This is to certify that the

dissertation entitled

**Neutral Detergent Fiber Concentration and Digestibility
in Corn Silage Influences Digesta Kinetics, Dry Matter
Intake, and Performance of Growing Steers**

presented by

Kent Eric Tjardes

has been accepted towards fulfillment
of the requirements for

Doctor of _philosophy_ degree in _Animal Science_

Daniel D. Buskirk

Major professor

Date___May 1, 2001___

PLACE IN RETURN BOX to remove this checkout from your record.
TO AVOID FINES return on or before date due.
MAY BE RECALLED with earlier due date if requested.

DATE DUE	DATE DUE	DATE DUE
JAN 1 0 2004		
0 7 2 7 0 4		

6/01 c:/CIRC/DateDue.p65-p.15

NEUTRAL DETERGENT FIBER CONCENTRATION AND DIGESTIBILITY IN
CORN SILAGE INFLUENCES DIGESTA KINETICS, DRY MATTER INTAKE,
AND PERFORMANCE OF GROWING STEERS

By

Kent Eric Tjardes

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Animal Science

2001

ABSTRACT

NEUTRAL DETERGENT FIBER CONCENTRATION AND DIGESTIBILITY IN CORN SILAGE INFLUENCES DIGESTA KINETICS, DRY MATTER INTAKE, AND PERFORMANCE OF GROWING STEERS

By

Kent Eric Tjardes

It is our hypothesis that corn silage high in fiber potentially limits dry matter intake (DMI) and performance of growing beef steers. Improving fiber digestibility and(or) reducing fiber concentration in corn silage should improve intake and performance if intake is limited by ruminal fill. The brown midrib-3 (*bm₃*) gene mutation has been incorporated into corn plants to improve fiber digestibility. In Experiment 1, the objective was to determine the effect of bm_3 corn silage on digestion (Trial 1) and performance (Trial 2) of growing steers. In Trial 1, eight ruminally fistulated Angus steers (224 ± 24 kg) were used in a replicated 4 × 4 Latin square design with a 2 × 2 factorial arrangement of treatments and 21-d periods. Steers had ad libitum access or were restricted to 80% intake of diets containing 86% bm_3 corn silage (BMCS) or corn silage from its isogenic normal counterpart (Control). BMCS resulted in increased DMI ($P < 0.01$) and improved total-tract digestibility of dry matter (DM) and neutral detergent fiber (NDF; $P < 0.05$). In Trial 2, 128 steer contemporaries to Trial 1 (245 ± 13 kg) were offered ad libitum access to BMCS or Control diets. After a 112-d treatment period, steers received a common finishing diet. During the 112-d treatment period, steers fed BMCS had higher DMI ($P < 0.05$) and similar body weight gain ($P > 0.10$), resulting in poorer feed efficiency ($P < 0.01$). Finishing and overall performance of steers was not different due to

treatment ($P > 0.10$). The objectives of Experiments 2 and 3 were to determine if corn silage high in NDF concentration would limit DMI and performance by physical fill. In Experiment 2, eight ruminally fistulated Holstein steers (198 ± 13 kg) were used in a replicated 4×4 Latin square design with a 2×2 factorial arrangement of treatments and 16-d periods. Treatment diets contained a normal hybrid (33.8% NDF; low-fiber; **LF**) or male-sterile (50.8% NDF; high-fiber, **HF**) corn silage. Diets were offered ad libitum to steers without or with rumen inert bulk (**RIB**) added at 25% of pretrial ruminal volume. Feeding HF reduced DMI and ruminal NDF turnover time ($P < 0.01$), but had no effect on ruminal digesta volume ($P > 0.10$). Addition of RIB also reduced DMI and NDF turnover time ($P < 0.01$). The RIB increased digesta + RIB volume ($P < 0.01$), but had no effect on digesta (minus RIB) volume ($P > 0.10$). In Experiment 3, twelve Angus (237 ± 13 kg) and twelve Holstein (235 ± 15 kg) steers were used in a crossover design consisting of six, 14-d periods. The LF and HF diets were alternated each period. The HF diet decreased DMI and gain over the entire trial ($P < 0.01$), and HF depressed DMI to a greater extent as steers increased body weight when compared to LF ($P < 0.01$). Holstein steers consumed more DM and gained faster than Angus steers ($P < 0.01$). Difference in total-tract DM digestibility was negatively correlated to difference in DMI ($r^2 = 0.23$; $P < 0.01$) for LF minus HF within Angus steers, but not for Holstein steers. Results from these experiments suggest that DMI of light-weight steers receiving corn silage diets within a wide range of NDF concentration was controlled by a combination of both physical and metabolic factors. In addition, the use of bm_3 to improve fiber digestibility of a corn silage based diet containing less than 40% NDF improved DMI but did not affect feedlot ADG.

ACKNOWLEDGMENTS

Finally, I am truly appreciative to my family and the role they played. I would like to thank my mother Gale, father Harry, and grandparents Eugene and Gladis for their continued love and financial support during my "long" college career. I want to thank my brother Kurt, my sisters Kara and Kristin, their husbands Al and Wade, and my future family Mike, Pam and Stacy, for there continual support towards me "finally" finishing. Last but not least, I would like to acknowledge the patience, encouragement, and love of my fiancé, Michelle Smiricky. I also appreciated her help dumping rumens, even though she refused to wear gloves.

TABLE OF CONTENTS

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF TABLES

CHAPTER 4

CHAPTER 5

LIST OF FIGURES

CHAPTER 5

APPENDIX A

APPENDIX B

LIST OF ABBREVIATIONS

ADF	acid detergent fiber
ADG	average daily gain
ADIN	acid detergent insoluble nitrogen
ADL	acid detergent lignin
bm_3	brown midrib-3 mutation
BMCS	brown midrib-3 corn silage based diet
BW	body weight
CF	crude fiber
CP	crude protein
Control	isogenic normal corn silage diet
cwt	100 pounds of body weight
d	day(s)
DE	digestible energy
DM	dry matter
DMI	dry matter intake
GE	gross energy
h	hour(s)
HF	high fiber diet containing male-sterile corn silage
i.d.	internal diameter
iNDF	indigestible neutral detergent fiber
k_d	digestion rate in the rumen
k_p	passage rate for the rumen
LF	low fiber diet containing normal corn silage
ME	metabolizable energy
n	number
NDF	neutral detergent fiber
NE_m	net energy of maintenance
NE_g	net energy of gain
OM	organic matter
P	probability that difference was due to chance alone
r^2	coefficient of determination
RIB	rumen inert bulk
SAS	Statistical Analysis System
s.c.	subcutaneous
SD	standard deviation
SEM	standard error of the least squares mean
VFA	volatile fatty acids
$\bar{x}$	mean

INTRODUCTION

Many producers background cattle or feed them a high forage growing ration before they are finished on a high concentrate ration. The use of backgrounding allows producers to 1) increase frame size of cattle and thereby increase their final weight at a similar body composition, 2) utilize less expensive feedstuffs, resulting in cheaper weight gains, and 3) hold cattle in order to sell them during the high part of the annual price cycle. In the southern part of the United States and Plains States, producers have the ability to use grazing as a method to background cattle. In these situations, cattle graze either cool-season native range or improved cool-season pastures (*e.g.* ryegrass, winter wheat, and rye). In the upper Midwest, because freezing temperatures and snow cover limits the use of year-round grazing, harvested forages are fed in many backgrounding or growing diets. Corn silage is often the primary ingredient in these growing rations in the upper Midwest.

Concentration of cell wall material in forage plants has been implicated as a major factor that influences forage intake by cattle. Many different molecules and molecular polymers make up the cell wall of corn plants. The number and structural interactions of these molecules and polymers can change during maturation of the plant and can vary due to genetic differences in hybrids. These variations contribute to differences in fiber concentrations and digestibility, and ultimately affect intake and performance of cattle.

Light-weight cattle have a relatively smaller ruminal capacity compared to mature cattle, and therefore have the potential for intake to be relatively more limited when diets contain a high concentration of fiber. However, it has been proposed that several mechanisms work in concert with one another to influence feed intake. These mechanisms

produce a number of signals that are summarized by intake centers of the central nervous system, which ultimately determine commencement and cessation of eating. These potential signals include rumen distension, propionate flux, circulating hormones and(or) neurotransmitters.

Being able to accurately estimate voluntary dry matter intake is important when trying to determine the nutrient requirements of cattle. Accurately estimating intake is also critical for predicting performance and efficiency of gain of cattle. Accurate predictions of feed efficiency and gain allow producers to estimate profitability and determine breakeven prices for buying and selling cattle. The understanding of how fiber concentration and digestibility in corn silage affects intake is important when considering the profitability in producing cattle. If intake can be manipulated through corn hybrid selection, harvesting hybrids at the optimal time, and(or) post-harvest modifications to improve gain and(or) feed efficiency, this could have dramatic effects on returns to management and labor.

The overall hypothesis of the research described in this dissertation is that corn silage high in fiber potentially limits intake and performance of light-weight steers by physical constraints in the rumen. Therefore, improving fiber digestibility or decreasing fiber concentration in corn silage should reduce the filling effect in the rumen, and increase intake and performance. The objectives of this research project were to:

1) determine the effects of increasing fiber digestibility of corn silage on digesta kinetics, DMI, growth, and feed efficiency of light-weight steers;

2) challenge growing steers with ruminal fill in the form of dietary NDF and inert bulk to determine if increased NDF concentration in corn silage limits DMI by rumen fill and influences digesta kinetics and diet digestibility;

3) determine if increased NDF concentration in corn silage depresses DMI and performance and influences diet digestibility as steers increase in BW; and

4) determine if Holstein and Angus steers respond differently to increased NDF concentration in corn silage.

Chapter 2 describes a digestion trial using 8 ruminally fistulated Angus steers and a performance trial using 128 Angus steers comparing brown midrib-3 corn silage to its isogenic normal control to address Objective 1. Chapter 3 describes an experiment in which 8 ruminally fistulated Holstein steers were challenged with rumen fill in the form of NDF and rumen inert bulk (Objective 2). Objectives 3 and 4 were addressed by feeding either a low-fiber or high-fiber diet to 12 Angus and 12 Holstein steers using a crossover design consisting of six, 14-day periods (Chapter 4).

CHAPTER 1

Literature Review

Regulation of Intake

Animal and dietary factors that control satiety and hunger, in turn regulating

intake, are complex and not fully understood. The regulation of DMI has been

differentiated into those factors that affect long-term and short-term control (Baile and

Forbes, 1974). Long-term control of intake is regulated by factors involved in

maintenance of energy inputs and outputs to achieve balance in body weight and

productive functions. Short-term regulators are those factors associated with controlling

meal initiation and termination, which have influence over meal size and inter-meal interval

within a day. Factors associated with short-term regulation of intake may more accurately

define daily fluctuations in intake. Factors that influence intake regulation have been

categorized into those associated with physical limitations, metabolic signals, and social

and environmental factors (Forbes, 1996). Physical regulation of DMI implies that intake

is limited by maximum flow of digesta throughout the gastrointestinal tract or physical

capacity of the gastrointestinal tract. Metabolic regulation occurs when absorbed fuels

trigger feedback mechanisms to terminate intake. These factors, involved in intake

regulation of forage, will be further discussed in the following sections.

Physical regulation

The theory that DMI is regulated by physical fill was first proposed sixty years ago

when (Lehmann, 1941) suggested that indigestible organic matter residue created bulk in

the gastrointestinal tract, limiting intake. Since that time, the theory has become widely accepted and much research has been conducted to better understand the mechanisms by which DMI is limited with physical control. Although the abomasum and large and small intestines have finite volumes, there is a general consensus that the physical capacity of these organs does not limit voluntary intake (Grovum, 1987; Forbes, 1995). The site in which physical distension regulates DMI generally has been regarded to be the reticulo-rumen. Ash and Kay (1957) reported that the reticulo-omasal orifice was sensitive to mechanical stimuli and its distension evoked rumination, indicating that the reticulo-omasal orifice may be a control mechanism for passage of particles from the reticulo-rumen. The discovery of tension receptors and mechanoreceptors concentrated in the reticulum and cranial rumen further suggest that the site of physical control of intake is the reticulo-rumen (Iggo, 1955; Leek, 1969). These tension receptors have been shown to send nerve impulses via the vagus and splanchnic nerves to brain centers when stimulated by distension (Leek, 1969). Epithelial mechanoreceptors are stimulated by both light mechanical and chemical stimuli (Leek, 1969).

Physical limitations to intake can be separated into animal and dietary affects. The primary animal effect that can impact DMI is capacity of the reticulo-rumen. Wardrop (1960) found a positive correlation between intake and weight of the empty reticulo-rumen in lambs. An increase in size of other abdominal organs, such as the pregnant uterus, reduces capacity of the reticulo-rumen and decreases DMI (Forbes, 1995). An increase in abdominal fat was also negatively correlated to DMI (NRC, 1987) and this may be due to a reduction on gut capacity and(or) may be due to satiety signals via leptin. Cattle with similar body fat but larger skeletal size have increased DMI (NRC, 1987).

Further discussion of differences in DMI between Holstein and beef breeds will be discussed later in this review.

Dietary characteristics which influence the digesta flow from the reticulo-rumen can play an important role in physical limitation of intake. The flow rate of digesta can be influenced by particle size, fragility, density, and chemical composition. Passage rate of particles is controlled by the reticulo-omasal orifice. Size reduction of large particles is required for passage from the reticulo-rumen. Poppi et al. (1985) reported that resistance to escape the reticulo-rumen increases for particles retained on a sieve aperture of 1.18 mm, for sheep and cattle. However, higher threshold sieve aperture sizes have been reported for steers (Dixon and Milligan, 1985) and dairy cattle (Cardoza and Mertens, 1986), in the range of 3 to 4 mm. Breakdown of large particles is primarily done through the process of rumination, with little or no further particle size reduction occurring once particles leave the reticulo-rumen (Poppi et al., 1980; Okine and Mathison, 1991). It has also been reported that rate of particle size reduction decreases with increasing BW (Welch, 1982; Illius and Gordon, 1991). Welch (1982) reported the rumination time per gram of cell wall contents decreased exponentially with increasing BW for sheep, goats and steers.

Increasing forage particle fragility increases the rate of particle size reduction and reduces particle retention time in the reticulo-rumen (Poppi et al., 1981; McLeod and Minson, 1988). Ulyatt et al. (1986) found a greater reduction in particle size by chewing for mature ryegrass that contained higher cell wall content and lower digestibility than for less mature ryegrass. They suggested that this greater particle size reduction was due to "brittleness" (*i.e.* fragility) which increased as the ryegrass matured.

Particle density also has an effect on physical control of intake. In order for a particle to pass from the reticulo-rumen, it must come into close proximity of the reticulo-omasal orifice at the second phase of reticular contraction (Allen and Mertens, 1988). The ability of a particle to come within close proximity of the orifice is dependent on particle density (Allen, 1996). Small, dense particles fall into the ventral rumen where they flow with the ventral currents into the reticulum (Wyburn, 1980). These particles are then close to the reticulo-omasal orifice and are expelled as it opens during the second reticular contraction (Midasch et al., 1994). Less dense particles are either trapped in the rumen mat (Faichney, 1986) or become propelled further away from the reticulo-omasal orifice when the rumen contracts (Lechner-Doll et al., 1991), resulting in these less dense particles having a slower rate of passage. Negative relationships between particle density and retention time in the reticulo-rumen have been reported in experiments using inert particles (Balch and Kelly, 1950; King and Moore, 1957; desBordes and Welch, 1984; Murphy et al., 1989) and experiments using labeled indigestible cell walls (Ehle, 1984; Ehle and Stern, 1986). Lechner-Doll et al. (1991) reported that the relationship between particle density and retention time in the reticulo-rumen was nearly linear. As density of inert particles increased from 0.9 to 1.5 g/mL, retention time decreased from 91 to 19 h for experiments using inert particles with different densities (Lechner-Doll et al., 1991).

In spite of the fact that digesta particles typically have a true specific gravity of 1.3 to 1.5 (Siciliano-Jones and Murphy, 1991), most digesta particles in the rumen are initially buoyant (Sutherland, 1988). This process is described in detail in a review by Allen (1996). As particles are swallowed, air becomes trapped within the void spaces, but this air eventually dissolves. Actively fermented particles remain buoyant because carbon

dioxide and methane are produced by fermentation of the potentially digestible organic matter and thereby decrease particle density. Density increases as fermentation continues and the amount of potentially fermentable organic matter is reduced, cell walls are disrupted, and less gas is associated with the digesta particles. This allows these particles to come into close proximity with the reticulo-omasal orifice and pass from the reticulum (Allen, 1996).

Metabolic regulation

If physical constraints on the gastrointestinal tract were the only method by which voluntary DMI were regulated, then more digestible feeds would be consumed at a much higher level than less digestible feeds. However, DMI of highly digestible feeds is not always greater, and their intake may be controlled by metabolic regulation. One theory of metabolic control of intake is based on the premise that an animal will consume nutrients until energy balance is achieved (Jones, 1972; Journet and Remond, 1976; De Jong, 1986). Illius and Jessop (1996) stated that an animal has, at any point in time, some maximal productive capacity. This capacity depends on the animal's genetic potential for growth and(or) lactation, and will vary over the animal's lifetime, according to stage of growth, reproductive status, physical and climatic environment, the animal's ability to store energy surpluses, etc. This theory is disputed by a review on intake control, in which Grovum (1987) cited several studies conducted with sheep, beef cattle, and dairy cattle where digestible energy intakes were relatively constant at moderate dietary energy densities, but declined at high dietary energy concentrations. He suggested that

maintenance of rumen function received priority over maintaining energy intake under high concentrate feeding.

A second theory states that metabolic feedback stemming from the animal's ability to utilize nutrients interacts with the balance of absorbed nutrients to regulate intake (Illius and Jessop, 1996). The ability to utilize nutrients depends on the animal's production potential. The metabolic feedback can be in the form of metabolites associated with energy metabolism, and hormones associated with homeorhetic and digestive control (Illius and Jessop, 1996).

In support of this second theory, epithelium chemoreceptors have been observed in the reticulum and the cranial sac of the rumen. These receptors are stimulated by acids, alkali, and hypo- and hyper-osmotic solutions (Leek, 1969). The osmolality of ruminal fluid can be highly variable depending on mineral salt content and fermentability of the diet (Allen, 2000). Satiety may be triggered by the osmolality stimulating the epithelial receptors in the reticulo-rumen (Grovum, 1995). However, Leek and Harding (1986) reported that the threshold for stimulation of receptors in response to hyper-osmotic solutions is between 700 and 1700 mOsm/kg, which is not in the physiological range. Osmolality of ruminal contents has been reported to be 250-300 mOsm/kg pre-feeding and increase within a few hours after a large meal to as high as 500 mOsm/kg (Warner and Stacy, 1968).

Large quantities of VFA are produced during ruminal fermentations. Therefore, several studies have investigated the possibility of these metabolites being associated with intake regulation. Undissociated VFA have been found to stimulate reticulo-rumen epithelial receptors in the range of 40 to 100 mM (Harding and Leek, 1972). Crichlow

and Leek (1980) reported that butyrate had a greater stimulatory effect on the epithelial receptors as compared to propionate, and that the stimulation was greater at lower pH. This is likely the effect of VFA absorption rate, because this rate is negatively associated with ruminal pH. Relative rate of absorption has been demonstrated to be butyrate > propionate > acetate (Dijkstra et al., 1993). It has been reported that VFA, particularly acetate and propionate, depress intake when infused into the rumen (Baile and Forbes, 1974; Forbes, 1995). However, De Jong et al. (1981) reported that the acetate concentration infused in the studies was unphysiological. De Jong et al. (1981) could not repeat the depression in intake when physiological levels were infused. Anil et al. (1993) infused sodium acetate continually into the rumen of lactating cows for 3 h. They observed little or no significant effects on intake when the rate of acetate infusion was similar to that normally produced in the rumen. Depression of intake only became obvious when infusion produced at least twice the normal concentration of acetate (Anil et al., 1993). Anil and Forbes (1980) observed that infusion of propionate into the hepatic vein depressed intake in sheep, but infusion into the jugular vein had no effect on intake. They also reported that denervation of the liver prevented the intake depressing effect of hepatic vein propionate infusion. Anil and Forbes (1980), therefore concluded that there may be propionate receptors in the liver.

Chemoreceptors, sensitive to only propionate, have not been identified in the liver to date (Allen, 2000). Andrews (1987) did report that there are thermo- and osmo-receptors in the liver that may be involved in satiety. Therefore, oxidizable fuels in the liver may have the ability to stimulate these receptors, and if the animal is unable to utilize these fuels, their buildup may shutdown intake.

Reductions in intake, as a result of propionate infusion, may also be mediated by an increase in insulin (Grovum, 1995). Plasma insulin has been shown to increase in response to hepatic infusion of propionate, but not infusion of acetate or jugular infusion of propionate in sheep (Manns and Boda, 1967). Secretions of insulin also may be induced by the sight of food in sheep (Bassett, 1975) and cattle (Vasilatos and Wangsness, 1980; Faverdin, 1986). Small doses of insulin have been shown to reduce intake in sheep (Dulphy and Faverdin, 1987; Foster et al., 1991)

Besides insulin, regulation of intake also can be controlled by additional hormones associated with energy status. Hormones associated with peripheral metabolism (*e.g.* glucagon, glucocorticoids, etc.) and the gut hormones associated with feeding (*e.g.* gastrin, secretin, cholecystokinin, etc.), as well as various neurotransmitters (*e.g.* serotonin, opioid peptides, neuropeptide Y, etc.) that have potential roles in intake control are reviewed in detail by Forbes (1995). The influence that several hormones and neurotransmitters potentially have on intake are summarized in Table 1-1. Understanding the interactions of these and other hormones and how they transmit signals to the hypothalamus are important areas for continued research.

