cows with high nutrient requirements fed high fiber diets so intake would more likely be limited by rumen capacity (Chapter 4). To isolate differences in forage fiber digestibility in unconfounded treatments, offering forages of the same species that contain similar fiber and protein concentrations but different fiber digestibilities would be appropriate. Such forages might be obtained by harvesting forages under different growing conditions, and taking advantage of variation in fiber composition associated with differences in heat, light, and temperature (Van Soest et al., 1978).

Objectives of this experiment were to obtain alfalfa silages with similar fiber and protein concentrations but differing fiber digestibilities, as measured by in vitro fermentation, and determine the effect of forage fiber digestibility on intake and production of early lactation dairy cows. A further objective was to measure feeding behavior and rumen characteristics to determine if changes were consistent with conditions of fill-limited intake.

MATERIALS AND METHODS

Forage Harvest and Selection

Two adjacent 8 ha fields of pure-stand alfalfa in their 2nd year of production on the campus of Michigan State University, East Lansing were used for this study. Regrowth between fields was staggered by early cutting of one field to provide a harvest approximately every 3 wk throughout the 1992 growing season. Forage NDF concentrations were monitored during plant growth; fields were cut and harvested when forage NDF was predicted to equal 40%. Forages were chopped and stored as silage in individual bags (Ag-Bag Corporation, Blair, NE). Objectives were to produce silages

with similar NDF and CP concentrations but different NDF digestibilities in sufficient quantities for this lactation study, as described in Chapter 5.

Out of six cuttings, one was destroyed by rain and five were successfully ensiled. Two months after the final harvest, post-ensiled samples were taken from four locations within each bag and analyzed for ash, CP, NDF, and NDF digestibility at 10, 24, and 120 h as estimated by in vitro fermentation with buffered rumen fluid (Goering and Van Soest, 1970). Four of the silages contained equal concentrations of NDF; among these, two differed ($P < .05$) in NDF digestibility by 5% units at each time of in vitro fermentation (Table 1). Consequently, these two forages were reserved for the lactation study and designated as low digestible fiber (**LDF**) and high digestible fiber (**HDF**) forages.

Experimental Design and Data Collection

Twelve multiparous Holstein cows in early lactation (13 ± 6 DIM; mean ± SD) were grouped by date of calving and assigned to one of two treatment diets in a two period balanced simple crossover design. Calving dates were distributed across 2.5 mo, therefore groups of cows commenced treatment at different times to attain starting dates at similar DIM. Cows were not bred until the experiment was completed. Treatment periods were 28 d in length, with the last 10 d used for data and sample collection. Diet ingredients were ground shelled corn, soybean meal, animal protein, minerals, vitamins, and one of the two reserved alfalfa silages that differed in NDF digestibility (Table 2). Values represent average ingredient and nutrient compositions from across the entire experiment. Rations were formulated to contain 35% NDF, at least 22% CP, and provide at least .5 kg/cow per d of the rumen undegraded protein supplement. Diets containing 35% NDF were found to limit intake by early lactation cows because of rumen fill (Chapter 4). All concentrate ingredients contained greater than 87% DM and were combined for each diet prior to the experiment. Except for mineral concentrations,

Table 1. Characteristics of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages prior to commencement of animal experiment.[1]

	LDF silage	HDF silage
Cutting date	7/27/92	8/17/92
Cutting number	2	3
Stage of maturity[2]	3.0	2.9
Leaf:stem DM ratio	1.0	1.1
DM, %	33.3	32.5
OM, % of DM	88.9	89.3
CP,[a] % of DM	26.2	24.5
NDF, % of DM	40.4	40.1
NDF digestibility[2], %		
10 h[a]	18.3	23.1
24 h[a]	39.6	44.8
120 h[a]	45.5	51.0

[1]n = 4 samples per forage.

[2]Estimated as mean stage by weight (Kalu and Fick, 1981); 2 = late vegetative, 3 = early bud, 4 = late bud.

[3]Determined from in vitro fermentation with buffered rumen fluid for length of time indicated.

[a]Nutrient concentration between forages differs significantly ($P < .05$).

Table 2. Ingredient and nutrient composition of low digestible fiber (LDF) and high digestible fiber (HDF) diets offered to 12 cows during the first 10 wk of lactation.

Ingredient Composition	LDF	HDF
	--------(% of diet DM)--------	
LDF alfalfa silage	83.3	...
HDF alfalfa silage	...	83.3
Ground shelled corn	11.8	11.8
44% Soybean meal	1.0	1.0
Protein supplement[1]	2.6	2.6
Dicalcium phosphate	.9	.9
Magnesium oxide	.02	.02
Trace mineral supplement	.33	.33
Vitamin supplement[2]	.03	.03

Nutrient Composition	LDF	SD[3]	HDF	SD
DM, %	37.0	1.8	38.0	1.1
	----------(% of diet DM)----------			
OM[a]	89.2	.2	89.6	.2
NDF[a]	36.7	.7	34.9	.6
ADF[a]	26.6	.5	24.6	.7
Hemicellulose	10.2	.6	10.3	.5
Cellulose[a]	20.4	.4	19.2	.5
Lignin[a]	6.2	.1	5.4	.2
CP[a]	23.9	.5	23.0	.3
RUP,[4] % of diet CP	27.3	ND[5]	27.5	ND
Ca	1.42	ND	1.37	ND
P	.58	ND	.56	ND
Mg	.28	ND	.26	ND

[1]Contains 55% meat and bone meal, 25% blood meal, 10% fish meal, and 10% feather meal.

[2]Contains 1733, 512, and 7.3 kIU/kg of DM of vitamins A, D, and E, respectively.

[3]Represents variation in chemical composition of samples composited weekly (n = 8/diet).

[4]RUP = rumen undegraded protein, calculated from NRC (1989).

[5]ND = not determined.

[a]Nutrient concentration between diets differs significantly ($P < .01$).

nutrient composition of the diets was determined from chemical analysis of individual feed ingredients.

Rations were mixed once daily and offered for ad libitum intake (10% refusal rate) as a TMR at 0800 and 2000 h, after cows were milked in their tie stalls. Feed amounts offered and refused were recorded daily. Forages were sampled daily (.5 kg), frozen, and composited weekly. Concentrate (.5 kg), diets (.5 kg), and feed refused (12.5% of orts) were sampled daily during collection days, frozen, and composited weekly. Milk yield was recorded daily. Milk samples were obtained on d 24 and 25 of each period for both milkings and individually analyzed for lactose, fat, and protein content with infrared spectroscopy by Michigan DHIA. Daily production of each component was determined in addition to SCM, using the equation of Tyrrell and Reid (1965). Cow BW was determined at 2200 h (d 24) and 1800 h (d 26) each period. Cows were scored for body condition (d 24) each period.

Fecal samples were obtained and frozen every 15 h from d 24 to 28 of each period to represent defecation every 3 h throughout a 24 h day. Sampling commenced at 0900 h on d 24 and continued at 2400 h (d 24), 1500 h (d 25), 0600 h and 2100 h (d 26), 1200 h (d 27), and 0300 h and 1800 h (d 28). Cows were not disturbed to obtain samples but were allowed to defecate naturally. The eight samples for each cow were composited on an equivalent wet basis (150 g samples). Feed disappearance, water intake, and jaw movements were measured continuously from d 19 to 24 each period with monitors and a computer data acquisition system (Chapter 2). Chewing monitors were placed on the cows 1 d prior to collection to allow for animal adaptation. Data were written to files every 5 s for each cow and variable. Cows remained in their stalls throughout the 5 d period, allowing for complete recording of all cow behavior.

Four of the twelve cows had a permanent rumen cannula and were used to investigate rumen digesta characteristics. Rumen digesta was manually removed from each cow via the cannula at 2200 h on d 24 (2 h postfeeding) and 1800 h on d 26 (2 h

prefeeding). A 10% aliquot of the digesta was separated during evacuation for sampling. Two digesta samples were obtained. A 600 g sample of the complete digesta was taken for determination of DM and nutrient composition. A second sample was strained through four layers of cheesecloth; the resulting fluid was immediately measured for pH and saved for VFA analysis. Both digesta and fluid samples were frozen immediately (-20°C) following collection. Total digesta weight and volume were determined. Digesta was returned to the rumen immediately following data collection.

Sample and Statistical Analysis

Diets, dietary ingredients, orts, feces, and rumen digesta were analyzed for nutrient concentrations. Samples were dried in a forced-air oven at 52°C for 72 h, ground with a Wiley mill (1-mm screen), and analyzed in duplicate for ash, NDF, ADF, lignin, and indigestible NDF. Ash and fiber analyses were performed using methods previously described (Chapter 4). Indigestible NDF was estimated as the NDF content of samples following in vitro fermentation in buffered rumen fluid (Goering and Van Soest, 1970) for 120 h without addition of pepsin. Cellulose content was calculated as ADF minus lignin content; hemicellulose content was calculated as NDF minus ADF content. Diets, dietary ingredients, orts, and feces were analyzed for CP (N x 6.25) using a modified Kjeldahl (Hach) procedure (Watkins et al., 1987). Mineral analysis of diets was performed using inductively coupled plasma spectroscopy (Northeast DHIA, Ithaca, NY). Oven DM was used in calculations for intake and nutrient digestibility. Concentrations of all nutrients, except DM, were expressed as a percentage of DM determined from forced-air oven drying at 105°C.

In addition to oven drying, forage DM was also determined by toluene distillation (AOAC, 1990). Frozen silage samples were thawed and blended with 100 ml H_2O to extract water soluble components. Following centrifugation at 26,000 x *g* for 30 min, sample supernatent was measured for pH and analyzed for organic acids using HPLC (Siegfried et al., 1984). The column used was Aminex HPX-87H, catalog

number 125-0140, 300 x 7.8 mm (Bio-Rad Laboratories, Richmond, CA). Column temperature was 50°C and solvent was .005 N H_2SO_4. Detection was by refractive index (Waters 410, Millipore Corp., Milford, MA).

Rates of digestible NDF digestion for LDF and HDF alfalfa silages and diets were determined from in vitro fermentation. Four samples of each silage and diet were incubated for 0, 3, 6, 12, 18, 24, 48, 72, and 120 h in buffered rumen fluid and analyzed for NDF content as earlier described for indigestible NDF analysis. The fractional rate of digestion was estimated for each sample as the negative slope of simple linear regression between the natural logarithm of digestible NDF remaining vs. time. This model assumes first order digestion with respect to digestible NDF concentration (Waldo, 1972). Values for times prior to 6 h were omitted from regression analysis to remove effects of fermentation lag from the rate estimate. Indigestible NDF was initially defined as NDF remaining after 120 h of fermentation and was subtracted from the total NDF remaining at each time point to obtain concentrations of digestible NDF. Estimates of indigestible NDF were iteratively adjusted to maximize the coefficient of determination for regression, as suggested by Mertens (1993). In vitro NDF digestibility and true DM digestibility were calculated for each sample following 12, 24, and 120 h of incubation. Digestibility of NDF was calculated as the percentage of prefermented NDF that had been fermented by 12, 24, or 120 h. True DM digestibility was calculated as non-NDF DM plus NDF that was fermented, as a percent of DM, by 12, 24, or 120 h. This calculation assumes that neutral detergent solubles have a digestibility of 100% (Van Soest, 1965).

Fecal output and apparent total tract digestibility of dietary nutrients were calculated using indigestible NDF as an internal marker (Cochran et al., 1986). Eating, ruminating, and drinking activities were determined from collected behavior data with previously developed algorithms (Chapter 2). Feeding behavior was summarized into

variables as performed by in Chapter 3. Across the three activities monitored, 90% of the collected computer data were considered acceptable.

Rumen fluid was centrifuged at 13,000 x *g* for 30 min, decanted, and the supernatent centrifuged at 26,000 x *g* for an additional 30 min. Concentration of VFA in the supernatent was determined with HPLC using the method earlier described for the analysis of silage acids. Concentration of major rumen VFA and their molar proportions were calculated. Fractional rate of NDF passage from the rumen (k_p), fractional rate of digestible NDF digestion in the rumen (k_d), apparent rumen digestibility as a percent of NDF intake, and apparent rumen digestibility as a percent of total tract NDF digestibility were calculated using indigestible NDF as an internal marker and rumen pool size estimates as described in Chapter 4.

All data were statistically analyzed using the specify model procedure of JMP (1991). The model used was consistent for balanced simple crossover designs with two treatments and two periods (Gill, 1978):

$$Y_{ijk} = \mu + C_i + P_j + T_k + E_{ijk}$$

where
μ = overall mean,
C_i = random effect of cow (i = 1 to 12),
P_j = random effect of period (j = 1 to 2),
T_k = fixed effect of treatment (k = 1 to 2),
E_{ijk} = residual, assumed normally distributed.

For variables measured from rumen cannulated cows, which included digesta composition and digestion kinetics, only four cows were utilized (i = 1 to 4). Interactions among the effects of cow, period, and treatment were assumed to be negligible and were not included in the model. Type III sums of squares were used to determine significance of treatment effects. When declared non-significant, treatment effects had probability values $> .10$.

RESULTS

Forage and Diet Composition

Although the NDF content of both alfalfa silages was similar in samples obtained prior to the lactation study (Table 1), analyses of samples taken throughout the duration of the study as the forages were being fed indicated that concentrations of all nutrients, except DM and hemicellulose, were significantly higher ($P < .01$) for LDF (Table 3). Mean NDF content of LDF was 1.8% units greater than HDF (40.6 vs. 38.8%) because of higher concentrations of both cellulose and lignin. Prior to the study, NDF concentrations were 40.4 and 40.1% for LDF and HDF silages, respectively; therefore, NDF content decreased for HDF silage between the two sampling times while LDF silage remained unchanged. Silage pH was lower for HDF and was consistent with its higher total organic acid content of 11.1% compared to 9.5% for LDF. Additionally, HDF contained a higher lactic:acetic acid ratio. No other organic acids were detected in either forage.

Differences in forage composition were reflected in the mean nutrient composition of both treatment diets (Table 2). Mean NDF contents were 36.7% for LDF and 34.9% for HDF diets, a difference of 1.8% units. Actual NDF content for LDF was greater than the formulated target of 35% because concentrate NDF contents were higher than anticipated. In vitro digestion characteristics of LDF and HDF silages and diets sampled during the study are presented in Table 4; digestion of silages is summarized in Figure 1. At each fermentation time, unfermented NDF as a percent of DM was significantly larger ($P < .01$) for LDF silages and diets compared to HDF. Thus, NDF digestibility and true DM digestibility were lower for LDF silages and diets compared to HDF at each fermentation time. After 24 h, NDF digestibility was 38.3% for diet LDF and 41.3% for diet HDF, a difference of 3% units. True DM digestibility after 24 h was 77.1% for diet LDF and 78.9% for diet HDF, a difference of 1.8% units. Approximately 50% of the difference in true DM digestibility between diets was due to differences in

Table 3. Nutrient composition of forages and concentrate sampled during animal experiment and used to formulate low digestible fiber (LDF) and high digestible fiber (HDF) diets.

	Alfalfa silage		
	LDF	HDF	Concentrate
n	17	17	8
DM, %			
52°C oven	32.8	33.9	89.2
Toluene	32.8	33.8	...
pH[a]	4.87	4.58	...
	----------(% of DM)----------		
OM[a]	89.4	89.8	88.4
NDF[a]	40.6	38.8	16.8
ADF[a]	31.2	29.2	3.4
Hemicellulose	9.4	9.6	13.4
Cellulose[a]	24.0	22.8	2.6
Lignin[a]	7.2	6.4	.8
CP[a]	24.7	23.3	20.3
Silage acids[a]			
Lactic	6.2	8.5	...
Acetic	3.3	2.6	...
Lactic:acetic ratio	1.9	3.3	...

[a]Nutrient concentration between forages differs significantly ($P < .01$).

Table 4. In vitro NDF digestion characteristics of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages and diets sampled during animal experiment.[1,2]

	Alfalfa silage		Diet	
	LDF	HDF	LDF	HDF
NDF, % of DM	40.6	38.8	36.7	34.9
Unfermented NDF, % of DM				
12 h	32.2	28.7	28.1	26.1
24 h	25.4	23.0	22.9	21.1
120 h	22.1	20.2	19.5	17.5
NDF digestibility, % of NDF				
12 h	21.7	25.6	24.2	27.4
24 h	38.3	40.2	38.3	41.3
120 h	45.4	47.9	46.9	49.8
True DM digestibility, %				
12 h	67.8	71.3	71.9	73.9
24 h	74.6	77.0	77.1	78.9
120 h	77.9	79.8	80.5	82.5
Rate of NDF digestion, h^{-1}	.112	.114	.126	.112

[1]Determined from in vitro fermentation with buffered rumen fluid for time indicated.

[2]Except for rate of NDF digestion, digestion parameters between treatments differ significantly for both forages and diets ($P < .01$).

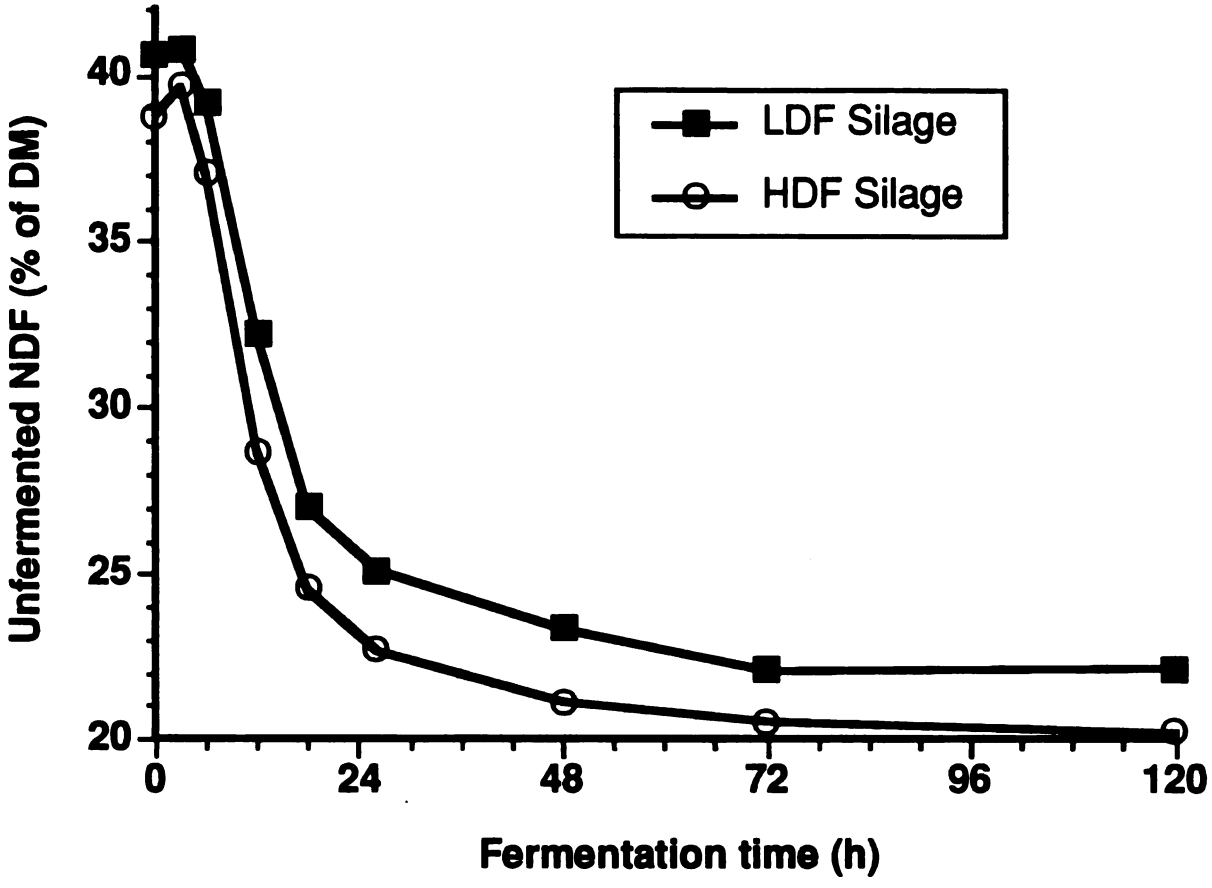


Figure 1. Digestion of low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silage NDF determined from in vitro fermentation in buffered rumen fluid for time indicated.

alfalfa silage NDF content, and 50% due to differences in alfalfa silage NDF digestibility. Fractional rates of digestible NDF digestion in vitro were not different for silages or diets, averaging .113 h^{-1} across silages and .119 h^{-1} across diets.

Cow Response

Daily milk production was significantly lower ($P < .02$) for cows receiving diet LDF compared to HDF (Table 5). These early lactation cows averaged 36.3 kg/d of milk when offered LDF and 38.2 kg/d when offered HDF, a difference of 1.9 kg/d. Milk fat, protein, and lactose contents, however, tended to be greater for diet LDF, resulting in no significant difference between diets for SCM production. Production of milk fat and protein were similar for both diets, averaging 1.47 and 1.02 kg/d, respectively. Lactose production was .08 kg/d higher ($P < .08$) for diet HDF compared to LDF. No differences between diets were observed for cow BW (mean = 616 kg) or body condition score (mean = 2.1).

Table 5. Milk production and body characteristics of 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.

Variable	LDF	HDF	SE	Probability > F value
Production, kg/d				
Milk	36.3	38.2	.5	.02
SCM	34.9	35.8	.6	NS[1]
Fat	1.46	1.48	.04	NS
Protein	1.00	1.03	.02	NS
Lactose	1.74	1.82	.03	.08
Milk composition, %				
Fat	4.03	3.88	.11	NS
Protein	2.76	2.71	.03	NS
Lactose	4.82	4.78	.03	NS
BW, kg	616	616	3	NS
Body condition score[2]	2.1	2.1	.1	NS

[1]NS = $P > .10$.

[2]Scale of 1 to 5; 1 = thin, 5 = obese.

Mean DMI was 19.4 kg/d for cows offered diet LDF and 20.4 kg/d when offered diet HDF (Table 6), a difference of 1.0 kg/d ($P < .01$). Intake of NDF was identical between treatments and averaged 7.1 kg/d. Intake of indigestible NDF was higher ($P < .09$) for diet LDF because this treatment contained higher concentrations of indigestible NDF. Fecal DM and NDF composition was similar between treatments, but indigestible NDF content of feces was significantly higher ($P < .01$) for diet LDF. Daily fecal excretion estimates of DM and NDF tended to be greater for cows receiving diet LDF. Apparent in vivo total tract digestibility of diet HDF was higher than diet LDF for the nutrients of DM, OM, NDF, ADF, hemicellulose, and cellulose ($P \leq .08$). Mean increase in digestibility across all nutrients was 4.2%. Similar digestibilities were obtained if lignin was used as an internal marker to calculate fecal output but treatment differences were slightly larger (6.9%, $P < .01$; Appendix Table 12).

Few differences in eating, ruminating, and drinking behavior were observed (Table 7). Cows averaged 12.5 eating bouts/d that were 27.0 min in length, for a total time spent eating of 327 min/d. Mean meal size of DM tended to be smaller for diet LDF compared to HDF and resulted in lower daily DMI for diet LDF as previously described. Cows receiving diet LDF ruminated during 13.7 bouts/d compared with 14.5 bouts/d for diet HDF ($P < .04$). Mean ruminating bout length, however, was longer ($P < .03$) for diet LDF (40.3 min) compared to diet HDF (38.2 min), resulting in no difference between treatments in daily time spent ruminating (mean = 546 min/d). Time spent eating or ruminating per unit of DM tended to be higher for diet LDF; total time spent chewing per unit of DM was significantly higher ($P < .08$) for diet LDF. Number of chews and chewing rates were not different between treatments for any activity. No drinking parameters were different between treatments.

Characterization of rumen digesta from four rumen cannulated cows also indicated few differences between diets. Volume of rumen digesta was greater 2 h postfeeding compared to 2 h prefeeding, however, no differences across treatments were

Table 6. Nutrient intake, fecal composition, fecal output, and apparent total tract digestibility for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.[1]

Variable	LDF	HDF	SE	Probability > F value
Intake, kg/d				
DM	19.4	20.4	.2	<.01
NDF	7.1	7.1	.1	NS[2]
Indigestible NDF[3]	3.8	3.6	.1	.09
CP	4.6	4.7	.1	NS
Fecal composition				
DM, %	14.4	14.1	.2	NS
NDF, % of DM	57.1	56.7	.2	NS
Indigestible NDF, % of DM	52.2	50.4	.4	.01
Fecal output, kg/d				
DM	7.3	7.1	.2	NS
NDF	4.2	4.0	.1	NS
Nutrient digestibility, %				
DM	62.6	65.2	.5	<.01
OM	63.5	66.2	.5	<.01
NDF	41.6	43.4	.6	.08
ADF	40.2	41.6	.7	NS
Lignin	-1.3	-5.5	1.3	.04
Hemicellulose	45.2	47.5	.8	.07
Cellulose	52.8	54.8	.7	.06
CP	73.8	74.8	.5	NS

[1]Calculated using indigestible NDF as an internal marker.

[2]NS = $P > .10$.

[3]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 7. Eating, ruminating, and drinking activities for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.

Variable	LDF	HDF	SE	Probability > F value
Eating bouts, /d	12.5	12.5	.4	NS[1]
Meal size, kg				
DM	1.60	1.64	.05	NS
NDF	.58	.57	.02	NS
Eating bout length, min	27.1	26.9	1.2	NS
Eating time				
min/d	327	327	7	NS
min/kg DM	17.5	16.5	.4	NS
min/kg NDF	47.9	47.5	1.3	NS
Eating chews, /d	18,503	19,347	702	NS
Eating chew rate, chew/min	56.2	59.0	1.3	NS
Water intake during meals, L/d	45.7	49.0	3.0	NS
Ruminating bouts, /d	13.7	14.5	.3	.04
Ruminating bout length, min	40.3	38.2	.6	.03
Ruminating time				
min/d	545	547	8	NS
min/kg DM	29.3	27.7	.7	NS
min/kg NDF	80.2	80.1	2.1	NS
Ruminating chews, /d	32,969	34,009	1059	NS
Ruminating chew rate, chews/min	59.6	61.5	1.2	NS
Total chewing time				
min/d	872	874	13	NS
min/kg DM	46.7	44.2	.9	.08
min/kg NDF	128	127	3	NS
Total chews, /d	51,472	53,356	1576	NS
Water intake, L/d	90.3	92.9	1.5	NS
Drinking bouts, /d	16.8	17.7	.7	NS
Drinking bout size, L	6.1	5.6	.3	NS
Drinking time, min/d	21.1	23.4	1.6	NS
Drinking rate, L/min	4.6	4.3	.2	NS

[1]NS = $P > .10$.

observed (Table 8). Mean rumen volume was 78.3 L across all determinations. Digesta NDF content tended to be higher for diet LDF and indigestible NDF content was 3.9% units higher ($P < .09$) for cows offered diet LDF. Average rumen pool size of nutrients was not different between treatments but tended to be greater for diet LDF compared to HDF for all nutrients measured.