Table 1-1. The influence of hormones and neurotransmitters in voluntary dry matter intake[a]

Hormones and neurotransmitters	Effect on dry matter intake
Metabolic hormones	
Glucagon	depresses
Growth hormone	may stimulate
Adrenaline	depresses
Gut peptides	
Cholecystokinin (CCK)	depresses
Pentagastrin	no effect
Somatostatin	depresses
Bombesin	depresses
Hormones associated with growth	
Cortisol	stimulates
B-agonists	no effect
Other hormones	
Estrogen	low doses stimulate, high doses depress
Vasopressin	depresses
Endorphins	not enough information
Satietin	may depress
Neurotransmitters and hormones associated with the central nervous system	
Serotonin	depresses
Opioid peptides	stimulates
Neuropeptide Y and peptide YY	stimulates
Growth hormone releasing factor	stimulates

[a]Adapted from Forbes (1995).

Integration of regulating factors

The physical and metabolic factors that have potential to affect intake of forages by ruminants include 1) distension of the gastrointestinal tract, 2) effects of ruminal fluid osmolality, 3) ability of tissues to metabolize nutrients (Forbes, 1996), 4) effects of VFA on the stomach, ruminal veins, and liver, 5) effect of peptides on smooth muscle tone in the digestive tract, 6) effects of circulating hormones, and 7) effects of various neurotransmitters (Grovum, 1987). Nerve impulses and chemical signals created by these factors are transmitted to the hypothalamus and(or) other satiety centers of the brain to control the initiation and termination of eating. The presence of multiple control mechanisms implies that intake may result from the summation of several responses. According to Illius and Jessop (1996), voluntary intake is ultimately a psychological phenomenon. It involves integration of various signals, and is a reflection of the biological system's flexibility to cope with variations in food supply, composition, and animal state (Illius and Jessop, 1996). Forbes and Provenza (2000) further theorized that animals integrate signals from the various visceral receptors, adipose tissue, social stimuli, and environmental factors, to generate a signal of total 'discomfort'. The animal then adjusts its DMI in attempt to minimize this discomfort.

The majority of research elucidating intake mechanisms has evaluated factors separately. There have been several studies, however, that have evaluated multiple factors affecting intake simultaneously, to determine possible synergy between factors. Adams and Forbes (1981) found that sodium acetate infusion into the rumen of sheep depressed intake by 12%, and a balloon in the rumen inflated with 1 L of water reduced intake by 18%. A combination of these two factors was apparently additive and depressed intake by

50%. In studies using dairy cattle, Anil et al. (1987) and Mbanya et al. (1993) reported that intake depressions from ruminal distension (balloon inflated with water) and the addition of VFA (either sodium acetate or sodium propionate) had either slight or non-significant affects alone, but in combination, resulted in a significant reduction in intake.

Because factors regulating intake in ruminants are not completely understood, many of the models predicting intake are empirical by nature rather than being mechanistic. There are numerous equations that predict voluntary intake of beef cattle. Intake has been found to be a function of body weight (Fox and Black, 1984), metabolizable energy (ARC, 1980), net energy of maintenance (NE_m; NRC, 1984, 1996), and dietary concentration of crude protein, ADF, and total digestible nutrients (Moore and Kunkle, 1999). The equations used by the NRC (1996) describe DMI as a function of dietary NE_m concentration, with adjustments for body fat, breed (beef vs Holstein or Holstein × beef), feed additives (monensin), temperature, and mud. The base equation for growing calves is:

$$DMI = (SBW^{0.75} * (0.2435 \, NE_m - 0.0466 \, NE_m^2 - 0.1128))/NE_m$$

and for growing yearlings is:

$$DMI = (SBW^{0.75} * (0.2435 \, NE_m - 0.0466 \, NE_m^2 - 0.0869))/NE_m$$

where:

DMI is dry matter intake in kg/d,

SBW is shrunk body wieght in kg, and

NE_m is net energy value of diet for maintenance in Mcal/kg.

These intake equations do not account for all the interactions between physiological, environmental, and management factors that regulate intake. However, the NRC (1996)

demonstrated during validation, that the growing calf equation accounted for 76.5% of the variation with a bias of only +0.16% for a data set containing the middle to upper range of dietary NE_m concentrations (Cornell data set), and 79.3% of the variation with a bias of only -0.49% for a data set containing the lower to middle range of dietary NE_m concentrations (Guelph data set). However, this same growing calf equation accounted for only 30.8% of the variation with a bias of -8.4% for a data set containing cattle fed all-forage diets (Alberta data set). The NRC (1996) subcommittee stated that no single, general equation can be applied in all production situations, and thereby recommend that beef cattle producers should develop intake prediction equations specific to given production situations. Such equations should account for a greater percentage of the variation in intake than would be possible with a generalized equation.

Fiber digestibility

Ruminants have evolved the ability to utilize forage as their sole source of nutrients (Hofmann, 1988). Forages remain an important feedstuff in ruminant animal productions systems within the United States, even though modern agricultural practices utilize substantial quantities of concentrate feeds in diets fed to both beef and dairy cattle (Jung and Allen, 1995). Forages alone may not meet the energy requirements of high producing dairy cows or rapidly growing steers (Galyean and Goetsch, 1993), therefore the quality of forage used in these production systems is of great importance when feeding high forage diets. According to Nelson and Moser (1994), forage quality is mainly considered in terms of plant factors affecting availability and digestibility of forage produced. Forage cell wall fractions have been implicated as a control mechanism for

forage intake (Waldo, 1986). Concentration and digestibility of cell walls potentially limits intake and energy availability of forage crops in both beef and dairy production systems (Jung and Allen, 1995). Oba and Allen (1999) evaluated the effects of the digestibility of NDF from forage on performance of dairy cows using treatment means across 13 sets of forage comparisons reported in the literature. They concluded that enhanced NDF digestibility of forage significantly increases DMI and milk yield. They further reported that for every one-unit increase in NDF digestibility in vitro or in situ, DMI was increased by 0.17 kg/d and 4% fat corrected milk was improved by 0.25 kg/d (Oba and Allen, 1999b). Buxton and Fales (1994), stated that no single factor impacts forage quality more than plant maturity.

The maturation of plant cells has been discussed in great detail in several reviews (Hatfield, 1993; Jung and Deetz, 1993; Moore and Hatfield, 1994; Jung and Allen, 1995). During the first stages of plant cell wall growth and development, the primary wall increases in size through elongation. The primary cell wall is composed of a composite of polysaccharides, proteins, and phenolic acids. Pectins, xylans, and cellulose are all deposited during primary growth, however, during this phase of growth no lignin is deposited (Jung and Allen, 1995). During the second phase, when cell elongation has ceased, the plant cell switches to secondary wall thickening. The cell wall becomes progressively thicker as it grows towards the center of the plant cell (Bacic et al., 1988). The polysaccharide material deposited during secondary thickening contains higher concentrations of cellulose than xylans, and pectins are no longer added to the walls (Jung and Allen, 1995). Lignin polymer deposition also begins with secondary wall thickening

16

(Terashima et al., 1993), beginning at the middle lamella/primary cell wall region and proceeding into the secondary wall (Jung and Allen, 1995).

As lignification proceeds from the primary to the secondary cell wall, there is a shift from guaiacyl- to syringyl-type lignin deposited (Terashima et al., 1993). In addition to continual lignification during secondary thickening as the plant matures, there is incorporation of arabinoxylan ferulate esters in the primary wall which forms cross-linkages between the xylans to lignin. The increase in lignin concentration and formation of cross-linkages between lignin and xylans potentially reduces cell wall digestibility. Akin and Chesson (1989) stated that lignin is the only internal chemical factor that has been demonstrated conclusively to negatively affect the extent of cell wall polysaccharide digestion. Merchen and Bourquin (1994) stated that the accumulation of phenolic material on plant cell surfaces could change surface chemistry sufficiently to inhibit cell wall digestion by ruminal microorganisms, thereby protecting the underlying cell wall from further attack.

There are also several extramural plant factors, external to the plant cell wall, that are detrimental to cell wall polysaccharide degradation. These factors include the cuticle, warty layer, and middle lamella of secondary thickened cell walls (Merchen and Bourquin, 1994). Akin (1979) stated that the cuticle is indigestible, and therefore one of the primary reasons ruminal microbes attack plant tissues at inner surfaces of broken cells. The warty layer, which is a lining on the inner surface of lignified cell walls (Engels and Brice, 1985) and middle lamella are probably poorly digested due to degree of lignification within these tissues (Engels and Schuurmans, 1992).

Effect of fiber modification on digestibility

In production systems where forage quality cannot be optimized, post-harvest treatments to improve forage digestibility and quality may be implemented. Techniques to modify forage digestibility include physical (*e.g.* grinding, pelleting and mechanical separation of plant parts) and chemical treatments (*e.g.* hydrolytic and oxidative treatments). Grinding or pelleting decreases particle size, increases surface area, and increases bulk density of leaf and stem fractions of forages (Laredo and Minson, 1975). Feed intake is consistently increased with grinding and pelleting. Greenhalgh and Reid (1973) reported that intake responses to grinding were greater for sheep than cattle (45 vs 11%) and greater in young animals than in mature ones (38 vs 17%). The intake of most ground forages generally increases with decreasing particle size and does not reach maximum until the mean particle size is less than 1 mm (Osbourn et al., 1976). Grinding and(or) pelleting generally reduces digestibility of the forage and the depression due to processing increases with increasing intake (Blaxter et al., 1956). The primary reduction in fiber digestion is due to shorter residence time in the gastrointestinal tract (Minson, 1963; Alwash and Thomas, 1974). The reduction in fiber digestibility may also be due to a depression in ruminal pH. Fine grinding and pelleting of forages drastically reduces the time that ruminants spend eating and ruminating (Weston and Hogan, 1967; Osuji et al., 1975). This consequently reduces saliva production (Osuji et al., 1975; Thomson and Beever, 1980) and decreases buffering capacity, which results in a depression in ruminal pH and a decrease in cell wall carbohydrate fermentation (Moore, 1964; Grant and Mertens, 1992a). The depression in digestion of grasses due to particle size reduction is greater than that of legumes (Waldo et al., 1972). This difference may exist because

grasses have a higher percentage of organic matter as structural carbohydrates (Thomson and Beever, 1980) and(or) grasses have higher concentrations of water-soluble carbohydrates which would more drastically depress ruminal pH (Osbourn et al., 1976).

Mechanical separation of plant materials is another method of physically processing forage in an attempt to improve quality. The simplest form involves leaf/stem fractionation of dried forage or crop residues. More involved processes include whole crop cereal harvesting and leaf protein concentration isolation from fresh forages. The processes are generally quite expensive, and they may not provide economic benefits (Berger et al., 1994).

Chemical treatments using hydrolytic and oxidative agents can be used to improve forage digestibility. Hydrolytic agents include alkali metal hydroxides (*e.g.* NaOH, KOH, and $Ca(OH)_2$), ammonia and urea. Sodium hydroxide is the most widely used alkali metal hydroxide, because it is more effective in improving forage digestibility and is less expensive when compared to KOH or $Ca(OH)_2$ (Bass et al., 1982; Owens et al., 1984). Alkali hydroxides improve forage digestibility by solubilizing hemicellulose, lignin and silica, and by hydrolyzing uronic and acetic acid esters (Rexen and Thomsen, 1976; Jackson, 1977; Klopfenstein, 1978; Chesson, 1981; Chesson et al., 1983). These chemicals may also increase rate of hydration, which is a necessary component of microbial degradation of fiber.

Ammonia and urea have similar modes of action, but are not as affective as NaOH in improving digestibility of forage. Ammoniation of forage has been shown to reduce the concentrations of NDF and hemicellulose, with no effect on cellulose, ADL and ADIN (Van Soest et al., 1984). The effect of urea on fiber digestibility is variable and may be the

19

result of urea having to be broken down to ammonia before it becomes active (Berger et al., 1994). Additionally, the water content of roughages, as well as temperature and intrinsic urease activity play a role in the breakdown of urea to ammonia (Williams and Innes, 1983).

Oxidative agents actively attack and degrade a major proportion of cell wall lignin (Chang and Allen, 1971). The net effects of oxidative agents on forage digestibility are due to the significant decrease in lignin content and increase in soluble carbohydrate concentration (Ben-Ghedalia et al., 1982; Ben-Ghedalia et al., 1983). Peroxides have similar effects on digestibility when compared to NaOH, but are more expensive (Berger et al., 1994). Ben-Ghedalia and Shefet (1983) reported that ozone treatment makes cell wall polysaccharides more available for digestion by microbes when compared to either untreated or NaOH treated forage. However, ozone treatment is impractical due to possible hazards and cost (Berger et al., 1994). Chlorine has been shown to improve fiber digestion, but potentially reduces DMI by as much as 50% (Yu et al., 1975; Ford et al., 1987). One oxidant that has shown potential for usage on residues in ruminant diets is SO_2. Sulfur dioxide-treatment of wheat straw has been shown to increase DMI, improve fiber digestibility (Ben-Ghedalia and Miron, 1987), and produce comparable gains to a barley-corn based diet when fed to sheep (Ben-Ghedalia et al., 1988).

Chemical treatments have the greatest improvements on fiber digestibility when used on mature lignified substrates, while reducing digestibility when used on more immature substrates that have high contents of cell solubles (Atwell et al., 1991; Cameron et al., 1991). They also have more influence on the digestibility of grasses as compared to

legumes, because grasses have a greater concentration of esterified hydroxycinnamic acids and potentially larger number of polysaccharide-lignin cross-linkages.

Effect of the brown midrib mutation on plant composition

Eyster (1926) was one of the earliest to report a brown pigment developing in cells in the midrib and leaf sheaths of maize (*Zea mays* L.). He found this characteristic to be homozygous recessive and designated it as brown midrib (**bm**). Jorgenson (1931) further observed that this pigmentation was found in the leaf midrib, stem, tassel, cob, and roots, but he could not identified any chemical that caused this pigmentation. It was later determined that the pigment was associated with all lignified tissues. To date, four mutations (*bm*$_1$, *bm*$_2$, *bm*$_3$, and *bm*$_4$) have been reported in maize (Neuffer et al., 1997).

Kuc and Nelson (1964), and Gee et al. (1968) were the first to observe that the brown midrib mutants were associated with lower lignin content, and less p-hydroxycinnamic acid bound to the lignin core, when compared to isogenic normal strains. Chabbert et al. (1994) reported that *bm*$_3$, when compared to isogenic normal, reduced lignin content by 18 to 30%, and content of p-coumaric acid was reduced 40 to 51%. They did not observe any difference in content of ester-bound ferulic acid between the two hybrids, but they found a 50% decrease in syringyl content and a slight increase in 5-OH guaiacyl residues in lignin from *bm*$_3$ (Chabbert et al., 1994). Grand et al. (1985) observed that the enzyme, O-methyltransferase, was reduced ten-fold for *bm*$_3$ when compared to isogenic normal. O-methyltransferase is involved in synthesis of methyloxylated ferulic and sinapic acids, which are precursors of guaiacyl and syringyl units of lignin, respectively (Grand et al., 1985; Vignols et al., 1995). Therefore,

improvements in cell wall digestibility of bm_3 could be a result of both reduction in lignin concentration and reduction in syringyl lignin content. Normally, syringyl-type lignin is more linear in structure and extends further into the secondary wall, thereby protecting a greater proportion of polysaccharides in the secondary wall from digestion compared to guaiacyl-type lignin. With bm, lignin would be more condensed and protective of the primary cell wall, however, the secondary cell wall would have greater potential for degradation because of less encroachment of lignin into this region (Jung and Deetz, 1993). Muller et al. (1972) showed that the *in vitro* digestion rates of DM, NDF, cellulose, and hemicellulose were faster for corn silage with bm_3 compared to isogenic normal.

Effect of the brown midrib mutation on intake and performance

Increased voluntary DMI has been observed for early (Rook et al., 1977; Block et al., 1981) and mid to late lactation (Sommerfeldt et al., 1979; Stallings et al., 1982) dairy cows fed bm_3 corn silage. In a majority of these experiments, increased DMI generally resulted in increased milk yield and(or) greater body weight gain. Oba and Allen (1999) reported a 9% increase in DMI and a 7% increase in milk yield when diets fed to dairy cows contained bm_3 over those fed isogenic normal corn silage. Tine et al. (2001) observed that DMI was 10.5% higher but milk yield was similar when bm_3 was compared to isogenic normal in diets fed to early lactating dairy cows. Keith et al. (1981) observed an increase in DMI when bm_3 was compared with isogenic normal corn silage fed to steers. They also reported improvements in ADG of steers fed bm_3 compared with isogenic normal, but did not observe any differences in feed conversion. When steers were

22

fed a 92% corn silage diet containing bm_3 compared to diets using a variety of commercial

hybrids, ADG was increased (McEwen et al., 1996). McEwen et al. (1996) also reported

that feeding a bm_3 corn silage diet resulted in increased feed efficiency compared with

diets containing corn silage from commercial hybrids.

In more recent studies, Oba and Allen (2000a, 2000b) stated that improvements in

DMI observed when feeding bm_3 compared to isogenic normal hybrids may be due to

alterations in meal size and frequency in addition to the increase in passage rate. They

proposed that fluctuations in ruminal pH and supply of metabolites may increase insulin

release and absorption of glucose, thereby increasing the frequency of meals and

improving DMI.

Effect of the brown midrib mutation on digestion

In previous literature, when bm_3 was compared with isogenic normal corn silage,

no difference in apparent total-tract DM digestibility was observed for lactating dairy

cows (Rook et al., 1977; Sommerfeldt et al., 1979; Oba and Allen, 1999a). However, a

6.6 percentage unit improvement in DM digestibility has been reported for sheep

consuming bm_3 (Stallings et al., 1982). In a study by Oba and Allen (1999), bm_3 was

compared with isogenic normal corn silage diets fed to lactating dairy cows in a crossover

design. As DMI increased with bm_3 compared to control, total-tract digestibility of NDF

decreased. When cows consumed similar amounts of bm_3 and isogenic normal silage

diets, there was a 6 unit increase in apparent total-tract digestibility of NDF for bm_3

compared with normal silage. However, this improvement in total-tract digestibility of

NDF for bm_3 corn silage was diminished when DMI increased. Oba and Allen (1999)

explained that higher passage rate associated with increased DMI could have reduced

ruminal retention time for bm_3 corn silage, which would have reduced total-tract

digestibility of NDF. In a later study, Oba and Allen (2000) observed an increase in

passage rate of NDF and a reduction in ruminal digestion rate of potentially digestible

NDF in dairy cows fed diets containing bm_3 relative to isogenic normal corn silage. Rook

et al. (1977) and Sommerfeldt et al. (1979) reported no differences in energy digestibility

for dairy cows fed diets containing either bm_3 or isogenic normal corn silage. Tine et al.

(2001) found that bm_3 corn silage provided greater amounts of energy when fed to dry

cows at maintenance due to increased fiber digestibility. However, difference in energy

digestibility between bm_3 and isogenic normal were small when diets were fed to early

lactating dairy cows. They concluded that the increases in milk production for bm_3

compared to isogenic normal in previous studies was likely due to the increases in DMI

for the bm_3 diet (Tine et al., 2001), which was previously pointed out by Oba and Allen

(1999).

Block et al. (1981) observed that bm_3 corn silage, fed at 65% of the diet to

lactating dairy cows, decreased acetate and increased molar proportion of propionate,

when compared to isogenic normal. In contrast, Rook et al. (1977) reported no difference

in molar proportions of either acetate or propionate between bm_3 and isogenic normal

when a 60% corn silage diet was fed to lactating dairy cows. However, when the

percentage of corn silage was 85%, Rook et al. (1977) did observe increases in molar

proportions of both acetate and propionate for bm_3. Rook et al. (1977), Block et al.

(1981), and Oba and Allen (2000a) reported that bm_3 reduced ruminal pH.

Fiber concentration

The NDF concentration of well-eared corn silage can range from less than 35% to greater than 55% (NRC, 1996). As discussed previously, the concentration of cell walls can have dramatic effects on intake as well as performance of animals. Besides modifying the fiber digestibility post-harvest, the concentration of fiber can be changed by altering the forage to concentrate ratio in the diet. A second method to alter fiber concentration can be accomplished by selecting hybrids with different NDF concentrations. As discussed previously, stage of maturation can also have a dramatic impact on fiber concentration. With corn hybrids, as the plant matures, there is a quadratic response on fiber concentration (St-Pierre et al., 1983; Bal et al., 1997). The filling of corn kernels with starch dilutes the NDF concentration of the entire plant. Once grain filling ceases and the corn plant continues to mature, subsequent NDF concentration increases with increasing dry matter content (Weaver et al., 1978; St-Pierre et al., 1983). A third method to alter fiber concentration of silage would be to use male-sterile corn hybrids compared to their isogenic normal counterparts. The use of male-sterile hybrids would prevent grain filling, therefore preventing starch from diluting the fiber concentration of the plant.

Effects of fiber concentration on intake and performance

Increasing dietary NDF concentration by increasing roughage to concentrate ratio has been shown to depress DMI of sheep (Aitchison et al., 1986) and dairy cows (Llamas-Lamas and Combs, 1991; Dado and Allen, 1995). This reduction is likely to occur when intake is being controlled by physical constraints on the rumen. Decreasing dietary NDF concentration by increasing concentrate in the diet may increase DMI if physical

constraints of the reticulo-rumen are limiting intake (Woody et al., 1983; Brennan et al., 1987). However, negative associative effects may occur with increasing concentrates in the diet, resulting in decreased fiber digestibility (Joanning et al., 1981; Grant and Mertens, 1992a; Grant and Mertens, 1992b). Intake may also become controlled by metabolic regulation with high levels of grain, resulting in decreased DMI (Muhamad et al., 1983; Woody et al., 1983).

Selecting hybrids with different fiber concentrations can have varied results on DMI and animal performance. These variations may be the result of the difference in fiber concentration being confounded by the differences in cell wall digestibility between hybrids. Orskov's group (Orskov et al., 1988; Reid et al., 1988; Orskov et al., 1991) found that straw produced from different barley hybrids contained different concentrations of NDF, and those with greater NDF concentration reduced DMI and performance of steers. In contrast, Bal et al. (2000a) found when comparing a corn hybrid (Garst 8751, 39.2% NDF) with a lower NDF corn hybrid (Cargill 3677, 32.8% NDF) that DMI was greater for the higher NDF corn hybrid, with no effect on milk production in dairy cows. The researchers also reported higher in situ NDF disappearance for the higher NDF corn hybrid (Bal et al., 2000b), and they concluded that the differences in intake were not affected by NDF content of the hybrid, but were likely the result of increased fiber digestibility (Bal et al., 2000a). However, the cows in this study were in mid to late lactation, and the high fiber diets contained approximately 29% NDF. Therefore, ruminal distension might not have been the major factor controlling DMI, but intake may have been regulated by metabolic factors. If this is true, then the higher propionate flux

associated with the lower fiber corn hybrid might have been more hypophagic than the higher fiber corn silage.

As discussed previously, as corn plants mature, there is a quadratic effect on fiber concentration. This has resulted in observed quadratic effects on DMI with feeder heifers (Chamberlain et al., 1971) and Holstein cows (St-Pierre et al., 1983). Intake was the lowest when corn was harvested at milk stage or when it was mature, but highest when it was harvested at the dough stage. Chamberlain et al. (1971), also observed a depression in ADG with the most mature corn silage. Bal et al. (1997), found that milk production was the lowest when dairy cows were fed a diet containing corn silage from immature corn plants. In a study using growing British breed steers, Joanning et al. (1981) observed that feeding immature corn silage reduced daily DMI, but had no effect on steer ADG. In contrast, Calder et al. (Calder et al., 1977) reported that stage of corn silage maturity had no affect on either DMI or ADG of yearling Hereford steers.

In a study comparing male-sterile to its isogenic normal corn hybrid, Stake et al. (1973) reported that steers consumed similar amounts of both silages when they received 1.81 kg/d of a protein/grain supplement and there was no difference in crude fiber between the hybrids. These researchers also reported no difference in steer ADG or efficiency of gain.

Effects of fiber concentration on digestion and digesta characteristics

Johnson and Combs (1992) and Dado and Allen (1995) found that, when ruminal distension was potentially limiting DMI of early lactating dairy cows, increasing dietary NDF concentration increased digesta volume and wet weight, decreased digesta DM

percentage, and thus resulted in no effect on weight of digesta DM. They also reported an increase in ruminal NDF weight (Johnson and Combs, 1992; Dado and Allen, 1995). Dado and Allen (1995) also found, with lactating dairy cows that increasing dietary fiber resulted in a faster passage rate of NDF and increased the amount of time spent ruminating and chewing. They reported that these factors likely compensated for the increased rumen fill and helped to maintain intake (Dado and Allen, 1995).

Johnson and Combs (1992) and Dado and Allen (1995) found that increasing dietary fiber concentration increased ruminal pH and acetate percentage, but reduced propionate percentage. Improved NDF digestibility for the high fiber diets was likely the result of improved conditions for fiber-digesting microorganisms within the gastrointestinal tract (Woodford et al., 1986; Grant and Mertens, 1992a, 1992b). Stake et al. (1973) reported that ruminal pH was greater, but concentration of total VFA and percentage of acetate were not affected, for male-sterile compared to normal corn silage fed to growing Holstein steers.

Dado and Allen (1995) found that increasing the dietary fiber concentration in diets fed to dairy cows decreased the apparent total-tract digestibilities of both DM and NDF. In previous research, when male-sterile was compared to normal corn silage in diets fed to growing steers, total-tract digestibility of crude fiber was improved, but digestibility of DM and energy were not influenced (Perry and Caldwell, 1969; Stake et al., 1973).

Rumen inert bulk

Addition of various quantities of rumen inert bulk (**RIB**) via permanent ruminal cannulae has been used to investigate physical capacity of the rumen. If rumen capacity is

limiting intake, then decreasing volume by reducing the utilizable reticulo-rumen space by addition of RIB should result in reduced dry matter intake. If intake is not reduced, it is concluded that intake is being limited by some factor other than physical fill.

Effects of rumen inert bulk on intake

Dado (1993) summarized 38 RIB treatments from 11 published studies, and reported that 92% of all treatments depressed intake. Average depression in dry matter intake was 94 ± 78 g of DM/L of RIB, with a minimum of -39 and a maximum of 300 g/L. The sources of RIB in these studies consisted of water-filled bladders, air-filled bladders, and polystyrene cubes. Experiments were conducted using sheep, steers, and lactating dairy cows. Dado (1993) also performed multiple regression analysis with the data to determine which factors significantly ($P > 0.01$) contributed to the variation in intake depression with RIB. It was concluded that 1) sheep had higher depressions compared to cattle, 2) animals of relatively smaller body weight within a species had greater depressions in intake, and 3) animals that tended to have higher requirements due to physiological states (*i.e.* growth or lactation) had greater depressions in intake compared to those at maintenance (Dado, 1993).

In a trial using mature steers (550 kg) fed low quality orchardgrass hay, Schettini et al. (1999) added either 50 or 100 tennis balls, weighted to specific gravity of either 1.1 or 1.3. They concluded that both volume and weight of the RIB were capable of depressing intake by 157 g of diet DM per L of RIB and 112 g of diet DM per kg of RIB, respectively. Since the RIB potentially had higher specific gravity than that of hay in the rumen, the RIB may have migrated out of the mat layer and sank. This would have

increased the potential for the tennis balls to migrate into the cardiac sac of the rumen and the reticulum. As a result, the weight of the RIB in the reticulum could have altered ruminal contractions (Kaske and Midasch, 1997) and(or) stimulated the mechanoreceptors around the cardia (Leek, 1969), which would reduce dry matter intake.

Effects of rumen inert bulk on digesta characteristics

When ruminal distension was potentially limiting to DMI of early lactating dairy cows, Dado and Allen (1995) observed that RIB, when added at 25% of pre-trial digesta volume to a diet containing 35% NDF, increased total ruminal volume (digesta + RIB) by only 9.2%, but decreased digesta volume by 14.3% and decreased DMI. This reduction in digesta volume suggests that the diet was potentially limiting to intake of these early lactation dairy cows due to physical constraints on the rumen. Johnson and Combs (1991) also found that when 25% RIB reduced DMI of early lactation dairy cows fed diets that contained either 26.1 or 28.5% NDF, total rumen volume increased an average of 15.2% and digesta volume decreased an average of 7.2%. In contrast, Johnson and Combs (1992) found that when 25% RIB did not influence DMI of late lactation dairy cows receiving diets containing less than 33% NDF, total ruminal volume increased 18.0%, but digesta volume was not significantly influenced. Since digesta volume was not influenced, this suggests that there was residual space in the rumen and the diet fed to these late lactation cows was not limiting intake by physical fill. Schettini et al. (1999) did not report the effect of RIB on ruminal volume when beef steers were fed low quality hay (70.3% NDF). However, they observed that addition of RIB decreased DMI and reduced digesta wet weight. Addition of RIB to dairy cows reduced digesta wet weight (Johnson

30

and Combs, 1991; Johnson and Combs, 1992), decreased amount of digesta DM and NDF (Johnson and Combs, 1991; Johnson and Combs, 1992; Dado and Allen, 1995), and increased passage rate of NDF (Dado and Allen, 1995). Johnson and Combs (1992) and Dado and Allen (1995) also found that the addition of RIB increased ruminal pH and acetate percentage, but reduced propionate percentage. Ruminal VFA concentrations may have been altered by RIB because of increased dilution rate of the ruminal contents, increased rate of VFA absorption as a result of increased mixing in the rumen, and(or) by a more rapid breakdown of fibrous particles caused from mechanical action of the RIB and(or) increased chewing.

Effects of rumen inert bulk on total-tract diet digestibility

Previous research with lactating dairy cows (Johnson and Combs 1991, 1992; Dado and Allen 1995) and beef steers (Schettini et al., 1999) reported that RIB had no effect on apparent total-tract digestibility of DM, NDF, or ADF, regardless of whether or not DMI was influenced. Waybright and Varga (1991) did report reductions in total-tract digestibility of DM, NDF, and ADF when RIB was added to sheep fed a 75% concentrate diet. They also reported that DMI and water intake were not affected by addition of RIB. The reduction in total-tract digestibility may have been the result of increased passage rate of the digesta through the gastrointestinal tract (Waybright and Varga, 1991).

Effects of cattle breed on intake, performance, and maintenance requirements

As discussed previously, increasing frame size of animals can increase dry matter intake. Frame sizes among beef breeds can vary considerably. The current NRC (1996)

intake prediction equations are adjusted by scaling frame sizes to an equivalent mature weight (frame-size equivalent weight) and this adjustment should account for the difference between beef breeds (Fox et al., 1988). However, these adjustments may not account for the differences in intake between Holsteins and beef breeds (Fox et al., 1988). Previous researchers have reported that Holstein and Holstein crossbred steers have 4.2 to 17.0% greater DMI when compared to British steers (Garrett, 1971; Dean et al., 1976; Thonney et al., 1981; Fox and Black, 1984). Fox et al. (1988) suggested that, relative to British-bred cattle, intake predictions should be increased 8% for Holsteins and 4% for Holstein × British-breed crosses.

The influence of breed-type on ADG in previous studies has been variable. Garrett (1971) reported no difference in ADG between Holstein and Hereford steers when they were fed either 70% sorghum or 44% barley diets. Dean et al. (1976) found a reduction in ADG of 0.2 to 0.4 kg/d for Holstein crossbred steers compared to British steers when they received a 65% sorghum diet. In a more recent study, Thonney et al. (Thonney, 1987) reported that Holstein steers gained 11% faster than Angus or Hereford steers when fed either high-moisture ear corn or corn silage based diets.

Equations by Fox and Black (1984) predict that Holstein steers require 12% more NE_m and NE_g than British breed steers. These equations are based on trials from Garrett (1971), Ayala (1974), Anrique (1976), and Crickenberger et al. (1978). In these trials, body weight gains for Holstein and beef steers were not significantly different. Garrett (1971) reported that protein gain per unit of food above maintenance was almost identical between Holstein and Hereford steers. The difference in energetic efficiency between the two breeds was related to the higher fat gain for Herefords, resulting in Herefords having

more energy retention (Garrett, 1971). Nour et al. (1981) also observed, when comparing steers at the same weight, that Holstein steers gained more muscle and less fat than Angus steers. The same group of researchers reported that Holstein steers consumed 10% more DM/d and gained 0.2 kg/d faster than Angus steers, but they did not report if there were any differences in energetic efficiency between the two breeds (Thonney et al., 1981). After completing an extensive review of previous literature pertaining to the differences in maintenance requirements among cattle of different breeds, the NRC (1996) subcommittee generalized that in growing cattle 1) *Bos indicus* breeds of cattle require 10% less energy for maintenance than beef breeds of *Bos taurus* cattle, with crossbreeds being intermediate, and 2) dairy or dual-purpose breeds of *Bos taurus* cattle apparently require about 20% more energy than beef breeds, with crossbreeds being intermediate.

Summary

Voluntary DMI of ruminants is controlled by physical and metabolic regulation. Distension in the gastrointestinal tract can limit voluntary DMI of ruminant animals, and may be the primary factor when they are fed high forage diets. Ruminal distension signals satiety through discomfort and the animal will adjust its DMI in attempt to minimize this discomfort. However, the reduction in DMI may reduce the supply of metabolic fuels thereby stimulating discomfort due to hunger. Determining how satiety and hunger interact to signal discomfort is an important area for future research. An understanding of these interactions is necessary to more clearly define how intake of higher fiber diets is regulated.

A knowledge of the plant factors that affect fiber digestibility and contribute to intake regulation is important. This knowledge allows us to determine the optimal time to harvest forage, select hybrids with improved digestibility, and apply post-harvesting methods to improve fiber digestion. These improvements in fiber digestibility may not only improve efficiency of forage utilization, but may also influence voluntary DMI.

Literature Cited

Adams, G. B., and J. M. Forbes. 1981. Additivity of effects of ruminal acetate and either portal propionate or rumen distension on food intake in sheep. Proc. Nutr. Soc. 40:44A (Abstr.).

Aitchison, E. M., M. Gill, M. S. Dhanoa, and D. F. Osbourn. 1986. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. Br. J. Nutr. 56:463-476.

Akin, D. E. 1979. Microscopic evaluation of forage digestion by rumen microorganisms--a review. J. Anim. Sci. 48:701-710.

Akin, D. E., and A. Chesson. 1989. Lignification as the major factor limiting forage feeding value especially in warm conditions. In: R. Desroches (ed.) Proc. XVI International Grassland Congress, Nice. p 1753-1760. Association Francaise pour la Production Fourragere, INRA, Versalles.

Allen, M. S. 1996. Physical constraints on voluntary intake of forages by ruminants. J. Anim. Sci. 74:3063-3075.

Allen, M. S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cows. J. Dairy Sci. 83:1598-1625.

Allen, M. S., and D. R. Mertens. 1988. Evaluating constraints on fiber digestion by rumen microbes. J. Nutr. 118:261-270.

Alwash, A. H., and P. C. Thomas. 1974. Effect of the size of hay particles on digestion in the sheep. J. Sci. Food Agric. 25:139-147.

Andrews, P. R. L. 1987. Vagal afferent innervation of the gastrointestinal tract. In: F. Cervero, and J. F. B. Morrison (ed.) Progress in Brain Research. p 65-86. Elsevier, Amsterdam, The Netherlands.

Anil, M. H., and J. M. Forbes. 1980. Feeding in sheep during intraportal infusions of short-chain fatty acids and the effect of liver denervation. J. Physiol. 298:407-414.

Anil, M. H., N. Jessop, and J. M. Forbes. 1987. Control of liver enzyme activity by the autonomic nerves in sheep. Proc. Nutr. Soc. 45:77A (Abstr.).

Anil, M. H., J. N. Mbanya, H. W. Symonds, and J. M. Forbes. 1993. Responses in the voluntary intake of hay or silage by lactating cows to intraruminal infusions of sodium acetate or sodium propionate, the tonicity of rumen fluid or rumen distension. Br. J. Nutr. 69:699-712.

Anrique, R. 1976. Body composition and efficiency of cattle as related to body type, size and sex. Ph.D. dissertation, Cornell Univ., Ithaca, NY.

ARC. 1980. The Nutrient Requirements of Ruminant Livestock. 7th ed. The Gresham Press, Surrey, England.

Ash, R. W., and R. N. B. Kay. 1957. Stimulation and inhibition of reticular contractions, rumination and parotid secretion from the forestomach of conscious sheep. J. Physiol. 149:43-57.

Atwell, D. G., N. R. Merchen, E. H. Jaster, G. C. Fahey, Jr., and L. L. Berger. 1991. Site and extent of nutrient digestion by sheep fed alkaline hydrogen peroxide-treated wheat straw-alfalfa hay combinations at restricted intakes. J. Anim. Sci. 69:1697-1706.

Ayala, H. 1974. Energy and protein utilization by cattle as related to breed, sex, level of intake and stage of growth. Ph.D. dissertation, Cornell Univ., Ithaca, NY.

Bacic, A., P. J. Harris, and B. A. Stone. 1988. Structure and function of plant cell walls. In: J. Preiss (ed.) Biochemistry of Plants. Vol 14. Carbohydrates. p 297-371. Academic Press, Inc., San Diego, CA.

Baile, C. A., and J. M. Forbes. 1974. Control of feed intake and regulation of energy balance in ruminants. Physiol. Rev. 54:160-214.

Bal, M. A., J. G. Coors, and R. D. Shaver. 1997. Impact of the maturity of corn for use as silage in the diets of dairy cows on intake, digestion, and milk production. J. Dairy Sci. 80:2497-2503.

Bal, M. A., R. D. Shaver, H. Al-Jobeile, J. G. Coors, and J. G. Lauer. 2000a. Corn silage hybrid effects of intake, digestion, and milk production by dairy cows. J. Dairy Sci. 83:2849-2858.

Bal, M. A., R. D. Shaver, K. J. Shinner, J. G. Coors, J. G. Lauer, R. J. Straub, and R. G. Koegel. 2000b. Stage of maturity, processing, and hybrid effects on ruminal degradation of whole-plant corn silage. Anim. Feed Sci. Technol. 86:83-94.

Balch, C. C., and A. Kelly. 1950. Factors affecting the utilization of food by dairy cows. 3. Specific gravity of digesta from the reticulo-rumen of cows. Br. J. Nutr. 4:395-398.

Bass, J. M., J. J. Parkins, and G. Fishwick. 1982. The effect of calcium hydroxide on the digestibility of chopped oat straw supplemented with a solution containing urea, calcium, phosphorus, sodium, trace elements and vitamins. Anim. Feed Sci. Technol. 7:93-100.

Bassett, J. M. 1975. Dietary and gastro-intestinal control of hormones regulating carbohydrate metabolism in ruminants. In: I. W. McDonald, and A. C. I. Warner (ed.) Digestion and Metabolism in the Ruminant. p 383-398. University of New England Publishing Unit, Aridale, Australia.

Ben-Ghedalia, D., and J. Miron. 1987. Intensive growth of lambs on sulfur dioxide-treated straw diets. Nutr. Rep. Int. 35:1129-1135.

Ben-Ghedalia, D., J. Miron, Y. Est, and E. Yosef. 1988. SO$_2$ treatment for converting straw into a concentrate-like feed: A growth study with lambs. Anim. Feed Sci. Technol. 19:219-229.

Ben-Ghedalia, D., and G. Shefet. 1983. Chemical treatments for increasing the digestibility of cotton straw. 2. Effect of ozone and sodium hydroxide treatments on the digestibility of cell-wall monosaccharides Sheep, straw composition. J. Agric. Sci. 100:401-406.

Ben-Ghedalia, D., G. Shefet, and Y. Dror. 1983. Chemical treatments for increasing the digestibility of cotton straw. 1. Effect of ozone and sodium hydroxide treatments on rumen metabolism and on the digestibility of cell walls and organic matter. J. Agric. Sci. 100:393-400.

Ben-Ghedalia, D., G. Shefet, J. Miron, and Y. Dror. 1982. Effect of ozone and sodium hydroxide treatments on some chemical characteristics of cotton straw for feeding ruminants. J. Sci. Food Agric. 33:1213-1218.

Berger, L. L., G. C. Fahey, Jr., L. D. Bourquin, and E. C. Titgemeyer. 1994. Modification of forage quality after harvest. In: G. C. Fahey, Jr. (ed.) Forage Quality, Evaluation, and Utilization. p 922-966. ASA-CSSA-SSSA, Madison, WI.

Blaxter, K. L., N. C. McGraham, and F. W. Wainman. 1956. Some observations on the digestibility of food by sheep, and on related problems. Br. J. Nutr. 10:69-91.

Block, E., L. D. Muller, L. C. Griel, Jr., and D. L. Garwood. 1981. Brown midrib-3-corn silage and heat extruded soybeans for early lactating dairy cows. J. Dairy Sci. 64:1813-1825.

Brennan, R. W., M. P. Hoffman, F. C. Parrish, F. Epplin, S. Bhide, and E. O. Heady. 1987. Effects of differing ratios of corn silage and corn grain on feedlot performance, carcass characteristics and projected economic returns. J. Anim. Sci. 64:23-31.

Buxton, D. R., and S. L. Fales. 1994. Plant environment and quality. In: G. C. Fahey, Jr. (ed.) Forage Quality, Evaluation, and Utilization. p 155-199. ASA-CSSA-SSSA, Madison, WI.

Calder, F. W., J. E. Langille, and J. W. G. Nicholson. 1977. Feeding value for beef steers of corn silage as affected by harvest dates and frost. Can. J. Anim. Sci. 57:65-73.

Cameron, M. G., G. C. J. Fahey, J. H. Clark, N. R. Merchen, and L. L. Berger. 1991. Effects of feeding alkaline hydrogen peroxide-treated wheat straw-based diets on intake, digestion, ruminal fermentation, and production responses by mid-lactation dairy cows. J. Anim. Sci. 69:1775-1787.

Cardoza, R. S., and D. R. Mertens. 1986. Effect of fiber source and content on threshold size for passage and fecal particle distribution. J. Dairy Sci. 69 (Suppl. 1):134 (Abstr.).

Chabbert, B., M. T. Tollier, B. Monties, Y. Barriere, and O. Argillier. 1994. Biological variability in lignification of maize: expression of the brown midrib bm3 mutation in three maize cultivars. J. Sci. Food Agric. 64:349-355.

Chamberlain, C. C., H. A. Fribourg, K. M. Barth, J. H. Felts, and J. M. Anderson. 1971. Effect of maturity of corn silage at harvest on the performance of feeder heifers. J. Anim. Sci. 33:161-166.

Chang, H.-M., and G. G. Allen. 1971. Oxidation. In: C. H. Ludwig (ed.) Lignins: Occurrence, Formation, Structure and Reactions. p 433-485. Wiley-Interscience, New York.

Chesson, A. 1981. Effects of sodium hydroxide on cereal straw in relation to the enhanced degradation of structural polysaccharides by rumen microorganisms. J. Sci. Food Agric. 32:745-758.

Chesson, A., A. H. Gordon, and J. A. Lomax. 1983. Substituent groups linked by alkali-labile bonds to arabinose and xylose residues of legumes, grass and cereal straw cell walls and their fate during digestion by rumen microorganisms. J. Sci. Food Agric. 34:1330-1340.