In a pattern similar to rumen volume, rumen fluid pH was higher 2 h prefeeding compared to 2 h postfeeding (Table 9). Although not significant, rumen pH tended to be higher for cows offered diet LDF (6.84 vs. 6.73). Differences in pH corresponded to a tendency for lower total VFA concentrations for diet LDF compared to HDF; differences between treatments 2 h postfeeding were significant ($P < .03$). The molar proportion of propionate in rumen fluid was lower ($P < .08$) for diet LDF, while acetate tended to be higher. Consequently, the acetate:propionate ratio was higher ($P < .10$) for diet LDF (3.4) compared to diet HDF (3.0). No differences between diets were detected for in vivo rumen NDF digestion kinetic and digestibility parameters (Table 10). Average NDF k_p was .028 and average digestible NDF k_d was .058. Apparent digestibility of NDF in the rumen averaged 32.4% of NDF intake and contributed 76.7% of total tract NDF digestibility.

DISCUSSION

Current systems of forage analysis and ration formulation do not account for differences in fiber digestibility (NRC, 1989). Fermentation of fiber in the rumen can contribute a significant portion of a dairy cow's total digestible energy intake (Galyean and Goetsch, 1993). Alfalfa forages with similar NDF concentrations have been shown to range in NDF digestibility from 25 to 55% after 30 h of in vitro fermentation (Allen et al., 1991), that is equivalent to a potential range in energy content of .33 Mcal of NE_L/kg of DM for forage containing 45% NDF. Forage fiber digestibility may also influence feed intake, especially if intake is limited by the physical capacity of the reticulorumen. Increasing the fraction of fiber that is potentially digestible subjects a larger portion of

Table 8. Rumen digesta characteristics for 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.

Variable	LDF	HDF	SE	Probability > F value
Volume, L				
2 h prefeeding	75.5	74.8	2.8	NS[1]
2 h postfeeding	82.5	80.5	4.7	NS
Average	79.0	77.6	3.8	NS
Composition[2]				
DM, %	13.8	13.7	.1	NS
NDF, % of DM	67.1	64.6	1.0	NS
Indigestible NDF,[3] % of DM	52.6	48.7	.9	.09
Mass,[2] kg				
Wet digesta	71.2	69.7	3.7	NS
DM	9.8	9.6	.4	NS
OM	8.8	8.6	.4	NS
NDF	6.6	6.2	.3	NS
ADF	4.7	4.3	.2	NS
Lignin	1.5	1.3	.1	NS
Hemicellulose	1.9	1.9	.1	NS
Cellulose	3.2	3.0	.2	NS
Indigestible NDF	5.1	4.7	.2	NS
Density,[2] kg/L	.91	.90	.01	NS

[1]NS = $P > .10$.

[2]Average of pre and postfeeding samples.

[3]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 9. Rumen fluid pH and VFA concentration of digesta from 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.

Variable	LDF	HDF	SE	Probability > F value
pH				
2 h prefeeding	6.93	6.78	.04	NS[1]
2 h postfeeding	6.74	6.69	.07	NS
Average	6.84	6.73	.06	NS
Total VFA concentration, mM				
2 h prefeeding	137.5	139.6	5.1	NS
2 h postfeeding	137.5	148.3	1.4	.03
Average	137.5	143.9	3.2	NS
VFA molar proportions[2]	--(% of total VFA)--			
Acetate	65.0	62.6	.6	NS
Propionate	19.0	20.7	.4	.08
Butyrate	8.5	8.7	.2	NS
Valerate	2.6	3.2	.1	NS
Branched-chain[3]	4.9	4.8	.2	NS
Acetate:propionate ratio	3.4	3.0	.1	.10

[1]NS = $P > .10$.

[2]Average of pre and postfeeding samples.

[3]isobutyrate + isovalerate.

Table 10. Rumen digestion kinetics of NDF and rumen apparent digestibility of NDF from 4 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.[1]

Variable	LDF	HDF	SE	Probability > F value
Digestion kinetics	----------(h^{-1})----------			
Fractional passage rate				
2 h prefeeding	.028	.029	.001	NS[2]
2 h postfeeding	.026	.028	.001	NS
Average	.027	.029	.001	NS
Fractional digestion rate				
2 h prefeeding	.063	.063	.007	NS
2 h postfeeding	.055	.054	.004	NS
Average	.058	.058	.004	NS
Rumen apparent digestibility				
	----------(% of NDF intake)----------			
2 h prefeeding	32.2	33.8	1.5	NS
2 h postfeeding	31.4	32.4	.3	NS
Average	31.7	33.1	.8	NS
	-----(% of total tract digestibility)------			
2 h prefeeding	77.5	78.5	2.2	NS
2 h postfeeding	75.6	75.3	.9	NS
Average	76.5	76.9	.7	NS

[1]Calculated using indigestible NDF as an internal marker and rumen pool size estimates.

[2]NS = $P > .10$.

the rumen fiber pool to both digestion and passage, which may increase the turnover rate of fiber within the rumen and allow for additional fiber consumption and DMI. If improved fiber digestion increases both DMI and energy density of the forage, a substantial increase in digestible DMI may be realized, as shown by Muller et al., 1972.

The first objective of this study was to obtain two alfalfa forages with similar NDF and protein concentrations but different NDF digestibilities to isolate the treatment effect of fiber digestibility. Equal NDF contents of the forages would also allow identical forage:concentrate ratios and one concentrate supplement to be used for both dietary treatments. Previous attempts to examine forage fiber digestibility have been unable to unconfound the effects of fiber digestibility, NDF content, fiber source, forage protein content, concentrate composition, or forage:concentrate ratio (Varga et al., 1984; Miller et al., 1990; Robinson and McQueen, 1992). Robinson and McQueen (1992) most successfully isolated the effect of NDF digestibility using two different maturities of timothy silage, however, this effect was still confounded with amount of a second forage source and with source of concentrate.

Selected forages initially met requirements that enabled an unconfounded fiber digestibility feeding trial (Table 1). Unfortunately, NDF content of HDF silage decreased between initial sampling and forage feedout, that was probably due to either a loss of cellulose between these two sampling periods (Table 3) or sampling bias during initial forage screening. The change in NDF content for silage HDF was predominantly due to a loss of digestible NDF (Figure 2). Loss of digestible fiber also was noted during fermentation for both silages based on samples taken prior to ensiling (Chapter 5). Loss of fiber during silage fermentation has been previously reported (Morrison, 1988). Clear interpretations of the results of this study are difficult to make since both NDF content and digestibility appeared to differ between diets at feedout. The difference in NDF content, however, may be related directly to the higher concentration of digestible fiber in HDF silage prior to the start of the trial. Consequently,

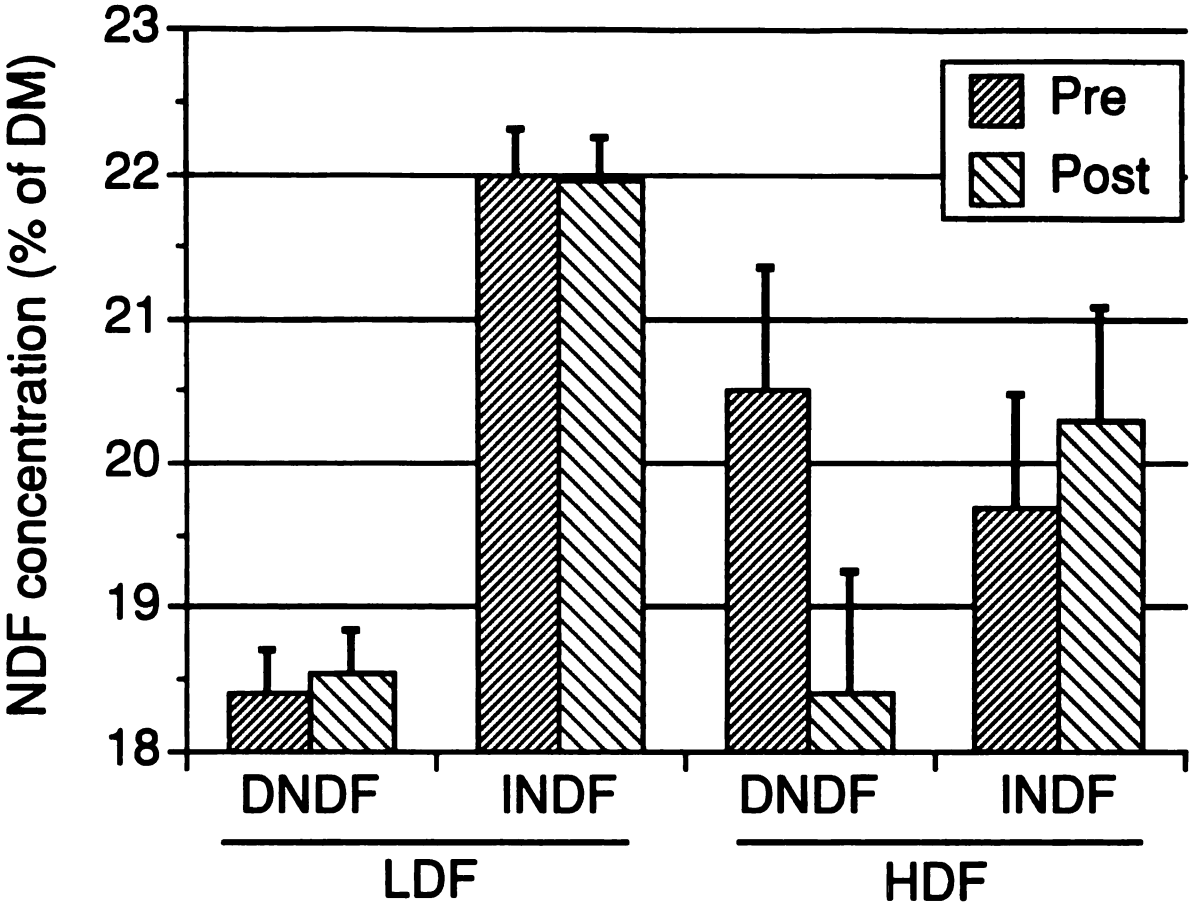


Figure 2. Concentration of digestible NDF (DNDF) and indigestible NDF (INDF) for low digestible fiber (LDF) and high digestible fiber (HDF) alfalfa silages following 120 h in vitro fermentation for samples taken prior to commencement of the lactation study (Pre) and samples taken during the lactation study (Post).

improvements in cow performance from feeding diet HDF may ultimately reflect the advantages of high fiber digestibility.

Lower lignin concentration for HDF silage was expected, because lignification of the plant cell wall is considered to be the primary limitation to its digestibility (Smith et al., 1972; USDA-ARS, 1993). Slight differences in CP content between the forages and diets was not a major concern. Both diets were considered to be in CP excess for the level of milk production expected. Amount of rumen undegraded protein was estimated to support 40 kg/d of milk, also above the expected milk production from these energy-limited diets.

Many of the cow responses to these diets are similar to those obtained with the 35% NDF diet fed in the trial reported in Chapter 4. Cows were estimated to be in negative energy balance because mean energy output (35.4 Mcal/d of NE_L) was equivalent to a dietary energy concentration of 1.80 Mcal of NE_L/kg of DM, a value likely to be an overestimate of the true energy content of these 83% alfalfa-based diets. Changes in BW were not calculated because they do not accurately reflect changes in body tissue for early lactation cows. During this period, changes in BW are confounded with increases in rumen digesta mass. Although high forage diets were used, high milk production was achieved, suggesting that silages were of excellent quality. Despite the relative small difference between diets LDF and HDF for NDF concentration (1.8% units) and NDF digestibility (3% units), significant increases in milk production were obtained with diet HDF. Other studies investigating fiber digestibility have also noted improvements in milk yield with higher digestibility (Varga et al., 1984; Robinson and McQueen, 1992), although others have not (Miller et al., 1990; Feng et al., 1993; McQueen and Robinson, 1993). Milk component concentrations tended to be higher for diet LDF, therefore, component and SCM yields were not different between diets. Rumen VFA suggest a trend toward increased microbial activity for diet HDF; differences in acetate:propionate ratio support the trend for higher milk fat content for

diet LDF. Varga et al. (1984) also observed higher milk fat content for a diet with lower fiber digestibility.

The most significant result in this study was the improvement in DMI with diet HDF. This increase was accompanied by increases in apparent in vivo DM and NDF digestibilities. Digestible DMI was calculated for each diet (Figure 3); approximately 90% of the improvement in digestible DMI with diet HDF was due to increased DMI and 10% was due to increased NDF digestibility. Almost all other studies with dairy cows have detected no increase in DMI with increases in fiber digestibility (Varga et al., 1984; Miller et al., 1990; Robinson and McQueen, 1992; Feng et al., 1993, McQueen and Robinson, 1993), with the exception of Llamas-lamas and Combs (1990). Lack of DMI increases may have been due to their use of cows whose intakes were not limited by rumen fill. We expected that intake of NDF would be higher and intake of indigestible NDF would be the same with diet HDF compared to diet LDF, if intake was limited by the presence of indigestible fiber in the rumen. On the contrary, intakes of NDF were equal while intakes of indigestible NDF tended to be lower with diet HDF (Table 6). These results suggest that increases in DMI were due to the lower NDF content of diet HDF.