Crichlow, E. C., and B. F. Leek. 1980. The importance of pH in relation to the acid-excitation of epithelial receptors in the reticulo-rumen of sheep. J. Physiol. 310:60P-61P (Abstr.).

Dado, R. G. 1993. Voluntary intake and feeding behavior of dairy cows in response to rumen fill from forage fiber. Ph. D. dissertation, Michigan State University, East Lansing.

Dado, R. G., and M. S. Allen. 1995. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk. J. Dairy Sci. 78:118-133.

De Jong, A. 1986. The role of metabolites and hormones as feedbacks in the control of food intake in ruminants. In: L. P. Milligan, W. L. Grovum, and A. Dobson (ed.) Control of Digestion and Metabolism in Ruminants. p 459-478. Pretice-Hall, Englewood Cliffs, NJ.

De Jong, A., A. B. Steffens, and L. De Ruiter. 1981. Effects of portal volatile fatty acid infusions on meal patterns and blood composition in goats. Physiol. and Behav. 27:683-689.

Dean, R. A., J. W. Holloway, J. V. Whiteman, D. F. Stephens, and R. Totusek. 1976. Feedlot performance of progeny of Hereford, Hereford x Holstein and Holstein cows. J. Anim. Sci. 42:1290-1296.

desBordes, C. K., and J. G. Welch. 1984. Influence of specific gravity on rumination and passage of indigestible particles. J. Anim. Sci. 59:470-475.

Dijkstra, J., H. Boer, J. van Bruchem, M. Bruining, and S. Tamminga. 1993. Absorption of volatile fatty acids from the rumen of lactating dairy cows as influenced by volatile fatty acid concentration, pH, and rumen liquid volume. Br. J. Nutr. 69:385-396.

Dixon, R. M., and L. P. Milligan. 1985. Removal of digesta components from the rumen of steers determined by sieving techniques and fluid, particulate and microbial markers. Br. J. Nutr. 53:347-362.

Dulphy, J. P., and P. Faverdin. 1987. Food ingestion in ruminants: modalities and associated phenomena. Reprod. Nutr. Devel. 27:129-155.

Ehle, F. R. 1984. Influence of feed particle density on particulate passage from rumen of Holstein cow. J. Dairy Sci. 67:693-697.

Ehle, F. R., and M. D. Stern. 1986. Influence of particle size and density on particulate passage through alimentary tract of Holstein heifers. J. Dairy Sci. 69:564-568.

Engels, F. M., and R. E. Brice. 1985. A barrier covering lignified cell walls of barley straw that restricts access by rumen microorganisms. Curr. Microbiol. 12:217-224.

Engels, F. M., and J. L. L. Schuurmans. 1992. Relationship between structural development of cell walls and degradation of tissues in maize stems. J. Sci. Food Agric. 59:45-51.

Eyster, W. H. 1926. Chromosome VIII in maize. Science. 64:22.

Faichney, G. J. 1986. The kinetics of particular matter in the rumen. In: L. P. Milligan, W. L. Grovum, and A. Dobson (ed.) Control of Digestion and Metabolism in Ruminants. p 173-195. Prentice-Hall, Englewood Cliffs, NJ.

Faverdin, P. 1986. Variations of blood insulin at feeding in the lactating cow. Reprod. Nutr. Devel. 26:381-382.

Forbes, J. M. 1995. Voluntary Food Intake and Diet Selection in Farm Animals. 1st ed. CAB International, Wallingford, U.K.

Forbes, J. M. 1996. Integration of regulatory signals controlling forage intake in ruminants. J. Anim. Sci. 74:3029-3035.

Forbes, J. M., and F. D. Provenza. 2000. Integration of learning and metabolic signals into a theory of dietary choice and food intake. In: P. B. Cronje (ed.) Ruminant Physiology - Digestion, Metabolism, Growth and Reproduction. p 3-19. CABI Publishing, New York, New York.

Ford, C. W., R. Elliott, and P. J. Maynard. 1987. The effect of chlorite delignification on digestibility of some grass forages and on intake and rumen microbial activity in sheep fed barley straw. J. Agric. Sci. 108:129-136.

Foster, L. A., N. K. Ames, and R. S. Emery. 1991. Food intake and serum insulin responses to intraventricular infusions of insulin and IGF-I. Physiol. and Behav. 50:745-749.

Fox, D. G., and J. R. Black. 1984. A system for predicting body composition and performance of growing cattle. J. Anim. Sci. 58:725-739.

Fox, D. G., C. J. Sniffen, and J. D. O'Connor. 1988. Adjusting nutrient requirements of beef cattle for animal and environmental variations. J. Anim. Sci. 70:1475-1495.

Galyean, M. L., and A. L. Goetsch. 1993. Utilization of forage fiber by ruminants. In: H. G. Jung, D. R. Buxton, R. D. Hatfield, and J. Ralph (ed.) Forage Cell Wall Structure and Digestibility. p 33-71. ASA-CSSA-SSSA, Madison, WI.

Garrett, W. N. 1971. Energetic efficiency of beef and dairy steers. J. Anim. Sci. 32:451-456.

Gee, M. S., O. E. Nelson, and J. Kuc. 1968. Abnormal lignins produced by the brown midrib mutants of maize. II. Comparative studies on normal and brown midrib-1 dimethylformamide lignins. Arch. Biochem. Biophys. 123:403-408.

Grand, C., P. Parmentier, A. Boudet, and A. M. Boudet. 1985. Comparison of lignins and of enzymes involved in lignification in normal and brown midrib (bm3) mutant corn seedlings. Physiol. Veg. 23:905-911.

Grant, R. J., and D. R. Mertens. 1992a. Development of buffer systems for pH control and evaluation of pH effects on fiber digestion in vitro. J. Dairy Sci. 75:1581-1587.

Grant, R. J., and D. R. Mertens. 1992b. Influence of buffer pH and raw corn starch addition on in vitro fiber digestion kinetics. J. Dairy Sci. 75:2762-2768.

Greenhalgh, J. F. D., and G. W. Reid. 1973. Long- and short-term effects on intake of pelleting a roughage for sheep. Anim. Prod. 19:77-86.

Grovum, W. L. 1987. A new look at what is controlling food intake. In: F. N. Owens (ed.) Symposium Proceedings, Feed Intake by Beef Cattle, Stillwater, OK. p 1-40.

Grovum, W. L. 1995. Mechanisms explaining the effects of short chain fatty acids on feed intake in ruminants - osmotic pressure, insulin and glucagon. In: W. V. Englehardt, S. Leonhard-Marek, G. Breves, and D. Geisecke (ed.) Ruminant Physiology: Digestion, Metabolism, Growth and Reproduction. p 173-197. Ferdinand Enke Verlag, Stuttgart, Germany.

Harding, R., and B. F. Leek. 1972. Rapidly adapting mechanoreceptors in the reticulo-rumen which also respond to chemicals. Proc. Physiol. Soc. 223:32P-33P.

Hatfield, R. D. 1993. Cell wall polysaccharide interactions and degradability. In: H. G. Jung, D. R. Buxton, R. D. Hatfield, and J. Ralph (ed.) Forage Cell Wall Structure and Digestibility. p 286-313. ASA-CSSA-SSSA, Madison, WI.

Hofmann, R. R. 1988. Anatomy of the gastro-intestinal tract. In: D. C. Church (ed.) The Ruminant Animal: Digestive, Physiology and Nutrition. p 14-43. Prentice Hall, Englewood Cliffs, NJ.

Iggo, A. 1955. Tension receptors in the stomach and the urinary bladder. J. Physiol. 128:593-607.

Illius, A. W., and I. J. Gordon. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. J. Agric. Sci. 116:145-157.

Illius, A. W., and N. S. Jessop. 1996. Metabolic constraints on voluntary intake in ruminants. J. Anim. Sci. 74:3052-3062.

Jackson, M. G. 1977. Review article: The alkali treatment of straws. Anim. Feed Sci. Technol. 2:105-130.

Joanning, S. W., D. E. Johnson, and B. P. Barry. 1981. Nutrient digestibility depressions in corn silage-corn grain mixtures fed to steers. J. Anim. Sci. 53:1095-1103.

Johnson, T. R., and D. K. Combs. 1991. Effects of prepartum diet, inert rumen bulk, and dietary polyethylene glycol on dry matter intake of lactating dairy cows. J. Dairy Sci. 74:933-944.

Johnson, T. R., and D. K. Combs. 1992. Effects of inert rumen bulk of dry matter intake in early and midlactation cows fed diets differing in forage content. J. Dairy Sci. 75:508-519.

Jones, G. M. 1972. Chemical factors and their relation to feed intake regulation in ruminants: A review. Can. J. Anim. Sci. 52:207-239.

Jorgenson, L. R. 1931. Brown midrib in maize and its linkage relations. J. Am. Soc. Agron. 23:549-557.

Journet, M., and B. Remond. 1976. Physiological factors affecting the voluntary intake of feed by cows: A review. Livest. Prod. Sci. 3:129-146.

Jung, H. G., and M. S. Allen. 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. J. Anim. Sci. 73:2774-2790.

Jung, H. G., and D. A. Deetz. 1993. Cell wall lignification and degradability. In: H. G. Jung, D. R. Buxton, R. D. Hatfield, and J. Ralph (ed.) Forage Cell Wall Structure and Digestibility. p 315-346. ASA-CSSA-SSSA, Madison, WI.

Kaske, M., and A. Midasch. 1997. Effects of experimentally-impaired reticular contractions on digesta passage in sheep. Br. J. Nutr. 78:97-110.

Keith, E. A., V. F. Colenbrander, T. W. Perry, and L. F. Bauman. 1981. Performance of feedlot cattle fed brown midrib-three or normal corn silage with various levels of additional corn grain. J. Anim. Sci. 52:8-13.

King, K. W., and W. E. C. Moore. 1957. Density and size as factors affecting passage rate of ingesta in the bovine and human digestive tracts. J. Dairy Sci. 40:528-536.

Klopfenstein, T. J. 1978. Chemical treatment of crop residues. J. Anim. Sci. 46:841-848.

Kuc, J., and O. E. Nelson. 1964. The abnormal lignins produced by the *brown-midrib* mutants of maize. Arch. Biochem. Biophys. 105:103-113.

Laredo, M. A., and D. J. Minson. 1975. The effect of pelleting on the voluntary intake and digestibility of leaf and stem fractions of three grasses. Br. J. Nutr. 33:159-170.

Lechner-Doll, M., M. Kaske, and W. V. Englehardt. 1991. Factors affecting the mean retention time of particles in the forestomachs of ruminants and camelids. In: T. Tsuda, Y. Sasaki, and R. Kawashima (ed.) Physiological Aspects of Digestion and Metabolism in Ruminants. p 445-482. Academic Press Inc., New York.

Leek, B. F. 1969. Reticulo-ruminal mechanoreceptors in sheep. J. Physiol. (Lond.). 202:585-609.

Leek, B. F., and R. H. Harding. 1986. Sensory nervous receptors in the ruminant stomach and the reflex control of reticulo-ruminal motility. In: I. W. McDonald, and A. C. I. Warner (ed.) Digestion and Metabolism in Ruminants. p 60-76. University of New England Publishing Unit, Aridale, Australia.

Lehmann, F. 1941. Die lehre vom ballast. Z. Tierphysiol. Tierernahr. Futterminttelkd. 5:155-173.

Llamas-Lamas, G., and D. K. Combs. 1991. Effect of forage to concentrate ratio and intake level on utilization of early vegetative alfalfa silage by dairy cows. J. Dairy Sci. 74:526-536.

Manns, J. G., and J. M. Boda. 1967. Insulin release by acetate, propionate, butyrate, and glucose in lambs and adult sheep. Am. J. Physiol. 212:747-755.

Mbanya, J. N., M. H. Anil, and J. M. Forbes. 1993. The voluntary intake of hay and silage by lactating cows in response to ruminal infusion of acetate or propionate, or both, with or without distension of the rumen by a balloon. Br. J. Nutr. 69:713-720.

McEwen, P. L., J. G. Buchanan-Smith, and M. G. Cameron. 1996. The influence of corn silage hybrid variety on beef steer growth performance. Ontario Beef Res. Update Univ. of Guelph, 43-48.

McLeod, M. N., and D. J. Minson. 1988. Large particle breakdown by cattle eating ryegrass and alfalfa. J. Anim. Sci. 66:992-999.

Merchen, N. R., and L. D. Bourquin. 1994. Processes of digestion and factors influencing digestion of forage-based diets by ruminants. In: G. C. Fahey, Jr. (ed.) Forage Quality, Evaluation, and Utilization. p 564-612. ASA-CSSA-SSSA, Madison, WI.

Midasch, A., M. Kaske, and J. Rehage. 1994. Sonographic investigation of reticular contractions in sheep, cows, and goats. In: D. Giesecke (ed.) Proceedings of the Society of Nutrition Physiology. p DLG-Verlag, Frankfurt, Germany.

Minson, D. J. 1963. The effect of pelleting and wagering on the feed value of roughage - A review. J. Br. Grassl. Soc. 18:39-44.

Moore, J. E., and W. E. Kunkle. 1999. Evaluation of equations for estimating voluntary intake of forages and forage-based diets. J. Anim. Sci. 77 (Suppl. 1):204 (Abstr.).

Moore, K. J., and R. D. Hatfield. 1994. Carbohydrate and forage quality. In: G. C. Fahey, Jr. (ed.) Forage Quality, Evaluation, and Utilization. p 229-280. ASA-CSSA-SSSA, Madison, WI.

Moore, L. A. 1964. Symposium on forage utilization: Nutritive value of forage as affected by physical form. Part I. General principles involved with ruminants and

effect of feeding pelleted or wafered forage to dairy cattle. J. Anim. Sci. 23:230-238.

Muhamad, Y. B., M. P. Hoffman, and H. L. Self. 1983. Influence of different ratios of corn and corn silage, housing systems and seasons on the performance of feedlot steers. J. Anim. Sci. 56:747-754.

Muller, L. D., V. L. Lechtenberg, L. F. Bauman, R. F. Barnes, and C. L. Rhykerd. 1972. In vivo evaluation of a brown midrib mutant of Zea mays L. J. Anim. Sci. 35:883-889.

Murphy, M. R., P. M. Kennedy, and J. G. Welch. 1989. Passage and rumination of inert particles varying in size and specific gravity as determined from analysis of faecal appearance using multicompartment models. Br. J. Nutr. 62:481-492.

Nelson, C. J., and L. E. Moser. 1994. Plant factors affecting forage quality. In: G. C. Fahey, Jr. (ed.) Forage Quality, Evaluation, and Utilization. p 115-154. ASA-CSSA-SSSA, Madison, WI.

Neuffer, M. G., E. H. Coe, and S. R. Wessler. 1997. Mutants of Maize. ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Nour, A. Y. M., M. L. Thonney, J. R. Stouffer, and W. R. C. White, Jr. 1981. Muscle, fat and bone in serially slaughtered large Holstein dairy or small Angus beef cattle fed corn or corn silage diets in one of two locations Carcasses. J. Anim. Sci. 52:512-521.

NRC. 1984. Nutrient Requirements of Beef Cattle. 6th ed. National Academy Press, Washington, DC.

NRC. 1987. Predicting Feed Intake of Food-Producing Animals. 1th ed. National Academy Press, Washington, DC.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. National Academy Press, Washington, DC.

Oba, M., and M. S. Allen. 1999a. Effects of brown midrib 3 mutation in corn silage on dry matter intake and productivity of high yielding dairy cows. J. Dairy Sci. 82:135-142.

Oba, M., and M. S. Allen. 1999b. Evaluation of the importance of the digestibility of neutral detergent fiber from forage: effects on dry matter intake and milk yield of dairy cows. J. Dairy Sci. 82:589-596.

Oba, M., and M. S. Allen. 2000a. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 1. Feeding behavior and nutrient utilization. J. Dairy Sci. 83:1333-1341.

Oba, M., and M. S. Allen. 2000b. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 2. Chewing activities. J. Dairy Sci. 83:1342-1349.

Okine, E. K., and G. W. Mathison. 1991. Effects of feed intake on particle distribution, passage of digesta, and extent of digestion in the gastrointestinal tract of cattle. J. Anim. Sci. 69:3435-3445.

Orskov, E. R., G. W. Reid, and M. Kay. 1988. Prediction of intake by cattle from degradation characteristics of roughages. Anim. Prod. 46:29-34.

Orskov, E. R., G. W. Reid, and M. Kay. 1991. Influence of straw quality and level of concentrate in a completely mixed diet on intake and growth rate in steers. Anim. Prod. 52:461-464.

Osbourn, D. F., D. E. Beever, and D. J. Thomson. 1976. The influence of physical processing on the intake, digestion and utilization of dried herbage. Proc. Nutr. Soc. 35:191-200.

Osuji, P. O., J. G. Gordon, and J. F. Webster. 1975. Energy exchanges associated with eating and rumination in sheep given grass diets of different physical forms. Br. J. Nutr. 34:59-71.

Owens, E., T. Klopfenstein, and N. A. Urio. 1984. Treatment with other chemicals. In: F. Sundstol, and E. Owen (ed.) Straw and Other Fibrous By-Products as Feed. p 248-275. Elsevier Science Publishers, Amsterdam, The Netherlands.

Perry, T. W., and D. M. Caldwell. 1969. Comparative nutritive value of silages made from high-sugar male sterile hybrid corn and regular starchy corn. J. Dairy Sci. 52:1119-1121.

Poppi, D., B. W. Norton, D. J. Minson, and R. E. Hendricksen. 1980. The validity of the critical size theory for particles leaving the rumen. J. Agric. Sci. 94:275-280.

Poppi, D. P., R. E. Hendricksen, and D. J. Minson. 1985. The relative resistance to escape of leaf and stem particles from the rumen of cattle and sheep. J Agric Sci. 105:9-14.

Poppi, D. P., D. J. Minson, and J. H. Termouth. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of feed in the reticulo-rumen. Aust. J. Agric. Res. 32:109-121.

Reid, G. W., E. R. Orskov, and M. Kay. 1988. A note on the effect of variety, type of straw and ammonia treatment on digestibility and on growth rate in steers. Anim. Prod. 47:157-160.

Rexen, F., and K. V. Thomsen. 1976. The effect on digestibility of a new techique for alkali treatment of straw. Anim. Feed Sci. Technol. 1:73-83.

Rook, J. A., L. D. Muller, and D. B. Shank. 1977. Intake and digestibility of brown-midrib corn silage by lactating dairy cows. J. Dairy Sci. 60:1894-1904.

Schettini, M. A., E. C. Prigge, and E. L. Nestor. 1999. Influence of mass and volume of ruminal contents on voluntary intake and digesta passage of a forage diet in steers. J. Anim. Sci. 77:1896-1904.

Siciliano-Jones, J., and M. R. Murphy. 1991. Specific gravity of various feedstuffs as affected by particle size and in vitro fermentation. J. Dairy Sci. 74:896-901.

Sommerfeldt, J. L., D. J. Schingoethe, and L. D. Muller. 1979. Brown-midrib corn silage for lactating dairy cows. J. Dairy Sci. 62:1611-1618.

Stake, P. E., M. J. Owens, D. J. Schingoethe, and H. H. Voelker. 1973. Comparative feeding value of high-sugar male sterile and regular dent corn silages. J. Dairy Sci. 56:1430-1444.

Stallings, C. C., B. M. Donaldson, J. W. Thomas, and E. C. Rossman. 1982. In vivo evaluation of brown-midrib corn silage by sheep and lactating dairy cows. J. Dairy Sci. 65:1945-1949.

St-Pierre, N. R., R. Bouchard, G. J. St Laurent, and C. Vinet. 1983. Effects of stage of maturity and frost on nutritive value of corn silage for lactating dairy cows. J. Dairy Sci. 66:1466-1473.

Sutherland, T. M. 1988. Particle separation in the forestomachs of sheep. In: A. Dobson, and M. J. Dobson (ed.) Aspects of Digestive Physiology in Ruminants. p 43-73. Cornell Univ. Press, Ithaca, NY.

Terashima, N., K. Fukushima, L.-F. He, and K. Takabe. 1993. Comprehensive model of the lignified plant cell wall. In: H. G. Jung, D. R. Buxton, R. D. Hatfield, and J. Ralph (ed.) Forage Cell Wall Structure and Digestibility. p 247-270. ASA-CSSA-SSSA, Madison, WI.

Thomson, D. J., and D. E. Beever. 1980. The effect of conservation and processing on the digestion of forages by ruminants. In: Y. Ruckebusch, and P. Thivend (ed.) Digestive Physiology and Metabolism in Ruminants. p 291-308. MTP Press Ltd., Lancaster, England.

Thonney, M. L. 1987. Growth, feed efficiency and variation of individually fed Angus, Polled Hereford and Holstein steers. J. Anim. Sci. 65:1-8.

Thonney, M. L., E. K. Heide, D. J. Duhaime, A. Y. M. Nour, and P. A. Oltenacu. 1981. Growth and feed efficiency of cattle of different mature sizes. J. Anim. Sci. 53:354-362.

Tine, M. A., K. R. Mcleod, R. A. Erdman, and R. L. Baldwin, VI. 2001. Effects of brown midrib corn silage on the energy balance of dairy cattle. J. Dairy Sci. 84:885-895.

Ulyatt, M. J., D. W. Dellow, A. John, C. S. W. Reid, and G. C. Waghorn. 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. In: L. P. Milligan, W. L. Grovum, and A. Dobson (ed.) Control of Digestion and Metabolism in Ruminants. p 498-515. Prentice-Hall, Englewood Cliffs, NJ.

Van Soest, P. J., A. Mascarehnas-Ferreira, and R. D. Hartley. 1984. Chemical properties of fibre in relation to nutritive quality of ammonia-treated forages. Anim. Feed Sci. Technol. 10:155-164.