Rumen digesta volume and rumen mass of NDF were similar between diets (Table 8), a finding similar to that of others (Llamas-lamas and Combs, 1990; Robinson and McQueen, 1992). Lower concentrations of indigestible NDF in diet HDF tended to promote lower concentrations of indigestible NDF in rumen digesta, however this decrease was not sufficient to significantly reduce rumen pool size of this component. Rumen turnover time of NDF was not significantly faster for diet HDF (mean = 21.6 h), consequently, changes in NDF digestibility did not increase clearance of NDF from the rumen. No differences in fractional rates of NDF digestion in and passage from the rumen were observed, and were not expected since these diets did not differ in in vitro rates of NDF digestion. Higher NDF digestibility may have resulted in a greater

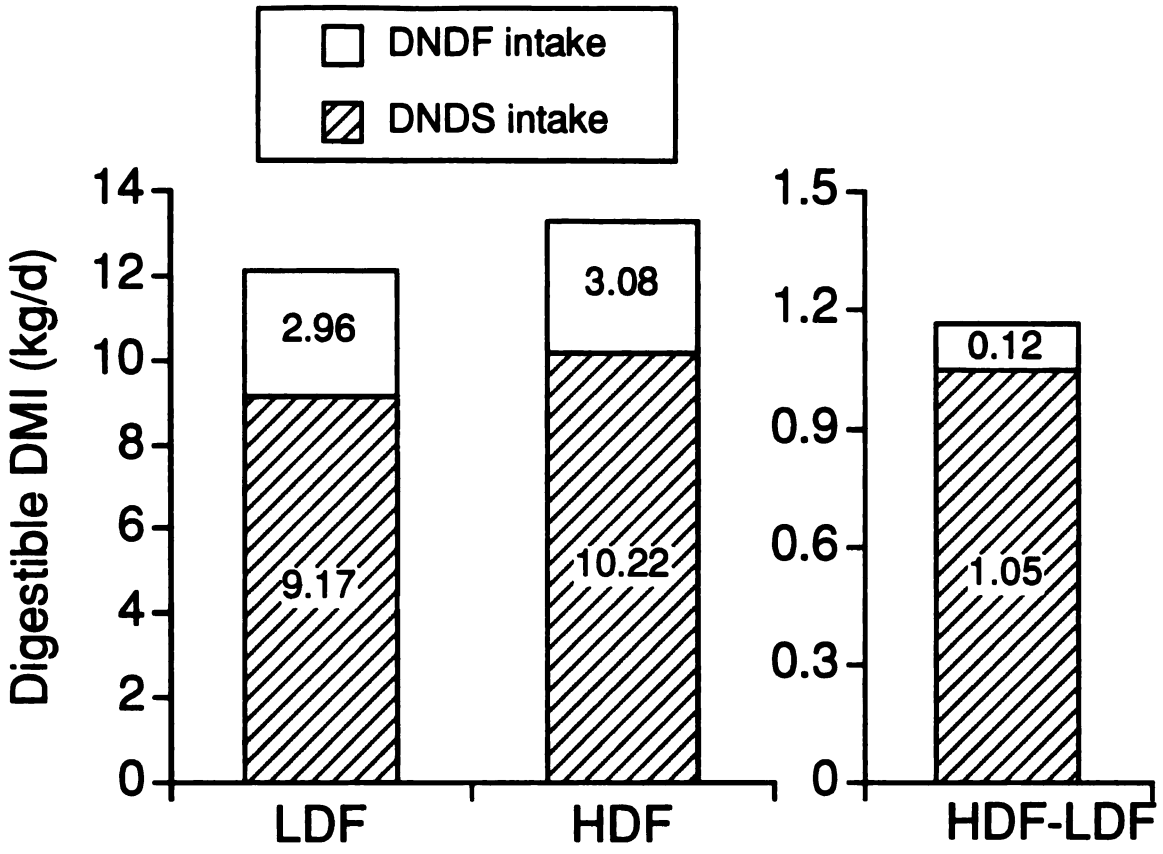


Figure 3. Contribution to digestible DMI from digestible NDF (DNDF) intake and digestible neutral detergent solubles (DNDS) intake for low digestible fiber (LDF) and high digestible fiber (HDF) diets offered to 12 early lactation cows.

digestible energy content for diet HDF, but appears to have had no affect on DMI. Differences in NDF digestibility between diets were small, and rumen digesta data were from only four cows, therefore, these results should be viewed as preliminary for describing the effect of fiber digestibility on DMI of early lactation cows.

Diet HDF resulted in more rumination bouts of shorter duration compared to diet LDF. Under conditions where intake was limited by rumen fill (Chapter 4), greater fill also was associated with more rumination bouts of shorter duration. Time spent chewing per unit of DM was higher for diet LDF, another characteristic of fill-limiting diets. These data do not provide substantial support to argue that either diet was more limited by rumen capacity than the other.

CONCLUSIONS

Ensiled alfalfa forages that differed in NDF digestibility by 5% units prior to commencement of a study with early lactation cows were offered as part of a high fiber ration. The alfalfa with higher fiber digestibility increased milk production and DMI by 1.9 and 1.0 kg/d, respectively. At the time of feeding, diets differed in both NDF content (1.8% units) and NDF digestibility (3% units), perhaps due to loss of digestible NDF in the higher quality forage during the trial. Equal NDF intake for these diets suggests that DMI was higher because of lower NDF concentration in the higher quality forage. Both DMI and NDF digestibility contributed to higher consumption of digestible DMI.

Isolating NDF digestibility as the sole treatment effect is difficult. If increases in fiber digestibility prior to ensiling promoted decreases in fiber content after ensiling, benefits to harvesting forages with higher fiber digestibility may be substantial. Further experimentation is required before differences in fiber digestibility can be claimed to have no effect on intake. Forages with larger differences in fiber digestibility at the time of feeding to cows with intake limited by physical fill are required to more closely examine this hypothesis. These forages may be difficult to obtain at only one location; cooperation among researchers at different locations may be required.

EPILOGUE

This research project sought to fulfill several objectives relative to the influence of forage quality on feed intake by cows in early stages of lactation. To adequately measure these effects, a computerized data acquisition system to monitor feeding behavior and rumen function was successfully developed and validated. Utilization of current computer technology enhances one's ability to make multiple observations on several animals simultaneously. The critical component of this system is the interpretive algorithm that summarizes large streams of data into variables that can easily be compared to evaluate treatment effects. At this time, five lactation studies have been conducted using this system to monitor feeding behavior. Due to the intensity in which variables can be measured, this, and similar systems like this, will serve as a valuable tool to investigate interactions between feed quality and animal response. Future experiments should seek to apply these techniques to free-roaming cows in group housing.

Before applying this measurement system to critical lactation experiments, a preliminary lactation study was conducted to examine the variation across cows and across days for several feeding behavior variables. Little information has been reported in the literature about such variation and how it might be used to design experiments to maximize statistical power and inference. Significant variation between cows was observed for many variables, including meal size, eating bouts, and total time spent chewing. The mean coefficient of variation for all variables was 21%. To detect contrast differences of 10% of means for all variables examined with 80% probability

required the use of 12 cows measured for 5 d in a Latin square design. Consequently, all subsequent experiments were designed in such a fashion.

Two lactation studies with cows 2 wk into lactation were conducted using these monitoring tools and additional measurements common to nutrition studies, such as rumen digesta evacuation, fecal collections, and diet analysis, to evaluate the effect of fiber concentration of the diet or extent of fiber digestibility on feed intake. In trial 1, cows were challenged with rumen fill in the form of dietary NDF or inert bulk to determine if filling characteristics of forage diets varied with fiber content, and if cows adapted to rumen fill by altering their feeding behavior. Addition of inert bulk decreased intake for cows receiving 35% NDF diets but not for cows receiving 25% NDF diets. Volume of rumen digesta plus inert bulk was similar for high fiber treatments whether or not inert bulk was present. Finally, fiber and inert bulk addition increased NDF passage from the rumen in a similar manner. These data support the hypothesis that cows receiving high fiber diets have intakes limited by the physical capacity of the reticulo-rumen. Changes in feeding behavior or rumen function were insufficient to maintain intake under conditions of high rumen fill. Added fiber and inert bulk altered aspects of rumination, rumen fermentation, and reticular motility in a similar fashion, demonstrating that NDF has rumen-filling characteristics.

In trial 2, cows were offered two diets that differed in the source of alfalfa silage used. Two silages were harvested in the summer of 1992 that contained similar concentrations of NDF (40%) but different digestibilities of NDF (40 vs. 45% after 24 h in vitro fermentation). High forage mixed diets were fed to determine if higher NDF digestibility resulted in increased intake and production. Higher fiber digestibility increased milk production and intake by 1.9 and 1.0 kg/d, respectively. At the time of feeding, however, diets differed in both NDF content (1.8% units) and NDF digestibility (3% units), perhaps due to loss of digestible NDF in the higher quality forage during the trial. Equal NDF intake for these diets suggests that DMI was

increased because of lower NDF concentration in the higher quality forage. Isolating NDF digestibility as the sole treatment effect was difficult. If increases in fiber digestibility prior to ensiling promote decreases in fiber content after ensiling, benefits to harvesting forages with higher fiber digestibility may be substantial.

In summary, forage fiber did appear to limit voluntary feed intake in early lactation dairy cows because of rumen fill. Future research is needed to determine what other dietary factors influence the fill value of different diets and whether cows of varying size, shape, stage of lactation, or some other trait vary in their ability to accommodate rumen fill. Low fiber digestibility may have also limited intake by cows, however, this treatment effect was confounded with fiber content of the diet. Forages with larger differences in fiber digestibility at the time of feeding are required to more closely examine this hypothesis. These forages may be difficult to obtain at only one location; cooperation among researchers at different locations may be required.

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APPENDIX

Table 1. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: computer board assignments in Labtech Notebook software setup.

Board no.	Terminal board[1]	Software board assignment	Function	Stall no.
0	DAS-8	DAS-8	water	11, 12
1	Exp-16: #4	Exp-16, gain=1	pH	1-12
2	Exp-16: #2, #3	Exp-16, gain=50	chewing	1-12
			motility	1-12
3	Exp-16: #1	Exp-16, gain=200	load	1-12
4	CTM-05: #1	CTM-05	water	1-5
5	CTM-05: #2	CTM-05	water	6-10

[1]See Appendix Figure 1 for location of terminal boards.

Table 2. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: channel characteristics of algorithm functions for data acquisition run under Labtech Notebook.[1]

Channel Name: Time

Channel No. -	1	Buffer size -	64
Channel type -	Time	No. of iterations -	1
Channel units -	Secs	No. of stages -	1
Time origin -	Elapsed time	Sampling rate, Hz -	0.200
Format -	SSSSS.SSS	Stage duration, sec -	2,000,000
Mode -	Cumulative	Start / stop method -	Immediate

Channel Name: Water 1

Channel No. -	2	Buffer size -	128
Channel type -	Counter	No. of iterations -	1
Channel units -	Counts	No. of stages -	1
Interface device -	4:CTM-05	Sampling rate, Hz -	0.200
Interface channel #-	1	Stage duration, sec -	2,000,000
Mode -	Cumulative	Start / stop method -	Immediate

Channel Name: Load 1

Channel No. -	14	Offset constant -	variable
Channel type -	Analog input	Buffer size -	128
Channel units -	Lbs.	No. of iterations -	1
Interface device -	3:DAS8/Exp16	No. of stages -	1
Interface channel # -	16	Sampling rate, Hz -	0.200
Input range -	±0.025V	Stage duration, sec -	2,000,000
Scale factor -	variable	Start / stop method -	Immediate

Channel Name: Chew raw 1

Channel No. -	26	Offset constant -	0
Channel type -	Analog input	Buffer size -	128
Channel units -	Volts	No. of iterations -	1
Interface device -	2:DAS8/Exp16	No. of stages -	1
Interface channel # -	48	Sampling rate, Hz -	4.0
Input range -	±0.1V	Stage duration, sec -	2,000,000
Scale factor -	100	Start / stop method -	Immediate

Table 2. (cont.)

Channel Name: Chew derivative 1

Channel No. -	38	Offset constant -	0
Channel type -	Calculated	Buffer size -	128
Channel units -	Volts	No. of iterations -	1
Operation -	dx/dt	No. of stages -	1
X input channel -	26	Sampling rate, Hz -	4.0
Y input channel -	•••	Stage duration, sec -	2,000,000
Parameter, r -	1	Start / stop method -	Immediate
Scale factor -	1		

Channel Name: Chew count 1

Channel No. -	50	Offset constant -	1
Channel type -	Calculated	Buffer size -	128
Channel units -	Chews	No. of iterations -	4,000,000
Operation -	Counter	No. of stages -	2
X input channel -	•••	Sampling rate, Hz -	1.0, 2.0
Y input channel -	•••	Stage duration, sec -	0, 0.5
Parameter, r -	1	Start / stop method -	Imm., On edge
Scale factor -	1	Trigger channel -	•••, 38
		Analog trigger value -	•••, -0.20
		Analog trigger polarity -	•••, Low
		No. of samples to save pretrigger -	•••, 0

Channel Name: Chews 1

Channel No. -	62	Offset constant -	0
Channel type -	Calculated	Buffer size -	128
Channel units -	Chews	No. of iterations -	1
Operation -	dx/dt	No. of stages -	1
X input channel -	50	Sampling rate, Hz -	0.200
Y input channel -	•••	Stage duration, sec -	2,000,000
Parameter, r -	0	Start / stop method -	Immediate
Scale factor -	1		

Channel Name: Motility raw 1

Channel No. -	74	Offset constant -	0
Channel type -	Analog input	Buffer size -	128
Channel units -	Volts	No. of iterations -	1
Interface device -	2:DAS8/Exp16	No. of stages -	1
Interface channel # -	32	Sampling rate, Hz -	4.0
Input range -	±0.1V	Stage duration, sec -	2,000,000
Scale factor -	200	Start / stop method -	Immediate

Table 2. (cont.)