Vasilatos, R., and P. J. Wangsness. 1980. Changes in concentrations of insulin, growth hormone and metabolites in plasma with spontaneous feeding in lactating dairy cows. J. Nutr. 110:1479-1487.

Vignols, F., J. Rigau, M. A. Torres, M. Capellades, and P. Puidgomenech. 1995. The brown midrib3 (bm3) mutation in maize occurs in the gene encoding caffeic acid O-methyltransferase. Plant Cell. 7:407-416.

Waldo, D. R. 1986. Effect of forage quality on intake and forage concentration interactions. J. Dairy Sci. 69:617-631.

Waldo, D. R., L. W. Smith, and E. L. Cox. 1972. Model of cellulose disappearance from the rumen. J. Dairy Sci. 55:125-129.

Wardrop, I. D. 1960. The post-natal growth of the visceral organs of the lamb. 2. The effect of diet on growth rate, with particular reference to the parts of the alimentary canal. J. Agric. Sci. 55:127-132.

Warner, A. C. I., and B. D. Stacy. 1968. The fate of water in the rumen. 2. Water balances throughout the feeding cycle in sheep. Br. J. Nutr. 22:389-410.

Waybright, T. R., and G. A. Varga. 1991. Effect of water-filled bags in the rumen of wethers on ruminal digesta kinetics and total tract nutrient digestibility. J. Anim. Sci. 69:2157-2167.

Weaver, D. E., C. E. Coppock, G. B. Lake, and R. W. Everett. 1978. Effect of maturation on compostition and in vitro dry matter digestibility of corn plant parts. J. Dairy Sci. 61:1782-1788.

Welch, J. G. 1982. Rumination, particle size and passage from the rumen. J. Anim. Sci. 54:885-894.

Weston, R. H., and J. P. Hogan. 1967. The digestion of chopped and ground roughages by sheep. I. The movement of digesta through the stomach. Aust. J. Agric. Res. 18:789-801.

Williams, P. V., and G. M. Innes. 1983. Factors affecting the hydrolysis of urea when applied to barley straw. Anim. Prod. 36:510=511 (Abstr.).

Woodford, J. A., N. A. Jorgensen, and G. P. Barrington. 1986. Impact of dietary fiber and physical form on performance of lactating dairy cows. J. Dairy Sci. 69:1035-1047.

Woody, H. D., D. G. Fox, and J. R. Black. 1983. Effect of diet grain content on performance of growing and finishing cattle. J. Anim. Sci. 57:717-728.

Wyburn, R. S. 1980. The mixing and propulsion of the stomach contents of ruminants. In: Y. Ruckebusch, and P. Thivend (ed.) Digestive Physiology and Metabolism in Ruminants. p 35-51. AVI Publishing Co. Inc., Westport, CN.

Yu, Y., J. W. Thomas, and R. S. Emery. 1975. Estimated nutritive value of treated forages for ruminants. J. Anim. Sci. 41:1742-1751.

CHAPTER 2

Brown Midrib-3 (*bm₃*) Corn Silage Improves Digestion but not Performance of Growing Beef Steers

Abstract

The brown midrib-3 (*bm₃*) gene mutation has been incorporated into corn plants to potentially improve fiber digestibility. The objectives of this study were to determine the effect of *bm₃* corn silage on digestion and performance of growing beef steers and to determine whether limiting intake would further enhance fiber digestibility of *bm₃* corn silage. A *bm₃* hybrid and its isogenic normal counterpart were harvested at three-quarters kernel milk line. Neutral detergent fiber, ADF, and ADL were 4.5, 6.9, and 1.9 units lower, respectively, and DM was 5.4 units higher for *bm₃* than for normal silage. In Trial 1, eight ruminally fistulated Angus crossbred steers (224 ± 24 kg) were randomly assigned to a 2 × 2 factorial arrangement of treatments in a replicated 4 × 4 Latin square design. Steers had ad libitum feed access or were restricted to 80% of ad libitum intake of diets containing 86% normal corn silage (**Control**) or *bm₃* corn silage (**BMCS**). The remainder of the diets consisted of soybean meal, urea, monensin, vitamins, and minerals. Dry matter intake was greater ($P < 0.01$) for steers offered ad libitum access to BMCS than for those with ad libitum access to the Control diet. The BMCS treatment resulted in improved ($P < 0.05$) apparent total-tract digestibility of DM, OM, NDF, and ADF. Mean concentration of total VFA and molar proportions of acetate were increased ($P < 0.05$) by feeding BMCS. There tended to be a DMI × hybrid interaction ($P = .16$) for apparent total-tract digestibility of NDF. When diets were offered ad libitum, BMCS increased NDF digestibility by 10.5 percentage units compared to with Control, but, when DMI was

limited, BMCS increased NDF digestibility by 15.8 percentage units. In Trial 2, 128 steer contemporaries of those used in Trial 1 (245 ± 13 kg) were offered ad libitum access to BMCS or Control diets as used in Trial 1. After a 112-d treatment period, concentrate in the diet was increased, and all steers were fed a common finishing diet. During the 112-d treatment period, steers receiving BMCS consumed 0.45 kg more DM/d ($P < 0.05$) and had similar ADG ($P > 0.10$), compared with those steers receiving the Control silage. This resulted in poorer ($P < 0.01$) feed efficiency for steers receiving BMCS. Finishing phase and overall performance of the steers was not different ($P > 0.10$) due to treatment. Although feeding BMCS in growth-phase diets resulted in increased daily DMI and improved digestibility of DM and fiber, it did not result in improved steer feedlot ADG compared with Control silage.

Introduction

Brown midrib mutations have been incorporated into corn plants to lower lignin concentration (Kuc and Nelson, 1964) and improve fiber digestibility compared with normal corn without the mutation. Muller et al. (1972) showed that the in vitro digestion rates of DM, NDF, cellulose, and hemicellulose were faster for corn silage with the brown midrib-3 (*bm₃*) mutation. Increased voluntary DMI has been observed for early (Rook et al., 1977; Block et al., 1981) and mid to late lactation (Sommerfeldt et al., 1979; Stallings et al., 1982) dairy cows fed *bm₃* corn silage. In a majority of these experiments, increased DMI generally resulted in increased milk yield and(or) greater BW gain. Oba and Allen (1999) reported a 9% increase in DMI and a 7% increase in milk yield when diets fed to dairy cows contained *bm₃* over those fed isogenic normal corn silage.

High levels of corn silage are often fed during the growth phase of beef cattle feeding systems in the upper Midwest (Ritchie et al., 1992). During this phase, the extent of ruminal fill and digestibility of fiber may limit animal performance. Feeding corn silage with the bm_3 mutation might improve growth performance as a result of increased fiber digestion and DMI.

Limit-feeding of a high roughage diet has been shown to improve total-tract digestibility of NDF in sheep (Colucci et al., 1989) and cattle (Colucci et al., 1989; Murphy et al., 1994). Oba and Allen (1999) reported a negative relationship between difference in NDF digestibility and difference in DMI for bm_3 and isogenic normal corn silage, for lactating dairy cows. Therefore, the objectives of this study were to determine the effects of bm_3 corn silage on fiber digestibility, voluntary DMI, growth, and feed efficiency of weanling beef steers and to determine whether limiting intake would further enhance fiber digestibility of the bm_3 corn silage.

Materials and Methods

A corn hybrid containing bm_3 (F657, Cargill Hybrid Seeds, Minneapolis, MN) and the same hybrid without the mutation (isogenic normal; 6208, Cargill Hybrid Seeds), were grown in adjoining 14.6-ha field plots at Michigan State University, East Lansing. Both hybrids were seeded on the same day in 76.2-cm rows to achieve a population of 69,200 seeds per hectare. As the corn approached maturity, DM for each hybrid was determined every third day to estimate desired time of harvest. Immediately before harvest, estimates of plant population were determined for each hybrid by counting the number of plants found in 5.3 m of a row, in 10 randomly selected sites. Four plants from each site were

51

weighed, chopped (Mighty Mac, Amerind MacKissic Inc., Parker Ford, PA), and DM was

determined by oven drying at 57°C. An estimate of DM yield per hectare was determined

by multiplying the plant population estimate by the plant DM weight. The two field plots

were harvested with a three-row silage chopper (Model 900, New Holland North America

Inc, New Holland, PA) set at 9.5-mm theoretical cut length, and ensiled in adjacent 150-T

concrete bunker silos at the Michigan State University Beef Cattle Teaching and Research

Center. Samples from every fourth silage load were collected, frozen immediately at -

20°C, and analyzed for CP by macro-Kjeldahl N (AOAC, 1984) before formulating the

experimental diets. Post-ensiled nutrient composition and fermentation characteristics of

the silages are presented in Table 2-1.

Trial 1

Eight Angus crossbred steers (224 ± 24 kg) were surgically fitted with 7.5-cm i.d.

ruminal cannulas (Model 4C, Bar Diamond Inc., Parma, ID) 4 wk before the start of the

trial. Eighteen days after surgery, cannulas were replaced with 10-cm i.d. ruminal

cannulas (Model 2C, Bar Diamond Inc.). At this time, steers were weighed and moved to

individual metabolism stalls for acclimation. Steers had ad libitum access to water and a

common corn silage diet (Table 2-2). Corn silage was the primary dietary ingredient, with

soybean meal and supplement added to meet or exceed requirements for metabolizable

protein, minerals, and vitamins (NRC, 1996). Feed offered and refused was recorded

daily, and, when DMI reached a plateau (< 5% difference in DMI for 4 d), DMI as a

percentage of body weight was calculated.

After acclimation, a 2 × 2 factorial arrangement of treatments was applied to a replicated 4 × 4 Latin square design balanced for carryover effects. Treatment periods were 21 d (14 d of adaptation and 7 d of collection). Treatment diets contained corn silage from a normal corn hybrid (**Control**) or the same hybrid with the brown midrib-3 mutation (**BMCS**; Table 2-2). The two diets were offered ad libitum or limited to 80% of ad libitum normal DMI. Preceding each period, steers were weighed, and ad libitum DMI as a percentage of body weight was estimated from DMI determined during acclimation. Treatments with limited DMI were fed 80% of this ad libitum DMI estimate. This procedure adjusted DMI for increasing BW during the 84-d trial.

Diets were mixed daily and fed at 1400, 2200, and 0600 the following day. Amounts fed and refused were recorded daily. Representative samples of complete mixed diets, individual ingredients, and orts were taken at each feeding on d 14 through 21 of each period and frozen immediately at -20°C.

Fecal output was determined using total fecal collection on d 15 through 18 of each period. Fecal collection bags were placed on each steer at 1400 on collection days. Accumulated feces were removed and weighed at each 24-h interval for the 4 d. A 0.5-kg representative sample was frozen at -20°C until analysis.

Five subsamples of whole ruminal contents from representative areas of the rumen were collected and composited every hour for 8 h starting at 0600 on d 15, 1400 on d 16, and 2200 on d 17, to represent an entire 24-h period. Fluid was separated from the particulate fraction by squeezing through four layers of cheesecloth. Ruminal fluid pH was determined immediately after collection. A 50-mL aliquot was frozen immediately at

-20°C for later analysis of VFA. An additional 50-mL aliquot was acidified with 1 mL of 6 N HCl and frozen at -20°C for later analysis of ruminal ammonia N concentration.

Total ruminal contents were removed at 1000 on d 19 and 1800 on d 21 of each period to determine ruminal volume and passage rate. Each animal's digesta was removed and placed in a 114-L open barrel. Ruminal content was weighed, and volume was determined. A 2.7-kg subsample was collected, and digesta were replaced. The subsample was frozen immediately at -20°C for later determination of indigestible NDF content.

Trial 2

One hundred twenty-eight weanling Angus crossbred beef steers (245 ± 13 kg) were used to determine the effects of feeding bm_3 corn silage on growth performance. Steers were blocked by weight and randomly assigned to eight replications of two dietary treatments with eight animals per pen (4.3 × 13.1 m, partially covered). Steers were fed once daily and had ad libitum access to Control and BMCS diets, as used in Trial 1, for 112 d. After this time, the percentage of concentrate in the diet was increased stepwise (four diets over 16 d) until steers were adapted to a common finishing diet that contained 15% normal corn silage (Table 2-2). Orts were weighed every 28 d during the entire feeding period. Complete mixed diets and individual feedstuffs were sampled every 15 d and frozen at -20°C until analysis. Steer weights at 0, 112, and 200 d were the average of full weights taken on two consecutive days. Steers were implanted at d 0 and 112 with 200 mg of progesterone and 20 mg of estradiol benzoate (IMPLUS-S, Upjohn Co., Kalamazoo, MI). Estimates of s.c. fat thickness and longissimus muscle area were

54

determined at d 0 and 112 using real-time ultrasound (Model SLC 200V Pie Medical, Classic Medical Supply Inc., Tequesta, FL) between the 12th and 13th rib. All steers were harvested at a commercial packing plant (Moyer Packing Co., Souderton, PA) on d 202 of the trial. Carcass measurements were recorded after a 48-h chill.

For both trials, experimental and surgical procedures were conducted according to those approved by the Michigan State University All University Committee on Animal Use and Care (AUF No. 07/97-093-00).

Sample Analysis

Feed and fecal samples were dried at 57°C and ground through a Wiley mill (Arthur H. Thomas, Philadelphia, PA) equipped with a 1-mm screen. Samples of rations and individual feedstuffs were composited for each period, and fecal samples were composited by animal for each period. Samples were then analyzed for DM, OM (Goering and Van Soest, 1970), NDF, ADF, and ADL (Van Soest et al., 1991; method A for NDF). Neutral detergent fiber, ADF, and ADL were corrected for ash. Feed samples were analyzed for CP by macro-Kjeldahl N (AOAC, 1984). Feed and fecal starch were measured by an enzymatic method (Karkalas, 1985) using a spectrophotometer (Spectra Max 190, Molecular Device Corp., Sunnyvale, CA) after samples were gelatinized with sodium hydroxide. Gross energy was determined for both feed and fecal samples by bomb calorimetry (1241 Adiabatic Calorimeter, Parr Instruments, Moline, IL; AOAC, 1984). Digestible energy was determined as the difference between intake of diet gross energy and output of fecal gross energy. Concentration of ME, NE_m, and NE_g in the diets were calculated from DE using NRC (1996) equations.

Ruminal VFA samples were allowed to thaw completely at room temperature (22 °C) before analysis. Samples were then mixed thoroughly, and 5-mL subsamples were transferred to high-speed centrifuge tubes. Samples were then acidified (pH < 3) with 90 μL of 12 N H_2SO_4, vortexed, and centrifuged (Model J2-21, Beckman Instruments Inc., Arlington Heights, IL) at 26,000 × g for 30 min. Concentrations of VFA in the supernate were then determined by HPLC (Waters 410 Differential Refractometer, Millipore Corp., Milford, MA) using an organic acid analysis column (300 mm × 7.8 mm i.d.; AMINEX HPX 87H Ion Exchange, Bio-Rad Laboratories, Hercules, CA) and 0.005 M H_2SO_4 at 0.6 mL·min^{-1} as the mobile phase.

Silage samples were allowed to thaw completely at room temperature before analysis. A 50-g subsample of silage plus 450 mL of distilled water were blended (Model STO-3500, STOMACHER Lab-Blender, Teckmar, Cincinnati, OH) for 5 min. Samples were strained through four layers of cheesecloth, and pH was determined. Five milliliters of solution was transferred to a high-speed centrifuge tube and acidified (pH < 3) with 90 μL of 12 N H_2SO_4 and centrifuged at 26,000 × g for 30 min. Concentrations of VFA in the supernate were determined by HPLC.

Ruminal samples were thawed completely at 22°C, mixed, and 5-mL subsamples were transferred to high-speed centrifuge tubes. Samples were then centrifuged at 26,000 × g for 30 min. Ruminal ammonia N concentrations were determined using a spectrophotometer (Model DU 7400, Beckman Instruments Inc., Schaumburg, IL) following the procedure described by Chaney and Marbach (1962).

Indigestible residues in feed and ruminal contents were determined using 120-h in vitro digestion according to procedures described by Dado and Allen (1995). Passage rate

of indigestible NDF from the rumen (k_p) was determined by dividing the rate of indigestible NDF intake by the indigestible NDF pool size, based on the two-pool, first-order model of rumen fiber digestion (Waldo et al., 1972). Ruminal NDF turnover time was determined by dividing ruminal NDF pool size by NDF intake per hour. These calculations assume that ruminal NDF pool sizes and fluxes are at steady state, and that 120-h in vitro indigestible NDF is an accurate measure of indigestible fiber in vivo.

Statistical Analysis

Intake, digestibility, VFA, digesta characteristics, and kinetic data for Trial 1 were analyzed using the Mixed Models procedure (SAS, 1996) as a 2 × 2 factorial arrangement of treatments. Compound symmetry was determined as the most appropriate covariance structure using the Schwarz Bayesian criterion (Littell et al., 1998). The model contained animal as a random effect and period, DMI level, hybrid, and DMI × hybrid as fixed effects. Interactions were considered significant at $P < 0.10$. In Trial 1, one steer that had ad libitum access to BMCS would not consume expected DMI of feed prior to collection for reasons unrelated to treatment. Therefore, data were omitted for this steer during that period. Due to the unbalanced design, data are presented as least squares means.

Ruminal pH and NH_3 N data for Trial 1 were analyzed using the Mixed Models procedure (SAS, 1996) as a 2 × 2 factorial arrangement of treatments with repeated measures over time. The covariance structure using unstructured correlation for period and autoregressive correlation for time was determined to be the most appropriate according to the Schwarz Bayesian criterion (Littell et al., 1998). The model contained

animal as a random effect and period, DMI level, hybrid, time, and their 2- and 3-way interactions as fixed effects. Interactions were considered significant at $P < 0.10$.

Data for Trial 2 were analyzed using the Mixed Models procedure (SAS, 1996) as a randomized complete block design using pen as the experimental unit. The model statement contained ADG, DMI, feed efficiency, and ultrasound data as the dependent variables and weight-block and treatment as the independent variables. Carcass data for 19 steers in Trial 2 were not obtained at the packing plant. Treatment effects for all data were considered different at a significance level of $P < 0.05$.

Results and Discussion

Isogenic normal corn was harvested 140 d following planting and was 4 percentage units higher in DM than the bm_3 at this time. The bm_3 corn was harvested 147 d following planting. Both hybrids were ensiled at three-fourths kernel milk line, but the DM concentration was greater for bm_3 than isogenic normal (Table 2-1). Previous literature indicates that adding the bm_3 mutation to corn results in slower growth (Miller and Geadelmann, 1983), delayed silking (Miller et al., 1983; Weller et al., 1985), and slower grain filling (Miller and Geadelmann, 1983), which may delay maturity by 7 to 14 d (Weller et al., 1985). Allen et al. (1997) compared 14 bm_3 corn hybrids with their respective isogenic normal counterparts and determined, that when the hybrids were harvested on the same date, the bm_3 hybrids were 3 percentage units lower in DM. In the current research, the percentage of CP was similar between the two hybrids. There was 6.3% more starch in the bm_3 corn silage compared with the isogenic normal corn silage. Neutral detergent fiber, ADF, and ADL were 4.5, 6.9, and 1.9 units lower, respectively,

for bm_3 than for isogenic normal. Oba and Allen (1999) observed reductions of 1.8, 1.3, and 0.8 units in NDF, ADF, and lignin for bm_3 corn silage.

Trial 1

Steers with ad libitum access to BMCS had a higher $(P < 0.01)$ daily DMI than steers with access to Control silage. This increase in DMI could be partially due to the lower NDF concentration and(or) increased NDF digestibility of BMCS. Oba and Allen (1999) reported a 9% increase in DMI when dairy cows received bm_3 corn silage compared with normal and attributed much of this increase to bm_3 silage being more readily degraded in the rumen and having a faster passage rate.

Digestibility of DM and OM was improved $(P < 0.05)$ by feeding BMCS compared with Control silage. The higher DM digestibility for BMCS could be due to the higher fiber digestibility and(or) the higher starch content in the diet. In previous literature, when bm_3 was compared with isogenic normal corn silage, no difference in apparent total-tract DM digestibility was observed for lactating dairy cows (Rook et al., 1977; Sommerfeldt et al., 1979; Oba and Allen, 1999); however, a 6.6 percentage unit improvement in DM digestibility has been reported for sheep (Stallings et al., 1982).

There was a trend for a DMI level $\times$ hybrid interaction $(P \leq 0.16)$ for apparent total-tract digestibility of NDF and ADF (Table 2-3). The magnitude of improvement in total-tract digestibility of NDF and ADF by feeding BMCS was dependent on DMI level. When BMCS was compared with Control at ad libitum intakes, there were 10.5 and 9.4 percentage unit improvements in total-tract digestibility of NDF and ADF, respectively. When intake was held constant between the two hybrids by limiting DMI, feeding BMCS

resulted in 15.8 and 15.4 percentage unit improvements in total-tract digestibility of NDF and ADF, respectively. Similar results were reported by Oba and Allen (1999), when bm_3 was compared with isogenic normal corn silage diets fed to lactating dairy cows in a crossover design. In that study, as DMI increased with bm_3 compared with control, total-tract digestibility of NDF decreased. When cows consumed similar amounts of bm_3 and isogenic normal silage diets, there was a 6 unit increase in apparent total-tract digestibility of NDF for bm_3 compared with normal silage. However, this improvement in total-tract digestibility of NDF for bm_3 corn silage was diminished when DMI was increased. Oba and Allen (1999) explained that higher passage rate associated with increased DMI could have reduced ruminal retention time for bm_3 corn silage, which should have reduced total-tract digestibility of NDF. Differences in apparent total-tract digestibility of NDF and ADF in the current trial can be explained in a similar manner. Limiting intake would have decreased passage rate and increased the ruminal retention time of the bm_3 corn silage, allowing a greater extent of fermentation in the rumen. Murphy et al. (1994) reported that, for every 1-kg reduction in DMI below ad libitum for steers fed corn silage-based diets, total-tract digestibility of NDF increased 4.1 units.

Apparent total-tract digestibility of starch was not affected ($P > 0.20$) by either hybrid or level of intake (Table 2-3). Oba and Allen (1999) also reported no difference in total-tract starch digestibility when either bm_3 or the same hybrid without the mutation was fed to lactating dairy cows. Murphy et al. (1994) observed that reducing DMI from ad libitum to 80% of ad libitum did not influence total-tract starch digestibility.

Gross energy digestibility tended to be improved ($P = 0.07$) by feeding BMCS compared with Control (Table 2-3). With a 10.5 percentage unit greater apparent total-

tract digestibility of NDF for BMCS than for Control silage and similar starch digestibility, GE digestibility would be predicted to be higher. The reason for lack of a significant increase in GE digestibility is not known but may be due to a decreased protein digestibility of BMCS. Rook et al. (1977) and Sommerfeldt et al. (1979) reported no differences in energy digestibility for dairy cows fed diets containing either bm_3 or isogenic normal corn silage. In the current study, the increased DMI and total-tract digestibility of energy by steers offered ad libitum intake of BMCS resulted in increased ($P < 0.05$) digestible energy intake for BMCS compared with Control silage.

Ruminal digesta characteristics and passage rate data are presented in Table 2-4. There were DMI level × hybrid interactions ($P < 0.10$) for digesta dry weight, digesta volume, percentage of ruminal NDF, and ruminal NDF turnover time. When steers had ad libitum access to BMCS and Control silage, digesta dry weight and digesta volume were increased by 5.2 and 4.1%, respectively. However, when intake was held constant by restricting DMI, feeding BMCS resulted in digesta dry weight and digesta volume being decreased by 7.7 and 7.0%, respectively. Ruminal NDF turnover time was 9% slower for ad libitum Control silage than for ad libitum BMCS. When intake was restricted, ruminal NDF turnover time was 23% slower for Control silage than for BMCS. Ruminal NDF turnover time for BMCS was similar ($P > 0.20$) when diets were fed at either DMI level. Ruminal passage rate of indigestible NDF was reduced ($P < 0.01$) by restriction of DMI but was not significantly affected by hybrid. The faster passage rate and similar turnover time for ad libitum BMCS than for limited BMCS suggests that digestion rate of BMCS was reduced by increasing DMI. Similar results were reported by Oba and Allen (2000), who observed an increase in passage rate of NDF and a reduction in digestion rate of

potentially digestible NDF when bm_3 relative to isogenic normal corn silage was fed to dairy cows.

Hybrid did not significantly influence ruminal pH ($P > 0.10$). There was a time × DMI interaction ($P < 0.001$) for ruminal pH. Therefore, ruminal pH data are presented as treatment least squares means over time after initial feeding (Figure 2-1). Ruminal pH reached the lowest point approximately 3 h after each feeding for both limit-fed treatments and then increased until the next feeding. Ruminal pH for steers receiving the limited diets continued this cyclic pattern for each additional feeding. Steers offered ad libitum access had decreasing ruminal pH from initial feeding until approximately 4 to 6 h after feeding. After this time, ruminal pH remained fairly constant with only slight fluctuations when additional feed was offered. The limited intake steers consumed all of their allotted feed rapidly at each of the feeding times, which would supply a large amount of fermentable substrate to the ruminal microbes in a short period of time, explaining the cyclic pattern for ruminal pH. Steers receiving the diets at ad libitum intakes were observed to consume feed throughout the period, which would result in a more constant pool of fermentable substrate in the rumen and a more consistent pH. A pattern in ruminal pH similar to the ad libitum treatments was observed by Rook et al. (1977), who reported that ruminal pH reached the lowest point approximately 4 h after feeding and then increased until the next feeding when an 85% corn silage diet was offered at ad libitum to lactating dairy cows. In contrast to these results, Rook et al. (1977) and Block et al. (1981) reported lower ruminal pH when bm_3 was compared to isogenic normal corn silage diets offered ad libitum to dairy cows.

Ruminal ammonia data are presented in Figure 2-2 as treatment least squares means over time after initial feeding, because of the time × DMI × hybrid interaction ($P <$ 0.05). Ruminal ammonia followed a cyclic pattern over the 24-h period for all treatments. In all four treatments, NH_3 N peaked approximately 1 h after each of the three feeding times. Limit-feeding resulted in higher ($P < 0.05$) NH_3 N at each of the peaks compared with ad libitum feeding. After reaching the peak, NH_3 N in both limit-fed treatments reached the lowest point approximately 4 h after feeding. Ruminal ammonia concentration in steers offered diets ad libitum declined more slowly and did not reach the lowest point until after 4 h after feeding. Murphy et al. (1994) found that restricting intake of steers fed a 75% corn silage diet resulted in higher peak concentrations of NH_3 N when compared with ad libitum DMI. In that study, the diets were balanced to contain similar daily intakes of CP by adding higher concentrations of soybean meal and urea to the limit-fed diets. As a result, steers receiving the limit-fed diets consumed more total protein shortly after feeding, resulting in a higher NH_3 N peak (Murphy et al., 1994). In the present study, even though the diets were balanced to contain similar concentrations of protein, the higher NH_3 N peak for steers receiving the limited intake diets could be explained in a similar manner. The feed-restricted steers probably consumed a larger initial meal size, which could be the cause of higher NH_3 N peak.

Steers with ad libitum access to Control silage had significantly higher NH_3 N concentration than those receiving ad libitum BMCS at 1 h after initial feeding. Limit-fed Control silage- and BMCS-fed steers had similar NH_3 N at 1 h after initial feeding. At 2 and 3 h after initial feeding, NH_3 N was higher ($P < 0.05$) for limit-fed Control steers than for limit-fed BMCS steers. The two treatments remained similar from 4 h after initial

63

feeding until additional feed was offered, at which time limit-fed Control steers again had higher concentrations NH_3 N after feeding. Murphy et al. (1994) observed that, as time after feeding increased, NH_3 N concentration of steers fed restricted intakes increased compared with steers offered ad libitum intakes. They explained that this could be from lack of NH_3 N assimilation into microbial protein as a result of decreased availability of fermentable substrate. In the present study, differences in ruminal ammonia concentrations between the limit-fed treatments could be due to an increase in availability of fermentable substrate for BMCS compared with Control silage. The lower concentration of NH_3 N caused by ad libitum BMCS compared to ad libitum Control silage could have resulted from an increased availability of fermentable substrate, a smaller initial meal size, faster liquid passage rate, lower protein digestibility, or any combination of these factors. When bm_3 was compared with isogenic normal corn silage in lactating dairy rations, no differences in NH_3 N were observed (Rook et al., 1977; Sommerfeldt et al., 1979; Block et al., 1981).

There was trend for a DMI level × hybrid interaction ($P < 0.15$) for total VFA concentration, and there was a DMI level × hybrid interaction ($P < 0.10$) for molar proportions of butyrate (Table 2-5). Steers with ad libitum access to BMCS had the highest ($P < 0.05$) concentration of total VFA compared with those fed the other three treatments. Total VFA were higher ($P < 0.05$) for ad libitum-fed Control steers than for limit-fed Control steers. There was a hybrid effect ($P < 0.001$) for molar proportions of acetate, and feeding BMCS at both DMI levels resulted in increased proportions of acetate. Feeding BMCS did not affect ($P < 0.20$) molar proportions of propionate. When bm_3 silage was fed to lactating dairy cows in rations containing 65% corn silage, Block et

al. (1981) observed an increase in molar proportion of propionate and a decrease in acetate. Rook et al. (1977) reported no difference in molar proportions of either acetate or propionate between bm_3 and isogenic normal when a 60% corn silage diet was fed to lactating dairy cows. When the percentage of corn silage was 85%, Rook et al. (1977) did observe increases in molar proportions of both acetate and propionate for bm_3.

Restricting DMI resulted in a reduction ($P < 0.01$) in total VFA concentration but increased ($P < 0.01$) molar proportions of acetate. Feeding both corn silage diets ad libitum resulted in a higher ($P < 0.05$) proportion of propionate. Rumsey et al. (1970) observed that increasing DMI from 0.5 to 2% of body weight for diets containing either all-concentrate or 88% hay resulted in increased concentration of total VFA, increased molar proportion of propionate, and decreased molar proportion of acetate. Galyean et al. (1979) also reported that feeding an 84% concentrate diet at increasing levels from one to two times maintenance tended to increase propionate and decrease acetate proportions. Total VFA concentration and molar percentages of acetate, propionate and butyrate over time, for this trial, are presented in APPENDIX A (Figures A-1 to A-4, respectively).

Trial 2

Feeding BMCS compared with Control silage during the 112-d growth phase resulted in a 0.43-kg increase in daily DMI (Table 2-6). The increase in DMI for steers receiving BMCS was consistent with the digestion trial data. Keith et al. (1981) also observed an increase (0.47 kg/d) in DMI when bm_3 was compared with isogenic normal corn silage fed to steers. When bm_3 was compared to isogenic normal in diets fed to lactating dairy cows, increases in DMI ranged from 3 to 9% (Sommerfeldt et al., 1979;

65

Stallings et al., 1982; Oba and Allen, 1999). Although there were improvements in fiber

and energy digestibility when fistulated steers received BMCS in Trial 1, ADG of feedlot

steers in Trial 2 was not influenced ($P > 0.20$) by hybrid. In addition, hybrid did not affect

($P > 0.20$) change in s.c. fat thickness or longissimus muscle area (0.20 vs 0.20 cm, and

17.6 vs 18.1 cm^2 for Control and BMCS, respectively). Based on energy concentration of

the diets from Trial 1 and DMI and BW from Trial 2, shrunk weight gain was predicted

(NRC, 1996) to be 0.13 kg/d greater for steers with ad libitum access to BMCS than for

Control steers. A possible explanation for the absence of observed ADG response in Trial

2 could be an increase in passage rate and a reduction in digestion rate of NDF for BMCS

by increasing DMI, as suggested by results in Trial 1. Steers in Trial 2 consumed 26%

more DM as a percentage of BW compared with cannulated steers in Trial 1 that had ad

libitum access to feed. This greater DMI in Trial 2 could have further increased passage

rate of BMCS and depressed DM digestion of BMCS, resulting in similar digestible DM

intake for both treatments. Oba and Allen (1999) observed that a large increase in DMI

resulted in lower digestibility of DM for *bm*₃ relative to isogenic normal corn silage. In the

current research, the increase in DMI and no change in ADG resulted in steers fed BMCS

having poorer ($P < 0.01$) feed efficiency. Keith et al. (1981) observed improvements in

ADG of steers fed *bm*₃ compared with isogenic normal but did not observe differences in

feed conversion. When steers were fed a 92% corn silage diet containing *bm*₃ compared

to diets using a variety of commercial hybrids, ADG was increased (McEwen et al., 1996).

McEwen et al. (1996) also reported that feeding a *bm*₃ corn silage diet resulted in

increased feed efficiency compared with diets containing corn silage from commercial

hybrids.

Average daily gain, daily DMI, and gain efficiency during the finishing phase and for the entire feeding period were not different ($P > 0.05$) between steers that had either received Control silage or BMCS during the growing period (Table 2-6). Consistent with there being no difference in ADG over the entire feeding period, there was no difference ($P > 0.10$) in final weight between the two treatments (Table 2-6). In addition, hot carcass weight, dressing percentage, s.c. fat thickness, longissimus muscle area, percentage of kidney-pelvic-heart fat, and marbling score were not significantly different between BMCS and Control steers (data not shown).

Implications

Although brown midrib-3 corn silage resulted in increased feed intake and improved digestibility of fiber, and was predicted to improve daily gains by 0.13 kg/d, no improvement in average daily gain was observed in the performance trial. In addition, poorer feed efficiency was observed for steers receiving brown midrib-3 corn silage in this trial. Reasons for the discrepancy between predicted and actual daily gains are not known and further research is warranted. Restricting feed intake may further improve fiber digestibility of brown midrib-3 corn silage. Knowledge gained from additional trials will be necessary for feedlot managers to make informed decisions on potential advantages or disadvantages of producing and feeding brown midrib corn silage.

Tables and Figures

Table 2-1. Post-ensiled nutrient composition and fermentation characteristics of isogenic normal and brown midrib-3 (bm_3) corn hybrids

	Corn hybrid	
Item	Isogenic normal	bm_3
Nutrient composition	----------------------- % in silage DM ----------------------	
DM	29.8	35.2
OM	96.3	96.6
CP	7.06	7.03
Starch	37.5	43.8
NDF[a]	44.0	39.5
ADF[a]	29.3	22.4
ADL[a]	3.68	1.78
Fermentation characteristics		
pH	3.66	3.79
Acetate, g/100 g DM	2.98	2.27
Propionate, g/100 g DM	0.37	1.00
Lactate, g/100 g DM	13.0	8.73

[a]Corrected for ash.

Table 2-2. Ingredient and nutrient composition of isogenic normal control (Control) and brown midrib-3 (BMCS) corn silage diets fed during the growing and finishing phases

Item	Growing diet[a]		Finishing diet
	Control	BMCS	
Ingredient composition, % in diet DM			
Isogenic corn silage	86.3	–	15.0
Brown midrib corn silage	–	86.3	–
Soybean meal, 44% CP	10.38	10.38	6.25
Cracked high-moisture corn	–	–	76.2
Ground shelled corn	0.21	0.21	0.17
Trace-mineralized salt[b]	0.64	0.64	0.5
Urea	0.47	0.47	0.37
Potassium chloride	0.36	0.36	0.28
Selenium 90[c]	0.07	0.07	0.05
Vitamin A[d]	0.01	0.01	0.01
Rumensin 80[e]	0.02	0.02	0.02
Dicalcium phosphate	0.14	0.14	0.11
Calcium carbonate	1.41	1.41	1.11
Nutrient composition, % in diet DM			
DM	35.6	43.2	64.6
OM	93.9	94.2	96.3
CP	12.9	12.9	12.7
NDF[f]	39.4	35.5	13.9
ADF[f]	26.4	20.4	7.1
ADL[f]	3.24	1.60	.95
Starch	33.6	39.0	53.7

[a]Control = isogenic normal corn silage diet; BMCS = brown midrib-3 corn silage diet.

[b]Composition (%): NaCl, 96-98.5; Zn, >0.35; Mn, >0.2; Fe, >0.2; Cu, >0.03; I, >0.007; Co, >0.005.

[c]Composition (%): Ca, >28.5; Se, 0.02.

[d]Contains 30,000 IU of vitamin A per gram.

[e]Contains 176 g of monensin per kg.

[f]Corrected for ash.

69

Table 2-3. Dry matter intake, fecal output, apparent total-tract digestibility, and energy concentration of isogenic normal control (Control) and brown midrib-3 (BMCS) corn silage diets offered ad libitum or 80% of ad libitum to steers (Trial 1)

Item	Ad Libitum		Limited			Effect,[b] P-value		
	Control	BMCS	Control	BMCS	SEM[a]	I	H	I × H
n	8	7	8	8				
DMI, kg/d	4.44	5.06	3.49	3.50	0.214	<0.01	<0.01	<0.01
Fecal output, kg/d	1.32	1.38	1.14	0.96	0.058	<0.01	0.23	<0.01
Apparent total-tract digestibility								
DM, %	70.4	73.1	67.4	72.7	1.29	0.29	0.02	0.33
OM, % DM	72.5	74.9	69.7	74.9	1.22	0.38	0.02	0.28
NDF, % DM	53.1	63.6	49.5	65.3	2.12	0.69	<0.01	0.16
ADF, % DM	56.1	65.5	52.1	67.5	2.04	0.69	<0.01	0.12
Starch, % DM	89.1	88.2	86.8	88.0	1.06	0.23	0.89	0.31
GE digestibility, %	72.1	74.1	70.7	74.0	1.22	0.58	0.07	0.61
DE intake, Mcal/d	13.7	15.6	10.5	10.9	0.79	<0.01	0.04	0.10
Energy concentration of diets[c]								
ME, Mcal/kg DM	2.53	2.55	2.48	2.55	0.042	0.72	0.42	0.61
NE_m, Mcal/kg DM	1.63	1.65	1.58	1.65	0.037	0.73	0.41	0.63
NE_g, Mcal/kg DM	1.02	1.04	0.983	1.04	0.033	0.73	0.42	0.64

[a]Standard error of the least squares mean.
[b]I = DMI main effect; H = hybrid main effect; I × H = DMI × hybrid interaction.
[c]Calculated from DE using NRC (1996) equations.

Table 2-4. Ruminal digesta characteristics and kinetics for steers receiving isogenic normal control (Control) and brown midrib-3 (BMCS) corn silage diets offered ad libitum or 80% of ad libitum (Trial 1)

| Item | Ad Libitum | | Limited | | | Effect,[b] P-value | | |
	Control	BMCS	Control	BMCS	SEM[a]	I	H	I × H
n	16	14	16	16				
DM, % at 57°C	11.85	12.46	11.06	11.33	0.432	<0.01	0.15	0.58
DM, kg	2.68	2.82	2.35	2.17	0.208	<0.01	0.86	0.09
Ruminal digesta volume, L	27.2	28.3	25.3	23.5	2.2	<0.01	0.66	0.07
Ruminal digesta density, kg/L	0.857	0.826	0.878	0.851	0.011	0.02	<0.01	0.83
Ruminal NDF, % DM	59.5	57.2	61.0	53.9	0.88	0.29	<0.01	<0.01
Ruminal NDF turnover time, h	23.8	21.8	27.6	22.5	0.97	<0.01	<0.01	0.05
k_p, %/h[c]	3.16	3.50	2.79	2.92	0.239	0.01	0.20	0.57

[a]Standard error of the least squares mean.
[b]I = DMI main effect; H = hybrid main effect; I × H = DMI × hybrid interaction.
[c]Ruminal passage rate of indigestible NDF.

Table 2-5. Ruminal VFA concentration for steers receiving isogenic normal control (Control) and brown midrib-3 (BMCS) corn silage diets offered ad libitum or 80% of ad libitum (Trial 1)

| Item | Ad Libitum | | Limited | | | Effect,[b] P-value | | |
	Control	BMCS	Control	BMCS	SEM[a]	I	H	I × H
n	192	168	192	192				
Total VFA, mM	105	108	103	103	2.1	<0.01	0.02	0.15
VFA, mol/100 mol								
Acetate	62.7	64.5	65.4	66.2	0.45	<0.01	<0.01	0.30
Propionate	20.8	20.7	19.9	19.4	0.58	0.04	0.53	0.61
Butyrate	11.5	9.8	10.0	9.7	0.43	0.03	<0.01	0.06
Valerate	0.53	1.07	0.51	1.10	0.07	0.95	<0.01	0.66
Branched chain[c]	3.06	2.74	3.04	2.61	0.14	0.56	0.01	0.64
Acetate:Propionate	3.10	3.17	3.37	3.49	0.11	0.01	0.32	0.77

[a]Standard error of the least squares mean.
[b]I = DMI main effect; H = hybrid main effect; I × H = DMI × hybrid interaction.
[c]Isobutyrate and isovalerate.