Channel Name: Motility average 1

Channel No. -	86	Offset constant -	0
Channel type -	Calculated	Buffer size -	128
Channel units -	Volts	No. of iterations -	1
Operation -	Block ave.	No. of stages -	1
X input channel -	74	Sampling rate, Hz -	1.0
Y input channel -	• • •	Stage duration, sec -	2,000,000
Parameter, r -	3	Start / stop method -	Immediate
Scale factor -	1		

Channel Name: Motility derivative 1

Channel No. -	98	Offset constant -	0
Channel type -	Calculated	Buffer size -	128
Channel units -	Volts	No. of iterations -	1
Operation -	dx/dt	No. of stages -	1
X input channel -	86	Sampling rate, Hz -	1.0
Y input channel -	• • •	Stage duration, sec -	2,000,000
Parameter, r -	0	Start / stop method -	Immediate
Scale factor -	1		

Channel Name: Contraction count 1

Channel No. -	110	Offset constant -	1
Channel type -	Calculated	Buffer size -	128
Channel units -	Contractions	No. of iterations -	2,000,000
Operation -	Counter	No. of stages -	2
X input channel -	• • •	Sampling rate, Hz -	1.0, 2.0
Y input channel -	• • •	Stage duration, sec -	0, 0.5
Parameter, r -	1	Start / stop method -	Imm., On edge
Scale factor -	1	Trigger channel -	• • •, 98
		Analog trigger value -	• • •, -0.10
		Analog trigger polarity -	• • •, Low
		No. of samples to save pretrigger -	• • •, 0

Channel Name: Contractions 1

Channel No. -	122	Offset constant -	0
Channel type -	Calculated	Buffer size -	128
Channel units -	Contractions	No. of iterations -	1
Operation -	dx/dt	No. of stages -	1
X input channel -	110	Sampling rate, Hz -	0.200
Y input channel -	• • •	Stage duration, sec -	2,000,000
Parameter, r -	0	Start / stop method -	Immediate
Scale factor -	1		

Table 2. (cont.)

Channel Name: pH 1

Channel No. -	134	Offset constant -	variable
Channel type -	Analog input	Buffer size -	64
Channel units -	pH	No. of iterations -	1
Interface device -	1:DAS8/Exp16	No. of stages -	1
Interface channel # -	64	Sampling rate, Hz -	0.200
Input range -	±5V	Stage duration, sec -	2,000,000
Scale factor -	variable	Start / stop method -	Immediate

[1]Setup designed for acquiring all five activities for one cow. Channel references specified for stall #1 only.

Table 3. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: channel assignments for a complete acquisition run under Labtech Notebook. Setup is designed for monitoring all five activities for 12 stalls.

		Labtech Notebook			
Channel no.	Name	Board no.	Channel no. of board	Reference channel	Output to file?
1	Time	--	--	--	Yes
2	Water 1	4	1	--	Yes
3	Water 2	4	2	--	Yes
4	Water 3	4	3	--	Yes
5	Water 4	4	4	--	Yes
6	Water 5	4	5	--	Yes
7	Water 6	5	1	--	Yes
8	Water 7	5	2	--	Yes
9	Water 8	5	3	--	Yes
10	Water 9	5	4	--	Yes
11	Water 10	5	5	--	Yes
12	Water 11	0	0	--	Yes
13	Water 12	0	1	--	Yes
14	Load 1	3	16	--	Yes
15	Load 2	3	17	--	Yes
16	Load 3	3	18	--	Yes
17	Load 4	3	19	--	Yes
18	Load 5	3	20	--	Yes
19	Load 6	3	21	--	Yes
20	Load 7	3	22	--	Yes
21	Load 8	3	23	--	Yes
22	Load 9	3	24	--	Yes
23	Load 10	3	25	--	Yes
24	Load 11	3	26	--	Yes
25	Load 12	3	27	--	Yes
26	Chew raw 1	2	48	--	No
27	Chew raw 2	2	49	--	No
28	Chew raw 3	2	50	--	No
29	Chew raw 4	2	51	--	No
30	Chew raw 5	2	52	--	No
31	Chew raw 6	2	53	--	No
32	Chew raw 7	2	56	--	No
33	Chew raw 8	2	57	--	No
34	Chew raw 9	2	58	--	No
35	Chew raw 10	2	59	--	No
36	Chew raw 11	2	60	--	No
37	Chew raw 12	2	61	--	No
38	Chew derivative 1	--	--	26	No

Table 3. (cont.)

Channel no.	Name	Labtech Notebook: Board no.	Labtech Notebook: Channel no. of board	Reference channel	Output to file?
39	Chew derivative 2	--	--	27	No
40	Chew derivative 3	--	--	28	No
41	Chew derivative 4	--	--	29	No
42	Chew derivative 5	--	--	30	No
43	Chew derivative 6	--	--	31	No
44	Chew derivative 7	--	--	32	No
45	Chew derivative 8	--	--	33	No
46	Chew derivative 9	--	--	34	No
47	Chew derivative 10	--	--	35	No
48	Chew derivative 11	--	--	36	No
49	Chew derivative 12	--	--	37	No
50	Chew count 1	--	--	38	No
51	Chew count 2	--	--	39	No
52	Chew count 3	--	--	40	No
53	Chew count 4	--	--	41	No
54	Chew count 5	--	--	42	No
55	Chew count 6	--	--	43	No
56	Chew count 7	--	--	44	No
57	Chew count 8	--	--	45	No
58	Chew count 9	--	--	46	No
59	Chew count 10	--	--	47	No
60	Chew count 11	--	--	48	No
61	Chew count 12	--	--	49	No
62	Chews 1	--	--	50	Yes
63	Chews 2	--	--	51	Yes
64	Chews 3	--	--	52	Yes
65	Chews 4	--	--	53	Yes
66	Chews 5	--	--	54	Yes
67	Chews 6	--	--	55	Yes
68	Chews 7	--	--	56	Yes
69	Chews 8	--	--	57	Yes
70	Chews 9	--	--	58	Yes
71	Chews 10	--	--	59	Yes
72	Chews 11	--	--	60	Yes
73	Chews 12	--	--	61	Yes
74	Motility raw 1	2	32	--	No
75	Motility raw 2	2	33	--	No
76	Motility raw 3	2	34	--	No
77	Motility raw 4	2	35	--	No
78	Motility raw 5	2	36	--	No
79	Motility raw 6	2	37	--	No

Table 3. (cont.)

Channel no.	Name	Labtech Notebook Board no.	Labtech Notebook Channel no. of board	Reference channel	Output to file?
80	Motility raw 7	2	40	--	No
81	Motility raw 8	2	41	--	No
82	Motility raw 9	2	42	--	No
83	Motility raw 10	2	43	--	No
84	Motility raw 11	2	44	--	No
85	Motility raw 12	2	45	--	No
86	Motility average 1	--	--	74	No
87	Motility average 2	--	--	75	No
88	Motility average 3	--	--	76	No
89	Motility average 4	--	--	77	No
90	Motility average 5	--	--	78	No
91	Motility average 6	--	--	79	No
92	Motility average 7	--	--	80	No
93	Motility average 8	--	--	81	No
94	Motility average 9	--	--	82	No
95	Motility average 10	--	--	83	No
96	Motility average 11	--	--	84	No
97	Motility average 12	--	--	85	No
98	Motility derivative 1	--	--	86	No
99	Motility derivative 2	--	--	87	No
100	Motility derivative 3	--	--	88	No
101	Motility derivative 4	--	--	89	No
102	Motility derivative 5	--	--	90	No
103	Motility derivative 6	--	--	91	No
104	Motility derivative 7	--	--	92	No
105	Motility derivative 8	--	--	93	No
106	Motility derivative 9	--	--	94	No
107	Motility derivative 10	--	--	95	No
108	Motility derivative 11	--	--	96	No
109	Motility derivative 12	--	--	97	No
110	Contraction count 1	--	--	98	No
111	Contraction count 2	--	--	99	No
112	Contraction count 3	--	--	100	No
113	Contraction count 4	--	--	101	No
114	Contraction count 5	--	--	102	No
115	Contraction count 6	--	--	103	No
116	Contraction count 7	--	--	104	No
117	Contraction count 8	--	--	105	No
118	Contraction count 9	--	--	106	No
119	Contraction count 10	--	--	107	No
120	Contraction count 11	--	--	108	No

Table 3. (cont.)

Channel no.	Name	Labtech Notebook Board no.	Labtech Notebook Channel no. of board	Reference channel	Output to file?
121	Contraction count 12	--	--	109	No
122	Contractions 1	--	--	110	Yes
123	Contractions 2	--	--	111	Yes
124	Contractions 3	--	--	112	Yes
125	Contractions 4	--	--	113	Yes
126	Contractions 5	--	--	114	Yes
127	Contractions 6	--	--	115	Yes
128	Contractions 7	--	--	116	Yes
129	Contractions 8	--	--	117	Yes
130	Contractions 9	--	--	118	Yes
131	Contractions 10	--	--	119	Yes
132	Contractions 11	--	--	120	Yes
133	Contractions 12	--	--	121	Yes
134	pH 1	1	64	--	Yes
135	pH 2	1	65	--	Yes
136	pH 3	1	66	--	Yes
137	pH 4	1	67	--	Yes
138	pH 5	1	68	--	Yes
139	pH 6	1	69	--	Yes
140	pH 7	1	70	--	Yes
141	pH 8	1	71	--	Yes
142	pH 9	1	72	--	Yes
143	pH 10	1	73	--	Yes
144	pH 11	1	74	--	Yes
145	pH 12	1	75	--	Yes

Table 4. Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle: feeding behavior data interpretation computer program for summarizing individual cow data into bouts of eating, ruminating, and drinking.[1]

```
*************************************************************************;
* File Name:    ChewIntp.sas;
* Date 1/20/93: Feeding behavior interpretive program, for IBM 3090-mainframe;
* Data form:    For individual cows measured continuously over several days;
* Input files:  Files generated by DA system and LABTECH NOTEBOOK;
* Output files: Bout summaries for contractions, eating, ruminating, and drinking;
*************************************************************************;

OPTION LS=132;
CMS FILEDEF DATA DISK S1P1COW1 PRN A;
CMS FILEDEF CONTSUM DISK CSS1P1C1 DAT A;
CMS FILEDEF EATPER DISK EPS1P1C1 DAT A;
CMS FILEDEF RUMPER DISK RPS1P1C1 DAT A;
CMS FILEDEF DRNKPER DISK DPS1P1C1 DAT A;

DATA ONE                                          /*READ DATA FILE*/;
  INFILE DATA FIRSTOBS=8;
  INPUT @2 TIME WMETR L1 CHEW PH C1;
  IF L1<-10 THEN L1=-5000;

DATA TWO                          /*BEGINNING LOAD ESTABLISHMENT*/;
  SET ONE(KEEP=L1); IF _N_=1 THEN TOT=50;
  IF L1=-5000 THEN DO; TOT=0; L1=0; L2=0; END;
  TOT+1; IF TOT>5; L2+L1;  IF TOT=11;
  L2=ROUND(L2/6,.1); DROP TOT L1; OUTPUT;

DATA TWO_A                    /*GETS THE LAST MEAL FOR SOME COWS*/;
  SET TWO END=LAST;  OUTPUT; IF LAST THEN DO; L2=-5000; OUTPUT;
      END;

DATA THREE                        /*BEGINNING LOAD ESTABLISHMENT*/;
  SET ONE(KEEP=L1);
  BY L1 NOTSORTED;
  IF L1=-5000 AND FIRST.L1=1 THEN DO; TOT=0; SET TWO_A; END;
  IF L1=-5000 AND FIRST.L1=0 THEN DO; TOT=0; L1=L2; END;
  IF _N_=1 THEN TOT=5; TOT+1; IF 1<TOT<6 THEN L1=L2;
  DROP L2 TOT;
```

Table 4. (cont.)

```
DATA FOUR                                    /*LOAD, WATER, MOVEMENT*/;
  MERGE ONE(DROP=L1 C1) THREE;
  WATERS=(WMETR-LAG(WMETR))*3.78/50    /*WATER IN LITERS*/;
 L2=LAG(L1); L3=LAG(L2); L4=LAG(L3); L5=LAG(L4);
 L6=LAG(L5); L7=LAG(L6); L8=LAG(L7); L9=LAG(L8);
 L10=LAG(L9); L11=LAG(L10); L12=LAG(L11); L13=LAG(L12);
 L14=LAG(L13); L15=LAG(L14); L16=LAG(L15); L17=LAG(L16);
 L18=LAG(L17); L19=LAG(L18); L20=LAG(L19); L21=LAG(L20);
 L22=LAG(L21);
  STDEV=STD(OF L1-L22);
  DROP WMETR L2-L22;

DATA FIVE            /*EATING AND RUMINATING DIFFERENTIATION*/;
  SET FOUR(KEEP=STDEV);
  IF STDEV<1 THEN DO; RTYPE=1; ETYPE=0; END;
  ELSE DO;  RTYPE=0; ETYPE=1; END;

DATA SIX             /*LOAD, WATER, CHEWS, PH DURING PAST 30 SEC.*/;
  SET FOUR(DROP=STDEV);
  SET FIVE(FIRSTOBS=12);
  LOAD+L1;
  TCHEWS+CHEW;
  IF WATERS>0 THEN DO; CHEW=0; RTYPE=0; ETYPE=0; COUNT+1; END;
  IF RTYPE=1 THEN RCHEW=CHEW; ELSE IF ETYPE=1 THEN ECHEW=CHEW;
  RCHEWS+RCHEW;  ECHEWS+ECHEW;
  TOT+1;
  WATER+WATERS;  PHS+PH;
  IF TOT=6; LOAD=LOAD/6; COUNT=COUNT/12;  PHS=PHS/6;
    DROP L1 CHEW TOT PH WATERS RTYPE ETYPE RCHEW ECHEW;
  OUTPUT;
  TCHEWS=0; LOAD=0; TOT=0; WATER=0; COUNT=0; RCHEWS=0;
ECHEWS=0;
  PHS=0;

DATA SEVEN                                   /*3 MIN. MOVING SUM OF CHEWS*/;
  SET SIX(KEEP=RCHEWS ECHEWS);
  R1=LAG(RCHEWS); R2=LAG(R1);  R3=LAG(R2);
  R4=LAG(R3);    R5=LAG(R4);  R6=LAG(R5);
  RCHEW=SUM(OF R1-R6);
  E1=LAG(ECHEWS); E2=LAG(E1);  E3=LAG(E2);
  E4=LAG(E3);    E5=LAG(E4);  E6=LAG(E5);
  ECHEW=SUM(OF E1-E6);
  DROP RCHEWS R1-R6 ECHEWS E1-E6;
```