Table 2-6. Performance for steers receiving isogenic normal control (Control) and brown midrib-3 mutation (BMCS) corn silage based diets for 112 d (Trial 2)

Items	Control	BMCS	SEM[a]	P-value
No. of pens	8	8		
Initial wt, kg	244	246	0.06	0.15
Growing period				
112-d wt, kg	359	359	2.01	0.90
ADG, kg	1.02	1.01	0.02	0.55
DMI, kg/d	7.04	7.47	0.12	0.04
Gain:Feed	0.145	0.135	0.001	<0.01
Subsequent finishing period				
Final wt, kg	509	516	3.52	0.17
ADG, kg	1.72	1.80	0.02	0.06
DMI, kg/d	9.98	10.08	0.10	0.49
Gain:Feed	0.172	0.179	0.004	0.23
Growing and finishing period				
ADG, kg	1.33	1.35	0.01	0.23
DMI, kg/d	8.35	8.63	0.08	0.06
Gain:Feed	0.159	0.157	0.002	0.52

[a]Standard error of the mean.
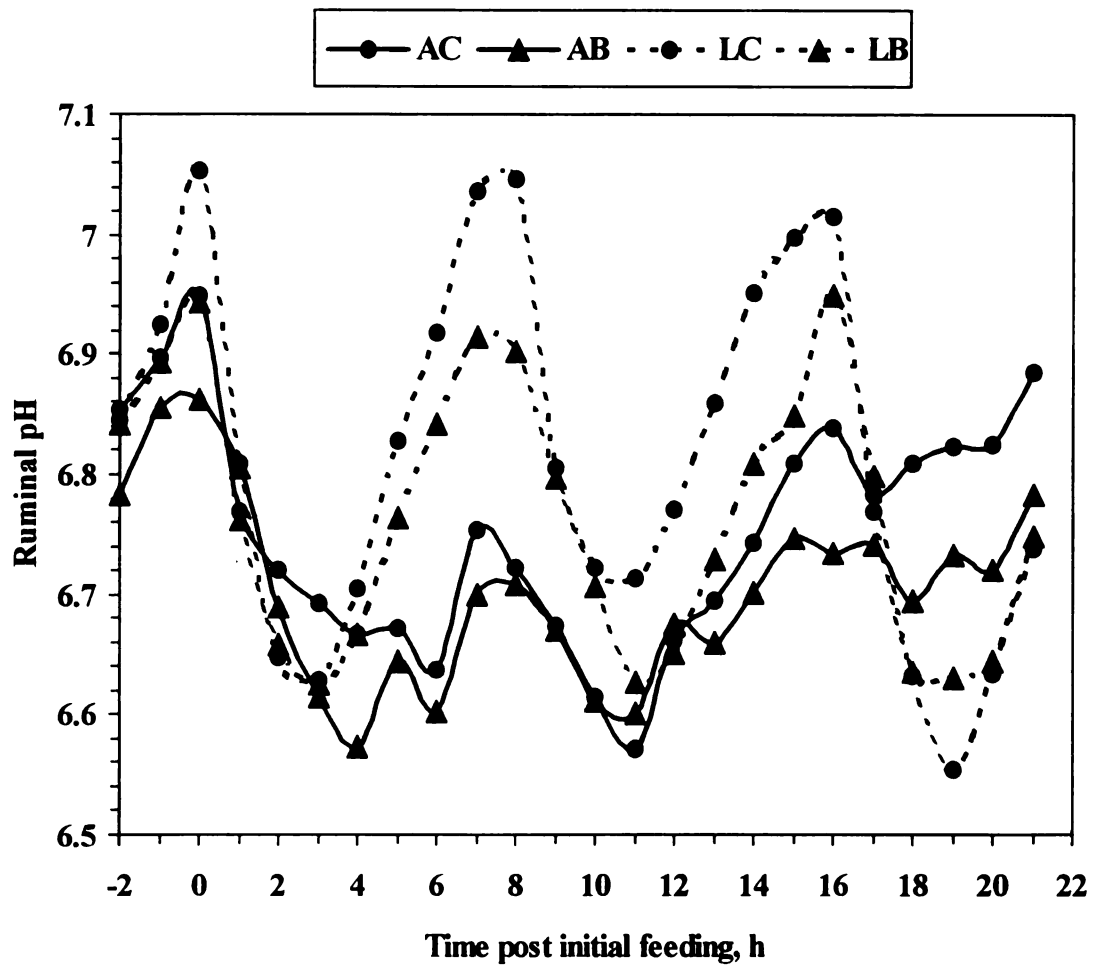
Figure 2-1. Effects of feeding ad libitum isogenic normal control (AC), ad libitum brown midrib-3 (AB), limited isogenic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on ruminal pH over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × DMI interaction ($P < 0.001$). SEM = 0.065.
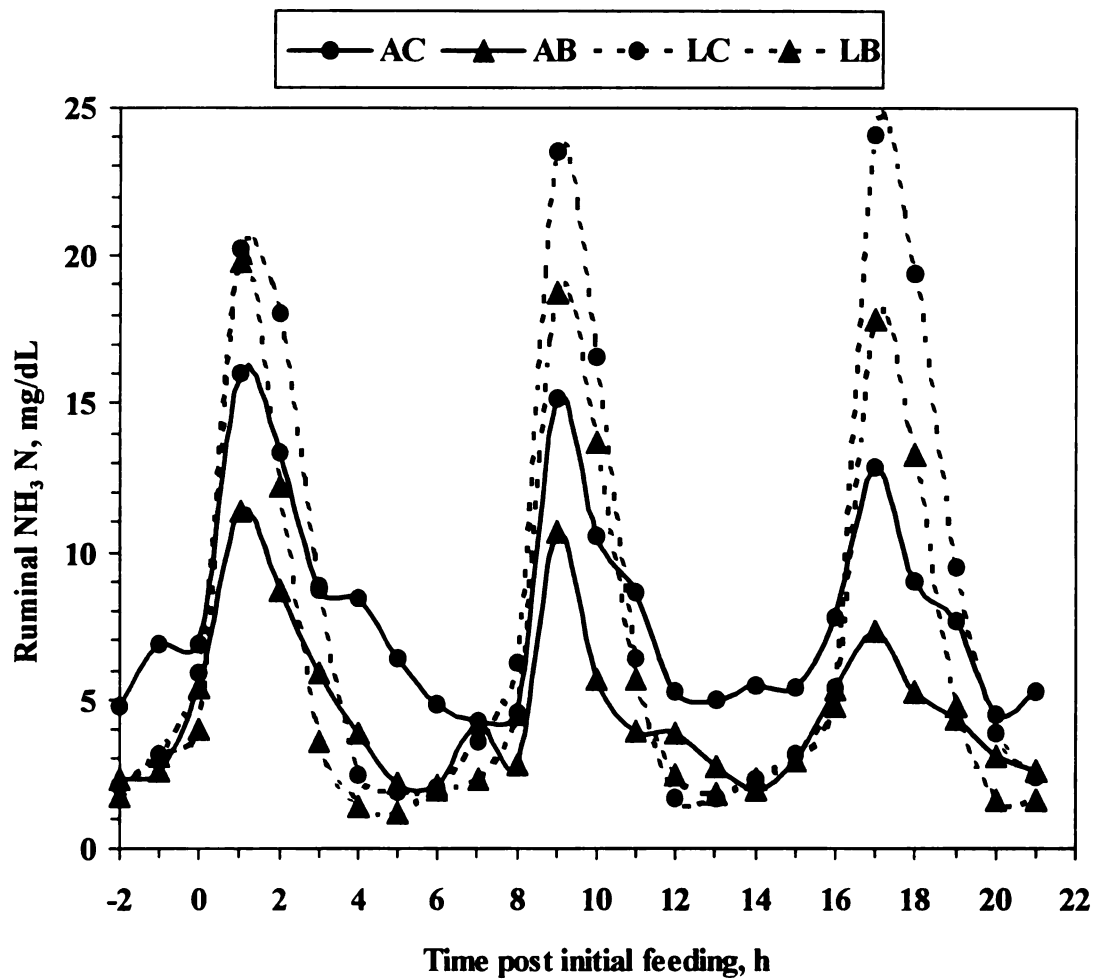
Figure 2-2. Effects of feeding ad libitum isogenic normal control (AC), ad libitum brown midrib-3 (AB), limited isogenic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on ruminal NH_3 N over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × DMI × hybrid interaction ($P < 0.05$). SEM = 1.13.

Literature Cited

Allen, M. S., M. Oba, D. Storck, and J. F. Beck. 1997. Effect of brown midrib 3 gene on forage quality and yield of corn hybrids. J. Dairy Sci. 80(Suppl. 1):157(Abstr.).

AOAC. 1984. Official Methods of Analysis. 14th ed. Association of Official Analytical Chemists, Washington, DC.

Block, E., L. D. Muller, L. C. Griel, Jr., and D. L. Garwood. 1981. Brown midrib-3-corn silage and heat extruded soybeans for early lactating dairy cows. J. Dairy Sci. 64:1813-1825.

Chaney, A. L., and E. P. Marbach. 1962. Modified reagents for determination of urea and ammonia. Clin. Chem. 8:130-132.

Colucci, P. E., G. K. Macleod, W. L. Grovum, L. W. Cahill, and I. McMillan. 1989. Comparative digestion in sheep and cattle fed different forage to concentrate ratios at high and low intakes. J. Dairy Sci. 72:1774-1785.

Dado, R. G., and M. S. Allen. 1995. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk. J. Dairy Sci. 78:118-133.

Galyean, M. L., D. G. Wagner, and F. N. Owens. 1979. Level of feed intake and site and extent of digestion of high concentrate diets by steers. J. Anim. Sci. 49:199-203.

Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agric. Handbook No. 379. ARS-USDA, Washington, DC.

Karkalas, J. 1985. An improved enzymatic method for the determination of native and modified starch. J. Sci. Food Agric. 36:1019-1027.

Keith, E. A., V. F. Colenbrander, T. W. Perry, and L. F. Bauman. 1981. Performance of feedlot cattle fed brown midrib-three or normal corn silage with various levels of additional corn grain. J. Anim. Sci. 52:8-13.

Kuc, J., and O. E. Nelson. 1964. The abnormal lignins produced by the *brown-midrib* mutants of maize. Arch. Biochem. Biophys. 105:103-113.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76:1216-1231.

McEwen, P. L., J. G. Buchanan-Smith, and M. G. Cameron. 1996. The influence of corn silage hybrid variety on beef steer growth performance. Ontario Beef Res. Update Univ of Guelph. pp43-48

Miller, J. E., and J. I. Geadelmann. 1983. Effect of the brown midrib-3 allele on early vigor and growth rate of maize. Crop Sci. 23:510-513.

Miller, J. E., J. L. Geadelmann, and G. C. Marten. 1983. Effect of the brown midrib-allele on maize silage quality and yield. Crop Sci. 23:493-496.

Muller, L. D., V. L. Lechtenberg, L. F. Bauman, R. F. Barnes, and C. L. Rhykerd. 1972. In vivo evaluation of a brown midrib mutant of *Zea mays L.* J. Anim. Sci. 35:883-889.

Murphy, T. A., S. C. Loerch, and B. A. Dehority. 1994. The influence of restricted feeding on site and extent of digestion and flow nitrogenous compounds to the duodenum in steers. J. Anim. Sci. 72:2487-2496.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. National Academy Press, Washington, DC.

Oba, M., and M. S. Allen. 1999. Effects of brown midrib 3 mutation in corn silage on dry matter intake and productivity of high yielding dairy cows. J. Dairy Sci. 82:135-142.

Oba, M., and M. S. Allen. 2000. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 3. Digestibility and microbial efficiency. J. Dairy Sci. 83:1350-1358.

Ritchie, H., R. Black, A. Booren, L. Copeland, J. Ferris, J. Lloyd, T. Louden, H. Person, and S. Rust. 1992. Type of Farming Systems Study: Beef feedlot survey. Agric. Exp. Station Res. Rep. 522. Michigan State University, East Lansing, MI.

Rook, J. A., L. D. Muller, and D. B. Shank. 1977. Intake and digestibility of brown-midrib corn silage by lactating dairy cows. J. Dairy Sci. 60:1894-1904.

Rumsey, T. S., P. A. Putnam, J. Bond, and R. R. Oltjen. 1970. Influence of level and type of diet on ruminal pH and VFA, respiratory rate and EKG patterns of steers. J. Anim. Sci. 31:608-616.

SAS. 1996. SAS/STAT User's Guide (Release 6.12). SAS Inst. Inc., Cary, NC.

Sommerfeldt, J. L., D. J. Schingoethe, and L. D. Muller. 1979. Brown-midrib corn silage for lactating dairy cows. J. Dairy Sci. 62:1611-1618.

Stallings, C. C., B. M. Donaldson, J. W. Thomas, and E. C. Rossman. 1982. In vivo evaluation of brown-midrib corn silage by sheep and lactating dairy cows. J. Dairy Sci. 65:1945-1949.

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods of dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74:3583-3597.

Waldo, D. R., L. W. Smith, and E. L. Cox. 1972. Model of cellulose disappearance from the rumen. J. Dairy Sci. 55:125-129.

Weller, R. F., R. H. Phipps, and A. Cooper. 1985. The effect of the brown midrib-3 gene on the maturity and yield of forage maize. Grass Forage Sci. 40:335-339.

CHAPTER 3

Neutral Detergent Fiber Concentration of Corn Silage and Rumen Inert Bulk Influences Dry Matter Intake and Ruminal Digesta Kinetics of Growing Steers

Abstract

The concentration of NDF in corn silage ranges from less than 35% to over 55%. Corn silage with high NDF concentration has the potential to reduce DMI because it has a greater filling effect in the rumen than low NDF corn silage. Our objective was to determine if high NDF corn silage-based diets limit intake of light-weight growing steers by challenging them with ruminal fill. Eight ruminally cannulated Holstein steers (198 ± 13 kg) were randomly assigned to a 2 × 2 factorial arrangement of treatments in a replicated 4 × 4 Latin square design with 16-d periods. Treatments were diets containing corn silage from a normal hybrid (low-fiber; **LF**) or its male-sterile isogenic counterpart (high-fiber; **HF**), offered ad libitum to steers with or without rumen inert bulk (**RIB**). The LF and HF diets contained 33.8 and 50.8% dietary NDF, respectively. Rumen inert bulk was added at 25% of pretrial ruminal volume in the form of plastic-coated tennis balls filled with sand to achieve a specific gravity of 1.1 (7.5 L). No fiber level × inert bulk interactions were detected for DMI or NDF intake ($P > 0.10$) suggesting that DMI was limited by physical fill at both levels of dietary fiber. Addition of RIB decreased DMI by an average of 10.7%, which was 65.5 g/L of added bulk. The HF treatment depressed DMI by an average of 15.5%, increased NDF intake 27.1%, and reduced ruminal NDF turnover time by 21.0% compared to LF ($P < 0.001$) with no effect on ruminal volume or amount of NDF in the rumen ($P > 0.10$). Addition of RIB also reduced ruminal NDF turnover time and amount of NDF in the rumen (11.8% and 20.7%, respectively; $P < 0.001$) with no change in ruminal digesta volume ($P > 0.10$). The HF treatment decreased

79

digestibility of DM and GE (5.5 and 5.7%, respectively; $P < 0.001$), but increased NDF

digestibility (10.4%; $P < 0.001$) compared to LF. Rumen inert bulk had no effect on

digestibility of DM, NDF, or GE ($P > 0.10$). Results from this trial suggest that DMI of

light-weight steers receiving corn-silage based diets within a wide range of NDF

concentration might be regulated by ruminal distension and metabolic signals to maintain

the balance between satiety and hunger.

Introduction

Distension in the gastrointestinal tract can limit voluntary DMI of ruminant animals

(Baile and Forbes, 1974; Forbes, 1996). Previous researchers have examined the effect of

reticulo-rumen fill on DMI by adding rumen inert bulk (**RIB**) to sheep (Egan, 1972;

Waybright and Varga, 1991), steers (Carr and Jacobson, 1967; Schettini et al., 1999), and

lactating dairy cows (Campling and Balch, 1961; Johnson and Combs, 1991, 1992; Dado

and Allen, 1996). A review of several studies by Dado (1993) indicated that the average

reduction in DMI, from RIB addition, was 94 g/L of RIB, and ranged from no change to a

depression in DMI of 300 g/L. The depression in intake was greatest for a) sheep, b)

animals with relatively lighter body weight within a species, and c) animals that tended to

be in physiological states with higher nutrient requirements (Dado, 1993).

Neutral detergent fiber is a measure of total insoluble fiber, and is related to the

filling effects of feeds in the rumen. Increasing the dietary NDF concentration, by

increasing roughage to concentrate ratio, depressed DMI of sheep (Aitchison et al., 1986)

and dairy cows (Llamas-Lamas and Combs, 1991; Dado and Allen, 1995). Increasing

dietary NDF concentration by addition of straw also reduced DMI and performance of steers (Orskov et al., 1988, 1991).

High levels of roughage are often fed during the growth phase of beef cattle feeding systems in the upper Midwest, and corn silage is the primary roughage source (Ritchie et al., 1992). Fiber concentration of corn silage can vary greatly; the average NDF for well-eared corn silage is 46.0% with a standard deviation of 6.5% (NRC, 1996). We hypothesized that corn silage high in NDF concentration limits DMI and animal performance of light-weight steers fed high roughage diets. Therefore, the objective of this trial was to determine if high NDF corn silage limits DMI by increasing ruminal fill.

Materials And Methods

A corn hybrid (5456, UAP Dyna-Gro, East Lansing, MI) and its male-sterile isogenic counterpart were planted in separate fields on the same day to achieve a population of approximately 66,700 plants/ha. The male-sterile hybrid was isolated from all other corn hybrids to prevent pollination. As the corn approached maturity, DM for each hybrid was determined every third day to estimate the desired time of harvest. The normal and male-sterile corn hybrids were harvested with a three-row silage chopper (Model 900, New Holland North America Inc., New Holland, PA) set at 1.3 cm theoretical cut length, and ensiled separately in adjacent 2.4-m dia. plastic silage bags (Ag Bag International, Warrenton, OR) at the Michigan State University Beef Cattle Teaching and Research Center. Before feeding, forages were analyzed for DM, NDF, CP, pH, and VFA. Post-ensiled nutrient composition and fermentation characteristics of the silages are presented in Table 3-1.

Experimental and surgical procedures in this trial were conducted according to those approved by the Michigan State University All University Committee on Animal Use and Care (AUF No. 07/99-089-00).

Eight Holstein steers (198 ± 13 kg) were surgically fitted with 7.5-cm i.d. rumen cannulas (Model 4C, Bar Diamond Inc., Parma, ID) 4 weeks before trial initiation. Eight days after surgery, cannulas were replaced with 10-cm i.d. rumen cannulas (Model 2C, Bar Diamond Inc.). At this time, steers were weighed and moved to individual metabolism stalls for acclimation for 14 days. Steers had ad libitum access to water and a common corn silage diet (Table 3-2). Corn silage from the normal (low-fiber) corn hybrid was the primary dietary ingredient, with soybean meal and supplement added to meet or exceed requirements for metabolizable protein, minerals, and vitamins (NRC, 1996). Feed offered and refused were recorded daily.

The eight fistulated steers were assigned to duplicated 4 × 4 Latin squares balanced for carryover effects with a 2 × 2 factorial arrangement of treatments. Steers were randomly assigned to treatment sequences within square. Factors evaluated were dietary NDF content and amount of rumen inert bulk. Concentrations of NDF in the diets were 33.8% (low-fiber; **LF**) or 50.8% (high-fiber; **HF**). The amount of RIB was 0 or 25% of the average pretrial ruminal digesta volume. Pretrial ruminal digesta volume was measured by manual evacuation of digesta. Rumen inert bulk consisted of 52 plastic-coated tennis balls (7.5 L; 1.1 specific gravity; Schettini et al., 1999). Treatment periods were 16 d, with 10 d for adaptation and the final 6 d for collection.

Diets were mixed once daily and offered at 0700 and 1900 daily to allow steers ad libitum access (≥ 10% orts) to the total mixed ration. Amounts fed and refused were

recorded daily. Representative samples of complete mixed diets, individual ingredients, and orts were taken at each feeding on d 10 through 16 of each period.

Fecal output was determined using total fecal collection for 4 d each period. Fecal collection bags were placed on each fistulated steer at 1300 on collection days starting on d 11. Accumulated feces were removed, weighed at each 24-h interval for the 4 d, and a 0.5 kg representative sample was retained.

Four subsamples of whole ruminal contents from representative areas of the rumen were collected and composited every 3 h for a 24-h period starting before morning feeding on d 11. Ruminal fluid was separated from the particulate fraction by squeezing through four layers of cheesecloth. Ruminal pH was determined immediately after collection. A 45-mL aliquot of fluid was frozen immediately at $-20°C$ for later analysis of ruminal VFA.

Total ruminal contents were removed at 1300 on d 15 and 16 of each period. Each animal's digesta was manually removed via the cannula and placed in a 114-L barrel. Weight and volume of the rumen contents were determined, and a 1-kg subsample was collected before replacing digesta. Immediately before digesta removal, headspace volume in the dorsal rumen was estimated at both evacuation times by filling the space with unweighted tennis balls of known volume. Following the evacuation on d 16, ruminal contents including RIB were switched among steers, within each square, to assist in adaptation to the next treatment.

Sample Analysis

Diets, individual ingredients, orts, ruminal contents, and fecal samples were dried immediately after collection at 57°C for 72 h in a forced-air oven and analyzed for DM

content. All samples were ground through a Wiley mill (Arthur H. Thomas, Philadelphia, PA) equipped with a 1-mm screen. Samples of the diets and dietary ingredients were composited for each period, and fecal samples were composited for each animal within period. Diets, individual ingredients, fecal, and ruminal content samples were analyzed for percentages of NDF, ADF, ADL, indigestible NDF, and ash. Neutral detergent fiber, ADF, and ADL were determined according to Van Soest et al. (1991; Method A for NDF) and corrected for ash. Ash content was determined after 5 h of oxidation at 500°C in a muffle furnace. Diet and individual ingredient samples were analyzed for CP by the combustion method (AOAC, 1990; Model FP-2000, LECO, St. Joseph, MI). Free glucose in the diets and feed ingredients was measured by an enzymatic method (Karkalas, 1985; glucose kit #510-A, Sigma Diagnostics Inc., St. Louis, MO) using a microplate reader (Spectra Max 190, Molecular Device Corp., Sunnyvale CA) after samples were extracted with deionized water. Starch in the diets, feed ingredients, and feces were measured by an enzymatic method (Karkalas, 1985; glucose kit #510-A) after samples were gelatinized with sodium hydroxide and digested with amylase (CRYSTALZYME 40 L, Vally Research Inc., South Bend, IN). Gross energy was determined for both feed and fecal samples by bomb calorimetry (AOAC, 1990; Model 1241 Adiabatic Calorimeter, Parr Instruments, Moline, IL). Digestible energy was determined as the difference between intake of diet gross energy and output of fecal gross energy. Concentrations of ME, NE_m, and NE_g in the diets were calculated from DE using published equations (NRC, 1996). Ruminal VFA, silage VFA, ruminal NDF turnover time, and passage rate of indigestible NDF were determined according to procedures described by Tjardes et al.

(2000). The concentrations of all nutrients were expressed as percentage of DM

determined from drying at 57°C.

Statistical Analysis

Intake, digestibility, VFA, digesta characteristics, and kinetic data were analyzed

based on a mixed effects model using MIXED procedure of SAS (SAS Inst. Inc., Cary,

N.C.). The model contained animal as a random effect and period, fiber level, RIB, and

fiber level × RIB as fixed effects. Using the Schwarz Bayesian criterion (Littell et al.,

1998), a first-order autoregressive error structure was determined as the most appropriate

residual covariance structure for repeated measures over period within animals. Main

effects were considered significant at $P < 0.05$ and two-way interactions were considered

significant at $P < 0.10$. One steer that had access to the high fiber diet with additional RIB

would not consume the expected DMI of feed before collection. Therefore, data were

omitted for this steer during that period. Due to the unbalanced design, data are presented

as least squares means.