Table 4. (cont.)

```
DATA EIGHT                          /*CONTRACTIONS DURING LAST 30 SEC*/;
  SET ONE(KEEP=C1);
  C2=LAG(C1); C3=LAG(C2); C4=LAG(C3); C5=SUM(OF C1-C4);
  IF C3>0 THEN C6=C5; ELSE C6=0;
  C7=LAG(C6); C8=LAG(C7);  C9=SUM(C7,C8);
  IF C9>0 THEN C10=0; ELSE C10=C6;
  IF C10>1 THEN C11=1; ELSE C11=0;
  DROP C1-C10;
  TOT+1;  CONT+C11;
  IF TOT=6; DROP TOT C11; OUTPUT;
  CONT=0; TOT=0;

DATA TEN                                /*DAILY SUM OF CONTRACTIONS*/;
  IF _N_= 1 THEN DO; FILE CONTSUM; PUT 'DAY' ' ' 'CONTRCT'; END;
  MERGE SIX(KEEP=TIME) EIGHT;
  TOT+1; CONTRACT+CONT;
  IF TOT=2880; TIME=TIME/86400;
  DROP TOT CONT;
  FILE CONTSUM LRECL=200;
  PUT TIME CONTRACT; TOT=0; CONTRACT=0;

DATA ELEVEN                             /*CHEWING TOTALS; 30 SEC FILE*/;
  MERGE SIX SEVEN(FIRSTOBS=4) EIGHT;
  IF RCHEW>75 AND RCHEWS>8 THEN RUMNATIN=1; ELSE RUMNATIN=0;
  IF ECHEW>75 AND ECHEWS>8 THEN EATING=1; ELSE EATING=0;
  RUMCHEWS=RUMNATIN*RCHEWS;
  EATCHEWS=EATING*ECHEWS;
  ICHEWS=TCHEWS-(RUMCHEWS+EATCHEWS);
  DROP TCHEWS RCHEWS RCHEW ECHEWS ECHEW;

DATA TWELVE                         /*TOTAL CHEWING EVERY FIVE MIN.*/;
  SET ELEVEN(DROP=LOAD COUNT WATER PHS CONT);
  TOT+1;  RUM+RUMNATIN;  EAT+EATING;
  RCHEW+RUMCHEWS;  ECHEW+EATCHEWS;  ICHEW+ICHEWS;
  IF TOT=10;  TIME=TIME/60;
  RUMNATIN=RUM/2; EATING=EAT/2;
  DROP TIME TOT RUM EAT RUMCHEWS EATCHEWS ICHEWS;
  OUTPUT; TOT=0;  RUM=0; EAT=0;
  RCHEW=0;  ECHEW=0;  ICHEW=0;

DATA THIRTEEN                           /*5 MIN SUMS OF CHEWING*/;
  SET TWELVE(KEEP=RCHEW ECHEW);
  R1=RCHEW;  R2=LAG(R1);  R3=LAG(R2);  RSUM=SUM(OF R1-R3);
  E1=ECHEW;  E2=LAG(E1);  E3=LAG(E2);  ESUM=SUM(OF E1-E3);
  DROP RCHEW R1-R3 ECHEW E1-E3;
```

Table 4. (cont.)

```
DATA FOURTEEN                /*EATING, RUMINATING CORRECTION*/;
  MERGE TWELVE THIRTEEN(FIRSTOBS=2);
  IF ESUM<RSUM THEN DO; RUMNATIN=EATING+RUMNATIN;
     EATING=0; RCHEW=ECHEW+RCHEW; ECHEW=0; END;
     ELSE DO; EATING=EATING+RUMNATIN;
     RUMNATIN=0; ECHEW=ECHEW+RCHEW; RCHEW=0; END;
  IF RUMNATIN>5 THEN RUMNATIN=5; IF EATING>5 THEN EATING=5;
  IDLE=5-(RUMNATIN+EATING);
  DROP ESUM RSUM;

DATA FIFTEEN        /*EXPANSION OF CHEWS FROM 5 MIN TO 30 SEC*/;
  SET FOURTEEN(KEEP=RUMNATIN EATING);
  RUM=RUMNATIN; EAT=EATING; DROP RUMNATIN EATING;
  OUTPUT; OUTPUT; OUTPUT; OUTPUT; OUTPUT;
  OUTPUT; OUTPUT; OUTPUT; OUTPUT; OUTPUT;

DATA SIXTEEN        /*CORRECTION OF 30 SEC TOTALS FOR CHEWS*/;
  MERGE ELEVEN FIFTEEN;
  IF RUM>EAT THEN DO; RUMNATIN=RUMNATIN+EATING; EATING=0;
  RUMCHEWS=RUMCHEWS+EATCHEWS; EATCHEWS=0; END;
  ELSE DO; EATING=EATING+RUMNATIN; RUMNATIN=0;
  EATCHEWS=EATCHEWS+RUMCHEWS; RUMCHEWS=0; END;
  IF STDEV<1 THEN STDEV=0;
  IF RUMNATIN>1 THEN RUMNATIN=1;
  IF EATING>1 THEN EATING=1;
  DROP COUNT RUM EAT;

DATA SEVENTEN(KEEP=L1)              /*STDEV OF LOAD FLAGGING*/;
  SET SIXTEEN(KEEP=LOAD STDEV); BY STDEV NOTSORTED;
  IF STDEV=0 AND FIRST.STDEV=1;
  L1=LOAD;

DATA EIGHTEEN(KEEP=L2)              /*STDEV OF LOAD FLAGGING*/;
  SET SIXTEEN(KEEP=LOAD STDEV); BY STDEV NOTSORTED;
  IF STDEV=0 AND LAST.STDEV=1; TOT+1;
  L2=LOAD; IF TOT>1;

DATA NINETEEN        /*STABLE LOADS BEFORE AND AFTER MEALS*/;
  SET SIXTEEN; BY STDEV NOTSORTED;
  IF STDEV=0 AND FIRST.STDEV=1 THEN SET SEVENTEN;
  IF STDEV=0 AND LAST.STDEV=1 THEN SET EIGHTEEN;
```

Table 4. (cont.)

```
DATA TWENTY          /*RUNNING SUMS FOR EAT AND RUM PERIODS*/;
  SET NINETEEN(KEEP=EATING RUMNATIN);
  R1=RUMNATIN; R2=LAG(R1); R3=LAG(R2); R4=LAG(R3);
  R5=LAG(R4); R6=LAG(R5); R7=LAG(R6); R8=LAG(R7);
  R9=LAG(R8); R10=LAG(R9); R11=LAG(R10); R12=LAG(R11);
  R13=LAG(R12); R14=LAG(R13); R15=LAG(R14);
  R16=SUM(OF R1-R10); R17=SUM(OF R1-R15);
  E1=EATING; E2=LAG(E1); E3=LAG(E2); E4=LAG(E3);
  E5=LAG(E4); E6=LAG(E5); E7=LAG(E6); E8=LAG(E7);
  E9=LAG(E8); E10=LAG(E9); E11=LAG(E10); E12=LAG(E11);
  E13=LAG(E12); E14=LAG(E13); E15=LAG(E14);
  E16=EATING; E17=SUM(OF E1-E15);
  DROP RUMNATIN R1-R15 EATING E1-E15;

DATA TW_ONE                                    /*EATING PERIODS*/;
  MERGE TWENTY(FIRSTOBS=16 KEEP=E17)
  TWENTY(FIRSTOBS=2 KEEP=E16)
  NINETEEN(KEEP=TIME L1 L2 WATER EATING EATCHEWS CONT PHS);
  IF E17=. THEN E17=E16;
  WATR+WATER; EAT+EATING/2; CHEWS+EATCHEWS; CONTR+CONT;
  IF E17=0 THEN E18=0; ELSE IF E16=1 THEN E18=1; ELSE E18=2;
  IF E18=LAG(E18) THEN E19=2; ELSE E19=E18;
  IF E19=2 THEN DELETE;
  IF E19=LAG(E19) THEN E20=2; ELSE E20=E19;
  IF E20=2 THEN DELETE;
  DROP WATER EATING EATCHEWS E16-E19 CONT;

DATA TW_TWO                              /*EATING PERIOD VARIABLES*/;
  SET TW_ONE; STARTIME=(LAG(TIME))/86400;
  STOPTIME=TIME/86400;
  DUR=ROUND(((STOPTIME-STARTIME)*1440),.1);
  EATCHEWS=CHEWS-LAG(CHEWS);
  EATING=EAT-LAG(EAT);
  STARTPH=ROUND(LAG(PHS),.01); STOPPH=ROUND(PHS,.01);
  WATER=ROUND(WATR-LAG(WATR),.1); CONT=CONTR-LAG(CONTR);
  STRTLOAD=ROUND(LAG(L1),.1); STOPLOAD=ROUND(L2,.1);
  IF _N_=1 THEN DELETE; IF E20=1 THEN DELETE;
  CHEWRATE=ROUND(EATCHEWS/EATING,.1);
  DROP TIME CHEWS EAT WATR L1 L2 E20 CONTR PHS;
```

Table 4. (cont.)

```
DATA TW_THREE                                   /*CLEAN UP DLOADS, PRINT*/;
  IF _N_ =1 THEN DO; FILE EATPER; PUT 'STARTIME' ' 'STOPTIME' '
     'DURATION' ' 'EATCHEWS' ' 'EATING' ' 'CHEWRATE' ' 'STARTPH' '
     'STOPPH' ' 'WATER' ' 'CONTRACTIONS' ' 'STARTLOAD' ' 'STOPLOAD'
     ' ' 'DLOAD' ' 'TIMELAST'; END;
  SET TW_TWO; LLOAD=LAG(STOPLOAD); DIF=LLOAD-STOPLOAD;
  IF DIF^>0 THEN DLOAD=STRTLOAD-STOPLOAD; ELSE DLOAD=DIF;
  IF DLOAD<.1 THEN DELETE;
  TIMELAST=ROUND(((STARTIME-LAG(STOPTIME))*1440),.1);
  DROP LLOAD DIF;
  STARTIME=ROUND(STARTIME,.0001);
  STOPTIME=ROUND(STOPTIME,.0001);
  FILE EATPER LRECL=200;
  PUT STARTIME STOPTIME DUR EATCHEWS EATING CHEWRATE
STARTPH
    STOPPH WATER CONT STRTLOAD STOPLOAD DLOAD TIMELAST;

DATA TW_FOUR                                    /*RUMINATING PERIODS*/;
  MERGE TWENTY(FIRSTOBS=16 KEEP=R17)
  TWENTY(FIRSTOBS=11 KEEP=R16)
  NINETEEN(KEEP=TIME WATER RUMNATIN RUMCHEWS CONT PHS);
  IF R17=. THEN R17=R16;
  WATR+WATER; RUM+RUMNATIN/2;  CHEWS+RUMCHEWS;
CONTR+CONT;
  IF R17=0 THEN R18=0; ELSE IF R16=10 THEN R18=1; ELSE R18=2;
  IF R18=LAG(R18) THEN R19=2; ELSE R19=R18;
  IF R19=2 THEN DELETE;
  IF R19=LAG(R19) THEN R20=2; ELSE R20=R19;
  IF R20=2 THEN DELETE;
  DROP WATER RUMNATIN RUMCHEWS R16-R19 CONT;

DATA TW_FIVE                            /*RUMINATING PERIOD VARIABLES*/;
  IF _N_ =1 THEN DO; FILE RUMPER; PUT 'STARTIME' ' 'STOPTIME' '
   'DURATION' ' 'TIMELAST' ' 'RUMCHEWS' ' 'RUMNATIN' ' 'CHEWRATE' '
   'STARTPH' ' 'STOPPH' ' 'WATER' ' 'CONT'; END;
  SET TW_FOUR; STARTIME=(LAG(TIME))/86400; STOPTIME=TIME/86400;
  DUR=ROUND(((STOPTIME-STARTIME)*1440),.1);   TIMELAST=LAG(DUR);
  RUMCHEWS=CHEWS-LAG(CHEWS);
  RUMNATIN=RUM-LAG(RUM);
  STARTPH=ROUND(LAG(PHS),.01);  STOPPH=ROUND(PHS,.01);
  WATER=ROUND(WATR-LAG(WATR),.1); CONT=CONTR-LAG(CONTR);
  IF _N_=1 THEN DELETE;  IF R20=1 THEN DELETE;
  IF _N_=3 THEN TIMELAST=.;
  CHEWRATE=ROUND(RUMCHEWS/RUMNATIN,.1);
  DROP TIME CHEWS RUM WATR R20 CONTR PHS;
  STARTIME=ROUND(STARTIME,.0001);
  STOPTIME=ROUND(STOPTIME,.0001);
  FILE RUMPER LRECL=200;
  PUT STARTIME STOPTIME DUR TIMELAST RUMCHEWS RUMNATIN
   CHEWRATE STARTPH STOPPH WATER CONT;
```

Table 4. (cont.)

```
DATA TW_SIX                                          /*WATER FLAGGING*/;
  SET ELEVEN(KEEP=TIME WATER COUNT);
  IF WATER>0 THEN F1=1; ELSE F1=0;
  F2=LAG(F1); F3=LAG(F2); F4=LAG(F3); F5=LAG(F4);
  F6=LAG(F5); F7=LAG(F6); F8=LAG(F7); FLAG=SUM(OF F1-F8);
  IF FLAG>0 THEN FLAG=1;
  WATERS+WATER; WTIMES+COUNT; DROP WATER COUNT F1-F8;

DATA TW_SEVEN                                        /*DRINKING PERIODS*/;
  SET TW_SIX; BY FLAG NOTSORTED;
  IF FIRST.FLAG=1;
  STARTIME=(LAG(TIME)-30)/86400;  STOPTIME=(TIME-240)/86400;
  DUR=ROUND(((STOPTIME-STARTIME)*1440),.1);
  DWATER=ROUND(WATERS-LAG2(WATERS),.01);
  WTIME=ROUND(WTIMES-LAG2(WTIMES),.01);
  DKRATE=ROUND(DWATER/WTIME,.01);
  IF WATERS=0 THEN DELETE;  IF FLAG=1 THEN DELETE;
  DROP TIME WATERS WTIMES FLAG;

DATA TW_EIGHT                                /*DRINKING BOUT FIX, PRINT*/;
  IF _N_ =1 THEN DO; FILE DRNKPER; PUT 'STARTIME' ' 'STOPTIME' '
   'DURATION' ' 'DWATER' ' 'WTIME' ' 'DKRATE' ' 'TIMELAST'; END;
  SET TW_SEVEN; IF DWATER<.09 THEN DELETE;
  TIMELAST=ROUND(((STARTIME-LAG(STOPTIME))*1440),.1);
  STARTIME=ROUND(STARTIME,.0001);
  STOPTIME=ROUND(STOPTIME,.0001);
  FILE DRNKPER LRECL=200;
  PUT STARTIME STOPTIME DUR DWATER WTIME DKRATE TIMELAST;
  RUN;
```

---

[1]Reticular contractions and ruminal pH are included in bout activities. Data input are cow files obtained from feeding behavior data acquisition system and Labtech Notebook. Data output are bout summaries in ASCII format. Current configuration is set for running on IBM 3090 mainframe computer using the Statistical Analysis System (SAS) software program.

Table 5. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: probability values for effects used to describe variation in experimental variables.[1]

	Source of variation				
Variable	Square	Treatment	Period within square	Cow within square	Square by Treatment
	(Probability > F)				
Production					
Milk	.0006	.0004	.5663	.0002	ns
4% FCM	.0001	.0091	.2187	.0027	ns
Fat	.0001	.2167	.2080	.0144	ns
Protein	.0008	.0001	.3385	.0010	ns
Lactose	.0031	.0001	.4222	.0009	ns
Milk composition					
Fat	.0481	.5036	.4783	.0045	ns
Protein	.0026	.0003	.0393	.0235	ns
Lactose	.0001	.0001	.0020	.0001	ns
Intake					
DM	.0065	.0001	.0019	.0222	.0360
NDF	.0011	.0039	.0124	.0516	.0338
Indigestible NDF	.0002	.0001	.0086	.0531	.0520
CP	.0091	.0001	.0011	.0232	.0298
Water intake					
Free water	.0043	.0009	.0059	.0001	ns
Total water	.0043	.0089	.0026	.0002	.0912
BW	.0001	.1565	.0045	.0001	ns
Empty BW	.0001	.0001	.0046	.0001	ns
Body condition score	.0001	.1672	.0044	.0001	ns
Nutrient digestibility					
DM	.0003	.0001	.3164	.0708	ns
OM	.0003	.0001	.5276	.1097	ns
NDF	.0236	.0019	.8119	.6939	ns
ADF	.0614	.9571	.8700	.1803	ns
Lignin	.0031	.0170	.0162	.6360	ns
Hemicellulose	.0215	.4481	.6518	.8898	ns
Cellulose	.0848	.4238	.9305	.1570	ns
CP	.0125	.4261	.0023	.2973	ns
Fecal output					
DM	.0070	.0140	.0107	.0248	.0763
NDF	.0021	.0017	.0426	.0757	.0965
Indigestible NDF	.0002	.0001	.0086	.0531	.0520
Fecal composition					
DM	...	...	...	...	...
NDF	...	...	...	...	...
Indigestible NDF	...	...	...	...	...

Table 5. (cont.)

Variable	Source of variation				
	Square	Treatment	Period within square	Cow within square	Square by Treatment
	(Probability > F)				
Fecal NDF particle size					
<600 µm	.0781	.0133	.0719	.2493	ns
600-1200 µm	.1536	.0027	.0533	.0501	ns
1200-2400 µm	.7260	.0001	.3868	.6490	.0927
>2400 µm	.1037	.7985	.1536	.4637	ns
Rumen volume					
Digesta	.0119	.0001	.0008	.0001	ns
Digesta + inert bulk	.0136	.0013	.0012	.0001	ns
Digesta + inert bulk + head space	.0098	.0005	.0003	.0001	ns
Digesta composition					
DM					
52°C	.0001	.0001	.0410	.0001	.0034
Toluene	...	...	...	...	...
NDF	.0013	.0001	.3677	.1073	ns
Rumen mass					
Wet digesta	.0083	.0001	.0010	.0003	ns
Wet digesta + inert bulk	.0116	.0001	.0014	.0002	ns
DM	.0010	.0001	.0135	.0055	ns
OM	.0002	.0001	.0130	.0034	ns
NDF	.0001	.0001	.0694	.0015	ns
ADF	.0001	.0001	.0411	.0020	ns
Lignin	.0001	.0001	.0137	.0026	ns
Hemicellulose	.0002	.0001	.0845	.0009	ns
Cellulose	.0001	.0001	.0492	.0008	ns
Indigestible NDF	.0001	.0001	.0355	.0009	ns
Density	.0002	.0001	.0458	.0087	ns
VFA concentrations					
Acetate	.0072	.0006	.0554	.0038	.0110
Propionate	.0656	.0001	.0683	.0009	ns
Butyrate	.0001	.0001	.7400	.0001	ns
Valerate	.0041	.0128	.1057	.0878	ns
Branched-chain	.0001	.0093	.0115	.0004	ns
Total	.0048	.0001	.0150	.0001	.0273
VFA molar proportions					
Acetate	.0785	.0001	.6122	.0057	ns
Propionate	.4357	.0001	.2146	.0070	ns
Butyrate	.0046	.3420	.5485	.1446	.0717
Valerate	.0307	.6570	.2204	.6007	ns
Branched-chain	.0001	.0025	.0189	.0164	.0629
Acetate:prop. ratio	.1606	.0001	.3034	.0022	ns
Fractional passage rate					
2 h prefeeding	.0035	.0001	.1088	.0001	.0497
2 h postfeeding	.0087	.0001	.2350	.0161	ns
Average	.0012	.0001	.2532	.0002	ns

Table 5. (cont.)

Variable	Source of variation				
	Square	Treatment	Period within square	Cow within square	Square by Treatment
	(Probability > F)				
Fractional digestion rate					
2 h prefeeding	.0916	.0005	.3734	.0074	ns
2 h postfeeding	.2924	.0620	.8788	.1041	ns
Average	.1191	.0044	.7265	.0235	ns
Rumen apparent digestibility					
% of NDF intake					
2 h prefeeding	.1922	.0001	.6478	.1899	ns
2 h postfeeding	.3317	.0001	.6112	.0311	.0904
Average	.1327	.0001	.4917	.0527	.0890
% of total tract digestibility					
2 h prefeeding	.0117	.0060	.9009	.5620	ns
2 h postfeeding	.0007	.0001	.1893	.0026	.0089
Average	.0007	.0001	.5278	.0895	.0767
Eating bouts	.0001	.4806	.6676	.0015	ns
Meal size					
Mean					
DM	.0001	.0002	.0057	.0002	.0678
NDF	.0001	.0079	.0367	.0037	ns
SD	...	...	...	...	...
Maximum	.4940	.4234	.0672	.2094	ns
Eating bout length	.0366	.0058	.6060	.0002	ns
Eating time					
min/d	.1324	.0004	.3142	.0020	ns
min/kg of DM	.0008	.0001	.0084	.0005	ns
min/kg of NDF	.0001	.0018	.0147	.0011	ns
Eating chews	.0040	.0001	.0360	.0001	.0925
Eating chew rate	.0079	.0509	.0009	.0001	ns
Water intake during meals	.8727	.0603	.0056	.0001	ns
Ruminating bouts	.7748	.0005	.0748	.0001	ns
Ruminating bout length	.0001	.0001	.0731	.0001	ns
Ruminating time					
min/d	.0001	.0001	.1408	.0440	ns
min/kg of DM	.0001	.0001	.0001	.0037	.0122
min/kg of NDF	.0002	.0001	.0004	.0048	.0084
Ruminating chews	.0001	.0001	.0340	.0001	ns
Ruminating chew rate	.0001	.0006	.0461	.0001	ns
Total chewing time					
min/d	.0005	.0001	.1783	.0106	ns
min/kg of DM	.0001	.0001	.0001	.0004	.0178
min/kg of NDF	.0001	.0001	.0005	.0022	.0223
Total chews	.0001	.0001	.0200	.0001	ns
Drinking bouts	.5299	.0219	.2975	.0002	ns
Drinking bout size	.4697	.5547	.6073	.0001	ns
Drinking time	.0001	.0759	.9973	.0001	ns
Drinking rate	.0001	.3139	.5454	.0001	ns

Table 5. (cont.)

Variable	Source of variation: Square	Treatment	Period within square	Cow within square	Square by Treatment
	(Probability > F)				
Reticular contractions					
Daily total					
Eating	.1567	.1070	.3526	.0127	ns
Ruminating	.0297	.0001	.0756	.0011	ns
Idle	.0005	.0003	.6604	.0078	ns
Total	.0005	.0051	.0170	.0001	ns
Frequency					
Eating	.9441	.0182	.2244	.0051	ns
Ruminating	.0001	.0001	.0038	.0001	ns
Idle	.0392	.3944	.7775	.0189	ns
Ruminal pH					
Daily pH					
Mean	.0002	.0004	.7380	.0282	ns
Variance	...	...	...	...	...
Minimum	.0110	.0028	.6474	.0839	ns
Maximum	.0002	.0005	.6630	.0232	ns
Range	.5522	.0971	.7520	.2011	ns
Hours below pH					
5.5	.2022	.0530	.5882	.4110	ns
6.0	.0075	.0049	.5463	.0861	ns
6.5	.0003	.0023	.7189	.0099	ns
7.0	.0016	.0170	.1725	.3775	.0301
Start of eating	.0003	.0004	.7514	.0455	ns
End of eating	.0003	.0004	.6953	.0648	ns
Start of rumination	.0006	.0005	.7482	.0268	ns
End of rumination	.0021	.0012	.9251	.0584	ns

[1]The statistical model used was appropriate for Latin square designs. A reduced model without square x treatment was used when this effect was not significant (P > .10).

Table 6. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: apparent total tract digestibility of nutrients using acid detergent lignin as an internal marker from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment			
Variable	LF+0	LF+B	HF+0	HF+B
Digestibility, %				
DM	66.8	65.9	65.2	63.3
OM	68.5	67.2	66.5	64.6
NDF	39.8	39.6	44.6	40.8
ADF	38.0	37.6	45.5	43.7
Indigestible NDF[1]	-16.4	-16.0	-1.5	-5.7
Hemicellulose	38.1	36.2	44.5	40.5
Cellulose	45.8	45.6	54.6	52.4
CP	65.2	65.1	70.0	67.4
Fecal output, kg/d				
DM	7.60	7.83	6.49	6.11
NDF	3.49	3.50	3.60	3.43
Lignin	.52	.51	.67	.61

[1]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 7. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: rumen digesta parameters 2 h prefeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Rumen volume, L								
Digesta	89.9[a]	75.4[b]	95.6[a]	78.6[b]	2.4	†	**	NS
Digesta + inert bulk	89.9[b]	97.6[a]	95.6[ab]	100.8[a]	2.4	†	*	NS
Digesta + inert bulk + head space	108.4[c]	115.7[ab]	110.1[bc]	119.3[a]	2.0	NS	**	NS
Digesta composition								
DM, %								
52°C oven	14.3[a]	12.4[b]	12.9[b]	10.4[c]	.2	**	**	NS
Toluene	12.3[a]	10.8[b]	11.9[ab]	8.1[c]	.6	*	**	NS
NDF, %	57.3[b]	56.8[b]	63.5[a]	63.6[a]	1.0	**	NS	NS
Rumen mass, kg								
Wet digesta	76.0[b]	63.1[c]	83.6[a]	68.3[c]	1.8	**	**	NS
Wet digesta + inert bulk	76.0[c]	85.3[ab]	83.6[b]	90.5[a]	1.8	**	**	NS
DM	10.8[a]	7.8[b]	10.8[a]	7.2[b]	.3	NS	**	NS
OM	9.6[a]	6.8[b]	9.5[a]	6.3[b]	.3	NS	**	NS
NDF	6.2[b]	4.4[c]	6.9[a]	4.6[c]	.2	*	**	NS
ADF	3.6[b]	2.6[c]	4.1[a]	2.8[c]	.1	**	**	NS
Lignin	.81[b]	.60[c]	.99[a]	.68[c]	.03	**	**	NS
Hemicellulose	2.6[a]	1.9[b]	2.8[a]	1.8[b]	.1	NS	**	NS
Cellulose	2.6[b]	1.9[c]	3.0[a]	2.0[c]	.1	*	**	NS
Indigestible NDF[2]	3.4[b]	2.4[c]	4.1[a]	2.7[c]	.1	**	**	†
Density, kg/L	.85[b]	.84[b]	.88[a]	.87[a]	.01	**	NS	NS

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

[1]Main effect levels differ, **$P < .01$, *$P < .05$, †$P < .10$.

[2]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 8. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: rumen digesta parameters 2 h postfeeding for 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
Rumen volume, L								
Digesta	89.8[b]	82.4[b]	101.9[a]	86.8[b]	2.8	**	**	NS
Digesta + inert bulk	89.8[b]	104.6[a]	101.9[a]	108.9[a]	2.8	**	**	NS
Digesta + inert bulk + head space	107.6[b]	120.2[a]	112.9[b]	122.9[a]	2.4	NS	**	NS
Digesta composition								
DM, %								
52°C oven	14.3[a]	13.2[b]	13.2[b]	10.7[c]	.3	**	**	*
Toluene	12.5[a]	11.9[a]	11.6[a]	8.3[b]	.7	**	*	†
NDF, %	53.7[b]	51.9[b]	59.9[a]	59.2[a]	.9	**	NS	NS
Rumen mass, kg								
Wet digesta	75.3[b]	67.4[c]	89.2[a]	75.5[b]	2.6	**	**	NS
Wet digesta + inert bulk	75.3[c]	89.6[b]	89.2[b]	97.7[a]	2.6	**	**	NS
DM	10.7[a]	8.8[b]	11.9[a]	8.2[b]	.4	NS	**	†
OM	9.4[a]	7.7[b]	10.4[a]	7.1[b]	.4	NS	**	†
NDF	5.8[b]	4.6[c]	7.1[a]	4.9[c]	.3	**	**	†
ADF	3.3[b]	2.6[c]	4.2[a]	2.9[bc]	.2	**	**	†
Lignin	.79[b]	.61[c]	1.02[a]	.70[bc]	.1	**	**	†
Hemicellulose	2.5[b]	2.0[c]	2.9[a]	2.0[c]	.1	†	**	*
Cellulose	2.5[b]	1.9[c]	3.1[a]	2.1[c]	.1	**	**	†
Indigestible NDF[2]	3.3[b]	2.5[c]	4.2[a]	2.9[c]	.1	**	**	*
Density, kg/L	.84[b]	.82[b]	.88[a]	.87[a]	.01	**	NS	NS

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

[1]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $\dagger P < .10$.

[2]Neutral detergent fiber residue after 120 h in vitro fermentation.

Table 9. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: concentration and molar proportion of VFA in rumen fluid 2 h prefeeding from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
VFA concentrations	----------(mmol/L)----------							
Acetate	77.8[a]	71.7[b]	78.1[a]	67.4[b]	2.0	NS	**	NS
Propionate	31.9[a]	26.2[b]	23.3[b]	17.7[c]	1.4	**	**	NS
Butyrate	13.0[a]	12.2[a]	12.6[a]	10.9[b]	.4	*	**	NS
Valerate	2.8[a]	2.3[b]	2.4[b]	1.9[c]	.1	**	**	NS
Branched-chain[2]	5.6[a]	4.9[b]	5.1[b]	4.9[b]	.2	NS	*	NS
Total	131.1[a]	117.3[b]	121.5[b]	102.9[c]	2.8	**	**	NS
VFA molar proportions	----------(% of total VFA)----------							
Acetate	59.4[c]	61.5[b]	64.3[a]	65.6[a]	.6	**	*	NS
Propionate	24.2[a]	21.8[b]	19.1[c]	17.1[c]	.8	**	*	NS
Butyrate	10.0	10.6	10.4	10.6	.3	NS	NS	NS
Valerate	2.1[a]	1.9[b]	2.0[ab]	1.8[b]	.1	†	*	NS
Branched-chain	4.3[b]	4.2[b]	4.2[b]	4.9[a]	.1	*	*	*
Acetate:propionate ratio	2.6[d]	3.0[c]	3.4[b]	3.9[a]	.1	**	**	NS

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

[1]Main effect levels differ, **$P < .01$, *$P < .05$, †$P < .10$.

[2]isobutyrate + isovalerate.

Table 10. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk: concentration and molar proportion of VFA in rumen fluid 2 h postfeeding from 12 cows receiving low fiber (LF) or high fiber (HF) diets without (+0) or with (+B) added rumen inert bulk.

	Treatment					Main effect[1] significance		
Variable	LF+0	LF+B	HF+0	HF+B	SE	F	B	FxB
VFA concentrations	----------(mmol/L)----------							
Acetate	77.4[a]	76.0[a]	77.3[a]	69.7[b]	1.8	NS	*	NS
Propionate	29.9[a]	26.6[ab]	25.2[b]	21.2[c]	1.2	**	**	NS
Butyrate	13.0[a]	12.8[a]	13.1[a]	11.1[b]	.3	*	**	**
Valerate	2.9	2.7	3.0	2.7	.1	NS	NS	NS
Branched-chain[2]	6.0	5.5	5.7	5.6	.2	NS	*	NS
Total	129.2[a]	123.6[a]	124.3[a]	110.4[b]	3.4	*	**	NS
VFA molar proportions	----------(% of total VFA)----------							
Acetate	60.1[b]	61.6[ab]	62.1[a]	63.1[a]	.7	*	†	NS
Propionate	22.9[a]	21.4[ab]	20.2[bc]	19.2[c]	.6	**	*	NS
Butyrate	10.0	10.4	10.6	10.0	.2	NS	NS	†
Valerate	2.2	2.2	2.4	2.4	.1	*	NS	NS
Branched-chain	4.7[b]	4.5[b]	4.7[b]	5.2[a]	.1	*	NS	*
Acetate:propionate ratio	2.7[c]	3.0[bc]	3.1[ab]	3.3[a]	.1	**	*	NS

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

[1]Main effect levels differ, $^{**}P < .01$, $^{*}P < .05$, $\dagger P < .10$.

[2]isobutyrate + isovalerate.

Table 11. Enhanced intake and production of cows offered ensiled alfalfa silage with higher neutral detergent fiber digestibility: probability values for effects used to describe variation in experimental variables.[1]

	Source of variation		
Variable	Cow	Period	Treatment
	(Probability > F)		
Production			
Milk	.0001	.4086	.0192
SCM	.0001	.8857	.3086
Fat	.0007	.7694	.7229
Protein	.0001	.0852	.1960
Lactose	.0001	.7149	.0837
Milk composition			
Fat	.0371	.3982	.3666
Protein	.0021	.1147	.2329
Lactose	.0052	.2255	.3966
BW	.0001	.0049	.9587
Body condition score	.0001	.0219	.5995
Intake			
DM	.0001	.0001	.0081
NDF	.0001	.0001	1.000
Indigestible NDF	.0009	.0001	.0872
CP	.0001	.0001	.7817
Fecal composition			
DM	.0072	.8248	.2594
NDF	.0041	.5080	.1875
Indigestible NDF	.0373	.1993	.0143
Fecal output			
DM	.0005	.0001	.4147
NDF	.0011	.0001	.3438
Nutrient digestibility			
DM	.7791	.3760	.0050
OM	.8073	.4300	.0037
NDF	.9503	.8626	.0778
ADF	.8501	.4910	.1964
Lignin	.6780	.0344	.0409
Hemicellulose	.2096	.3427	.0688
Cellulose	.6457	.9446	.0633
CP	.1768	.3554	.2071
Eating bouts	.0687	.3856	.9188
Meal size			
DM	.0113	.0010	.5527
NDF	.0122	.0007	.6014
Eating bout length	.0504	.2212	.9280
Eating time			
min/d	.0009	.2571	.9885
min/kg of DM	.0057	.0028	.1132
min/kg of NDF	.0160	.0041	.8358

Table 11 (cont.)

Variable	Source of variation		
	Cow	Period	Treatment
	(Probability > F)		
Eating chews	.0686	.4947	.4151
Eating chew rate	.0079	.9751	.1758
Water intake during meals	.0042	.0574	.4430
Ruminating bouts	.0009	.0700	.0415
Ruminating bout length	.0008	.5795	.0255
Ruminating time			
min/d	.0030	.0255	.8738
min/kg of DM	.0008	.0033	.1199
min/kg of NDF	.0021	.0035	.9561
Ruminating chews	.0622	.1842	.5033
Ruminating chew rate	.2210	.6125	.2826
Total chewing time			
min/d	.0036	.0463	.9153
min/kg of DM	.0016	.0011	.0753
min/kg of NDF	.0058	.0017	.9067
Total chews	.0863	.2312	.4175
Water intake	.0001	.0002	.5676
Drinking bouts	.0007	.3897	.4190
Drinking bout size	.0006	.8102	.2369
Drinking time	.0121	.6340	.3343
Drinking rate	.0014	.5331	.3470
Rumen digesta volume			
2 h prefeeding	.0679	.0215	.8657
2 h postfeeding	.2698	.0651	.7937
Average	.1497	.0404	.8199
Rumen digesta composition			
DM	.2780	.3846	.7536
NDF	.7512	.4120	.2134
Indigestible NDF	.6813	.6100	.0885
Rumen digesta mass			
Wet digesta	.1797	.0566	.7995
DM	.1059	.0400	.7166
OM	.1018	.0392	.6940
NDF	.1865	.0732	.5162
ADF	.1832	.0717	.4082
Lignin	.1714	.0733	.2785
Hemicellulose	.1993	.0820	.8778
Cellulose	.1856	.0696	.4768
Indigestible NDF	.1587	.0651	.3250
Rumen digesta density	.6464	.0474	.3333
Rumen pH			
2 h prefeeding	.0927	.1355	.1213
2 h postfeeding	.2215	.1605	.6142
Average	.1691	.1482	.2983
Total rumen VFA concentration			
2 h prefeeding	.5460	.1150	.7995
2 h postfeeding	.0547	.0634	.0322

Table 11 (cont.)

Variable	Source of variation		
	Cow	Period	Treatment
	(Probability > F)		
Average	.3951	.0995	.2957
Rumen VFA molar proportions			
Acetate	.7105	.4615	.1264
Propionate	.4729	.3571	.0787
Butyrate	.1306	.0770	.5769
Valerate	.5459	.1856	.1178
Branched-chain	.2819	.2613	.7642
Acet:Prop. ratio	.6079	.8229	.1007
Fractional passage rate			
2 h prefeeding	.5037	.8039	.3753
2 h postfeeding	.6915	1.000	.2929
Average	.6915	.8039	.3753
Fractional digestion rate			
2 h prefeeding	.6642	.8741	.9457
2 h postfeeding	.1916	.6364	.8253
Average	.4253	.7142	1.000
Rumen apparent NDF digestibility			
% of NDF intake			
2 h prefeeding	.8236	.8264	.5070
2 h postfeeding	.0309	.4880	.1116
Average	.3624	.9562	.3573
% of total tract digestibility			
2 h prefeeding	.8130	.9207	.7679
2 h postfeeding	.0997	.2062	.8270
Average	.1292	.2910	.6936

[1]The statistical model used was appropriate for balanced simple crossover designs.

Table 12. Enhanced intake and production of cows offered ensiled alfalfa silage with higher neutral detergent fiber digestibility: apparent total tract digestibility of nutrients using acid detergent lignin as an internal marker for 12 early lactation cows receiving low digestible fiber (LDF) or high digestible fiber (HDF) diets.

Variable	LDF	HDF	SE	Probability > F value
Fecal output, kg/d				
DM	7.2	6.8	.1	.008
NDF	4.1	3.8	.1	.003
Nutrient digestibility, %				
DM	63.0	67.0	.2	.001
OM	63.9	68.0	.3	.001
NDF	42.3	46.3	.4	.001
ADF	40.9	44.6	.4	.001
Indigestible NDF[1]	1.1	5.0	1.2	.05
Hemicellulose	45.8	50.1	.9	.006
Cellulose	53.4	57.0	.5	.001
CP	74.2	76.1	.3	.001

[1]Neutral detergent fiber residue after 120 h in vitro fermentation.

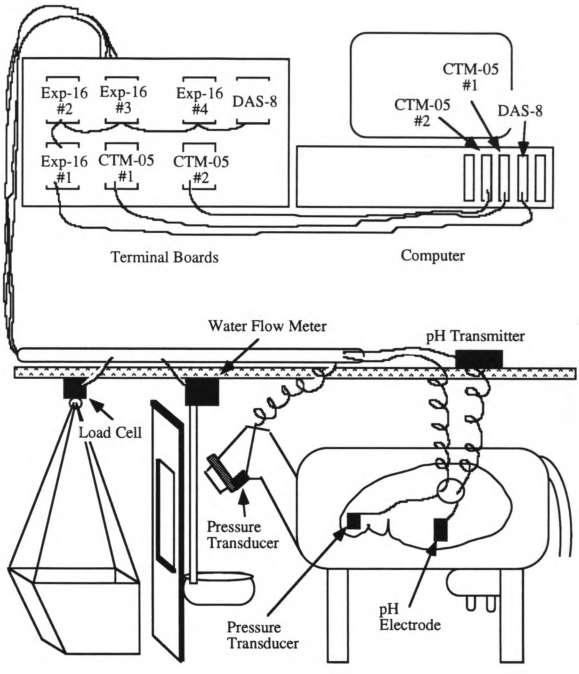


Figure 1. Schematic of complete data acquisition system for continuous monitoring of feed intake, water intake, chewing activity, reticular motility, and ruminal pH of cannulated cows at Michigan State University Dairy Teaching and Research Farm.