Results And Discussion

Normal and male-sterile hybrids were harvested 127 d following planting. At time

of harvest, the male-sterile hybrid had 4.8% less DM than the normal hybrid (31.5 vs

36.3% DM, respectively). The DM of silage from the male-sterile hybrid was 5.7% lower

after ensiling (Table 3-1). Stake et al. (1973) reported that the male-sterile corn silage

contained 2.0% less DM even when the male-sterile corn hybrid was harvested one week

after a regular dent corn hybrid. Perry and Caldwell, (1969) harvested a male-sterile corn

hybrid one month after a typical dent corn hybrid and observed that the male-sterile corn silage contained 13.2% less DM. Neither trial reported if the male-sterile and normal corn hybrids were of similar genetics or if the hybrids required a similar number of growing degree days for maturation.

Since the male-sterile corn hybrid was barren and devoid of grain, the male-sterile as compared to normal corn silage had lower starch (3.3 vs 32.0%, respectively) but greater NDF and ADF concentration (Table 3-1). The male-sterile corn silage contained 0.7% less CP than normal. Stake et al. (1973) observed no difference in crude fiber value between normal and male-sterile hybrids, however, the male-sterile contained 2.4% greater CP. Perry and Caldwell (1969) reported that both crude fiber and CP were higher for male-sterile when compared to normal (30.3 vs 21.3%, and 10.9 vs 8.4%, for crude fiber and CP, respectively).

Total soluble carbohydrate content of male-sterile corn hybrids ranges from 15 to 16% as compared to 8 to 10% for normal corn hybrids (Fisher and Fairey, 1979). During the ensiling process, the soluble carbohydrates would have been readily fermented (Stake et al., 1973). Stake et al. (1973) reported that the soluble carbohydrates would have been transformed to lactic acid, however, they failed to report if the ethanol content of male-sterile corn silage increased during fermentation. In the current study, the male-sterile corn silage had greater concentrations of acetate, propionate, lactate, and ethanol as compared to the normal corn silage (0.6, 0.3, 2.2, and 7.0%, respectively). The higher concentration of fermentation acids resulted in the male-sterile corn silage having 0.15 unit lower pH compared to the normal corn silage. Since the male-sterile corn silage contained a greater concentration of ethanol, steers receiving HF would have consumed up to 350

mL of ethanol over the entire day. No adverse signs related to ethanol ingestion were observed among steers. Previous research has shown that steers weighing 227 kg were able to tolerate 140 mL of ethanol pulse dosed into the rumen, however, they exhibited signs of intoxication when they received a pulse dose of 250 mL (Bruning and Yokoyama, 1988).

Feeding HF compared to LF resulted in an average reduction in steer DMI of 0.7 kg/d ($P < 0.001$; Table 3-3). Previous research has demonstrated that increased dietary NDF by straw addition, decreased DMI of steers (Reid et al., 1988; Orskov et al., 1991). Stake (1973) reported that steers consumed similar intakes of male-sterile and normal corn silage when they were receiving 1.81 kg/d of a protein/grain supplement and there was no difference in the crude fiber values between the two hybrids.

Addition of RIB depressed DMI of both LF and HF diets an average of 65 g/L of RIB ($P < 0.001$). Schettini et al. (1999) reported a reduction of 157 g/L of RIB when low quality orchard grass hay (70.3% NDF) was fed to beef steers with an initial weight of 550 kg. Mowat (1963) reported a reduction of up to 112 g/L of RIB when good quality hay (37.8% NDF) was fed to Holstein steers with an initial weight of 227 kg. Dado and Allen (1995) reported that DMI of a 25% NDF diet fed to early lactation dairy cows (17 d postpartum) was not affected by RIB addition, however, DMI of a 35% NDF diet was depressed by 95 g/L of RIB. They concluded that DMI of cows receiving the high fiber diet was under greater control by ruminal distension (Dado and Allen, 1995). In the current study, the fact that RIB decreased DMI in both diets and the lack of a fiber level × RIB interaction suggests that DMI was limited by physical fill at both levels of dietary fiber.

Increasing concentration of dietary fiber did not affect ruminal digesta volume or wet digesta weight ($P > 0.10$), but decreased digesta DM percentage and weight ($P < 0.05$; Table 3-3). Feeding HF compared to LF increased the concentration of NDF and indigestible NDF of the ruminal digesta ($P < 0.001$), however, amount of both NDF and indigestible NDF in the rumen was not affected by fiber treatments ($P > 0.10$). Johnson and Combs (1992) and Dado and Allen (1995), found that with early lactating dairy cows, increasing dietary NDF concentration increased digesta volume and wet weight, decreased digesta DM percentage, resulting in no effect on weight of digesta DM. They also reported an increase in ruminal NDF weight when concentration of dietary NDF was increased (Johnson and Combs, 1992; Dado and Allen, 1995). In these previous studies with early lactation dairy cows, DMI of the low NDF diets was likely not regulated by ruminal distension. When dietary NDF concentration was increased, the digesta volume was increased and ruminal fill began to limit DMI. In the current study, digesta volume was not increased when the dietary NDF concentration was increased, suggesting that DMI was limited by ruminal distension at both levels of dietary fiber.

Addition of RIB to both LF and HF, increased total ruminal volume (digesta + RIB) by 23.2% ($P < 0.01$), but did not influence digesta volume ($P > 0.10$; Table 3-3). The addition of RIB, increased wet weight of digesta + RIB ($P < 0.01$), but had no effect on wet digesta weight alone ($P > 0.10$). Dado and Allen (1995) observed that when a diet containing 35% NDF was fed to early lactating dairy cows, RIB added at 25% of pre-trial digesta volume increased total ruminal volume by only 6.2%, but decreased digesta volume by 16.3%. In the same trial, when the diet contained 25% NDF and 25% RIB was added, total ruminal volume was increased by 11.3% and digesta volume was decreased

by 12.1% (Dado and Allen, 1995). Johnson and Combs (1991) found that when 25% RIB reduced DMI of early lactation dairy cows fed diets that contained either 26.1 or 28.5% NDF, total rumen volume increased an average of 15.2% and digesta volume decreased an average of 7.2%. However, Johnson and Combs (1992) found that when 25% RIB did not influence DMI of late lactation dairy cows, total ruminal volume increased 18.0%, but digesta volume was not significantly influenced. Schettini et al. (1999) did not report the effect of RIB on ruminal volume, when beef steers were fed low quality hay (70.3% NDF), however they observed that addition of RIB reduced digesta wet weight. The lack of reduction in digesta volume in the current study, suggest that ruminal distension was not the only factor regulating DMI of the LF and HF diets. The addition of the RIB is expected to have increased stimulation of the tension receptors (Leek, 1969) contributing to satiety. However, the reduction in DMI would have reduced the amount of absorbed metabolic fuels potentially increasing the stimulation of hunger (Illius and Jessop, 1996) and DMI was the result of a balance between hunger and satiety (Forbes and Provenza, 2000).

Addition of RIB reduced the percentages and amounts of digesta DM, NDF, and indigestible NDF ($P < 0.01$; Table 3-3). These reductions are consistent with Dado and Allen (1995) who found that RIB not only reduced percentage DM of digesta, but also reduced the amounts of digesta DM, NDF and indigestible NDF. Johnson and Combs (1991, 1992) also reported that RIB reduced digesta wet weight and decreased amounts of digesta DM and NDF.

Increasing dietary fiber concentration and the addition of RIB both increased ruminal NDF turnover rate ($P < 0.05$). Similar results were observed by Dado and Allen

(1995), who found that with lactating dairy cows, passage rate of NDF was faster when dietary fiber and RIB were increased. They also noted that increasing dietary fiber and the addition of RIB increased the amount of time spent ruminating and chewing. Dado and Allen (1995) reported that these factors likely compensated for the increased rumen fill and helped to maintain intake. In the current study, increased NDF turnover rate and the faster passage rate of indigestible NDF were potentially due to the increased ruminal fill and(or) increased ruminating and chewing. However, RIB weight in the reticulum (Kaske and Midasch, 1997) and(or) RIB stimulation of mechanoreceptors around the cardia (Leek, 1969) may have also contributed to the faster passage rates, because a few of the weighted tennis balls were observed to be in the reticulum during ruminal content evacuation.

Ruminal pH, lactate, and VFA data are presented in Table 3-4. Ruminal pH was decreased and concentrations of lactate and total VFA were increased by feeding LF compared to HF ($P < 0.05$). In addition, molar percentages of propionate and butyrate were greater and acetate was reduced for LF ($P \leq 0.05$). This was likely the result of having greater starch content in the LF diet (Grant and Mertens, 1992b). Stake et al. (1973) reported that ruminal pH was greater, but concentration of total VFA and percentage of acetate were not affected for male-sterile compared to normal corn silage fed to growing Holstein steers.

Fiber level × RIB interactions were detected for total VFA concentration, and molar percentages of acetate and butyrate ($P < 0.10$). Addition of RIB to LF decreased total VFA concentration and butyrate percentage by 10.3 and 18.3%, respectively. Total VFA concentration and butyrate percentage were only decreased by 6.2 and 12.9% when

RIB was added to HF. Molar percentage of acetate was increased by 4.7 and 2.6%, when RIB was added to LF and HF, respectively. There was no fiber level × RIB interaction for molar percentage of propionate ($P > 0.05$). Ruminal VFA concentrations may have been altered by RIB because of increased dilution rate of the ruminal contents, increased rate of VFA absorption from increased mixing in the rumen, and(or) by a more rapid breakdown of fibrous particles. Similar to the current study, Johnson and Combs (1992) and Dado and Allen (1995) found that both the addition of RIB and increasing dietary fiber concentration increased ruminal pH and acetate percentage, but reduced propionate percentage.

Feeding LF as compared to HF not only reduced ruminal pH and resulted in higher molar percentages of propionate, but resulted in more daily variations in pH (Figure 4-1) and percentage of propionate (Figure 4-2). Greater fluctuation in ruminal pH and percentage of propionate might indicate a more pulsatile energy supply to the blood from the rumen. This agrees with Oba and Allen (2000) who reported that the more pulsatile supply of energy may have increased the rate of metabolite utilization which would have stimulated hunger sooner, shortening intermeal interval which would have the potential to increase DMI. However, blood metabolite and feeding behavior data collected concurrently would be necessary to confirm this hypothesis. Total ruminal VFA concentrations, molar percentages of acetate and butyrate over time, for this trial, are presented in APPENDIX B (Figures B-1 to B-3, respectively).

Addition of RIB had no effect on apparent total-tract digestibility of DM, NDF, ADF, starch, or GE ($P > 0.10$; Table 3-5). Previous research with lactating dairy cows (Johnson and Combs 1991, 1992; Dado and Allen 1995) and beef steers (Schettini et al.,

91

1999) also reported that RIB had no effect on apparent total-tract digestibility of DM, NDF, or ADF. Waybright and Varga (1991) did report reductions in total-tract digestibility of DM, NDF and ADF when RIB was added to sheep fed a 75% concentrate diet. In the current study, even though there was no decrease in total-tract digestibility of GE with the addition of RIB, the decrease in DMI resulted in there being an average reduction in DE intake of 1.45 Mcal/d ($P < 0.001$).

The HF compared to the LF treatment had lower apparent total-tract digestibility of DM and GE ($P < 0.001$; Table 3-5), but greater total-tract digestibility of NDF and ADF ($P < 0.01$). The difference in DM and GE digestibility was primarily the result of the male-sterile hybrid having a higher NDF and lower starch content than the normal corn silage. Improved NDF digestibility for the HF treatment was likely the result of improved conditions for fiber-digesting microorganisms within the gastrointestinal tract (Woodford et al., 1986; Grant and Mertens, 1992a, 1992b) as suggested by the greater ruminal pH and percentage of acetate. In previous research, when male-sterile was compared to normal corn silage in diets fed to growing steers, crude fiber digestibility was improved, but digestibility of DM and energy were not influenced (Perry and Caldwell, 1969; Stake et al., 1973). Stake et al. (1973) reported no difference in ADG or efficiency of gain when steers had ad libitum access to either male-sterile or a normal corn hybrid. In the current study, increasing dietary fiber decreased NE_m and NE_g by 17.3 and 28.4%, respectively ($P < 0.001$). Based on energy concentrations, feeding HF as compared to LF reduced predicted shrunk weight gain (NRC, 1996) by 71.7% (0.15 vs 0.53 kg/d for HF and LF, respectively). The HF treatment also had a 67.6% poorer predicted efficiency of gain, when compared to LF.

Illius and Jessop (1996) suggested that voluntary DMI is ultimately a psychological phenomenon, involving the integration of many metabolic signals by the central nervous system. Forbes and Provenza (2000) further theorized that animals integrate signals from the various visceral receptors, adipose tissue, social stimuli, and environmental factors, to generate a signal of total 'discomfort'. The animal then adjusts its DMI in attempt to minimize this discomfort. In the current study, the lack of reduction in digesta volume with a depression in DMI as a result of RIB addition and increase of fiber concentration, suggests that the steers might have regulated DMI in an attempt to minimize discomfort. The RIB addition and increase in NDF concentration would have distended the rumen and would have potentially increased animal discomfort. The reduction in DMI would have reduced absorbed metabolic fuels causing increased discomfort due to hunger. The steers might have altered meal size and inter-meal interval in an attempt to reduce discomfort from ruminal distension, but would have attempted to consume enough DM in order to reduce the stimulus of hunger. Feeding behavior and blood metabolite data collected simultaneously would be necessary to confirm this hypothesis of animals eating to minimize discomfort.

Implications

Results from this study indicate that the NDF content of corn silage can limit intake when fed to light-weight steers. The lack of reduction in digesta volume with addition of inert fill suggests that feed intake was not regulated by ruminal distension alone. Intake regulation of corn silage diets may be the result of steers attempting to minimize discomfort due to satiety and hunger as a result of ruminal distension and lack of

metabolic fuels. Further research is necessary to more directly define how the metabolic

signals interact to regulate intake of corn silage-based diets.

Tables and Figures

Table 3-1. Post-ensiled nutrient composition and fermentation characteristics of normal and male-sterile corn hybrids

	Corn hybrid	
Item	Normal	Male-sterile
Nutrient composition, % in silage DM[a]		
DM	36.7	31.0
CP	6.91	6.18
NDF[b]	38.6	56.7
ADF[b]	22.7	32.3
Starch	32.0	3.3
Fermentation characteristics[c]		
pH	3.61	3.46
Acetate, g/100 g DM	0.80	1.42
Propionate, g/100 g DM	–	0.30
Ethanol, g/100 g DM	0.52	7.57
Lactate, g/100 g DM	5.67	7.88

[a]During trial analysis.
[b]Corrected for ash.
[c]Pre-trial analysis.

Table 3-2. Ingredient and nutrient composition of normal (Low-fiber) and male-sterile (High-fiber) corn silage diets

Item	Low-fiber	High-fiber
Ingredient composition, % in diet DM		
Normal corn silage	87.72	–
Male-sterile corn silage	–	85.76
Soybean meal, 44% CP	9.04	11.07
Ground shelled corn	0.21	0.20
Trace mineralized salt[a]	0.62	0.61
Urea	0.46	0.45
Potassium chloride	0.34	0.34
Selenium 90[b]	0.07	0.06
Vitamin A[c]	0.01	0.01
Rumensin 80[d]	0.02	0.02
Dicalcium phosphate	0.13	0.13
Calcium carbonate	1.37	1.34
Nutrient composition		
DM, %	39.3	30.3
CP, % DM	11.4	11.2
NDF, % DM[e]	33.8	50.8
indigestible NDF, % NDF	43.2	36.0
ADF, % DM[e]	20.3	30.1
ADL, % DM[e]	2.07	2.72
ADL, % NDF	6.12	5.35
Starch, % DM	29.1	4.2
Free glucose, % DM	0.12	0.05

[a]Composition (%): NaCl, 96-98.5; Zn, > 0.35; Mn, > 0.2; Fe, > 0.2; Cu, > 0.03; I, > 0.007; Co, > 0.005.

[b]Composition (%): Ca, > 28.5; Se, 0.02.

[c]Contains 30,000 IU of vitamin A per gram.

[d]Contains 176 g of monensin per kg.

[e]Corrected for ash.

Table 3-3. Dry matter intake, NDF intake, and ruminal digesta characteristics and kinetics of normal (Low fiber) and male-sterile (High fiber) corn silage based diets with and without rumen inert bulk (RIB)

Item	Low fiber Control	Low fiber RIB	High fiber Control	High fiber RIB	SEM[a]	Effect[b], P-value Fiber	Effect[b], P-value RIB	Effect[b], P-value F × B
DMI, kg/d	4.92	4.47	4.23	3.70	0.14	<0.001	<0.001	0.63
NDF intake, kg/d	1.66	1.51	2.15	1.88	0.06	<0.001	<0.001	0.13
Ruminal volume, L								
Digesta + RIB	28.7	35.5	29.1	35.2	2.14	0.98	<0.001	0.73
Digesta	28.7	28.0	29.1	27.6	2.14	0.98	0.29	0.73
Headspace[c]	3.22	3.88	4.24	5.58	0.52	0.02	0.08	0.28
Digesta composition								
DM, % at 57°C	13.1	11.3	11.7	9.4	0.38	<0.001	<0.001	0.20
NDF, % DM	56.0	52.9	61.2	55.3	1.02	<0.001	<0.001	0.03
iNDF, % DM[d]	37.6	34.8	42.1	37.6	1.25	0.004	0.004	0.39
Rumen mass, kg								
Wet digesta + RIB	24.3	33.3	25.9	35.1	1.84	0.03	<0.001	0.86
Wet digesta	24.3	24.4	25.9	26.3	1.84	0.03	0.71	0.86
DM	3.16	2.78	3.03	2.50	0.20	0.04	<0.001	0.42
NDF	1.78	1.46	1.84	1.41	0.13	0.92	<0.001	0.42
iNDF[d]	1.18	0.96	1.30	0.94	0.72	0.48	<0.001	0.24
Density, kg/L	0.85	0.88	0.89	0.95	0.01	<0.001	<0.001	0.12
iNDF k_p, %/h[e]	2.68	2.98	2.65	3.24	0.18	0.37	0.001	0.19
Ruminal NDF turnover time, h	25.9	23.2	20.8	18.0	1.40	<0.001	0.002	0.97

[a]Standard error of the least squares mean.

[b]Fiber = Fiber level main effect; RIB = rumen inert bulk main effect; F × B = Fiber level × rumen inert bulk interaction.

[c]Volume of space in dosal rumen.

[d]Indigestible NDF.

[e]Passage rate of indigestible NDF.

Table 3-4. Ruminal pH, lactate, and VFA of normal (Low-fiber) and male-sterile (High-fiber) corn silage-based diets with and without rumen inert bulk (RIB)

Item	Low-fiber		High fiber			Effect[b], P-value		
	Control	RIB	Control	RIB	SEM[a]	Fiber	RIB	F × B
pH	6.43	6.56	6.72	6.74	0.08	0.003	0.20	0.38
Lactate, mM	0.70	0.60	0.47	0.41	0.11	0.02	0.38	0.84
Total VFA, mM	112.6	101.0	94.2	88.4	3.2	<0.001	<0.001	0.01
VFA, mol/100 mol								
Acetate	62.1	65.0	68.7	70.5	0.4	<0.001	<0.001	0.03
Propionate	23.8	22.7	18.5	18.0	0.5	<0.001	0.05	0.41
Butyrate	10.30	8.41	9.39	8.18	0.33	0.05	<0.001	0.06
Valerate	0.96	1.12	0.93	0.99	0.04	0.02	0.001	0.03
Isobutyrate	1.04	1.12	0.88	0.89	0.03	<0.001	0.05	0.11
Isovalerate	1.92	1.72	1.55	1.48	0.14	0.002	0.16	<0.001

[a]Standard error of the least squares mean.

[b]Fiber = fiber level main effect; RIB = rumen inert bulk main effect; F × B = fiber level × rumen inert bulk interaction.

Table 3-5. Apparent total tract digestibility, and energy concentration of normal (Low fiber) and male-sterile (High fiber) corn silage based diets with and without rumen inert bulk (RIB)

	Low fiber		High fiber			Effect[b], P-value		
Item	Control	RIB	Control	RIB	SEM[a]	Fiber	RIB	F × B
Apparent total tract digestibility								
DM, %	70.1	69.6	65.6	63.2	0.87	<0.001	0.12	0.27
NDF, % DM	47.8	46.0	58.8	55.7	1.35	<0.001	0.11	0.64
ADF, % DM	50.7	49.1	60.0	57.1	1.21	<0.001	0.11	0.59
Starch, % DM	98.8	98.8	98.8	97.1	1.06	0.44	0.42	0.42
GE digestibility, %	69.6	69.3	65.0	62.6	0.87	<0.001	0.14	0.27
DE intake, Mcal/d	13.7	12.4	10.5	8.9	0.43	<0.001	<0.001	0.49
Energy concentration of diets[c]								
ME, Mcal/kg DM	2.28	2.27	2.04	1.97	0.03	<0.001	0.15	0.27
NE_m, Mcal/kg DM	1.41	1.40	1.19	1.12	0.03	<0.001	0.15	0.27
NE_g, Mcal/kg DM	0.82	0.82	0.63	0.56	0.02	<0.001	0.15	0.27

[a]Standard error of the least squares mean.

[b]Fiber = Fiber level main effect; RIB = rumen inert bulk main effect; F × B = Fiber level × rumen inert bulk interaction.

[c]Calculated from DE using NRC (1996) equations.

Figure 3-1. Effects of feeding a normal corn hybrid (low-fiber; **LF**) or its male-sterile counterpart (high-fiber; **HF**), without or with rumen inert bulk (**RIB**) on ruminal pH over time. Feed offered at 0, 12 h. Time × fiber level interaction ($P < 0.0001$). SEM = 0.09.
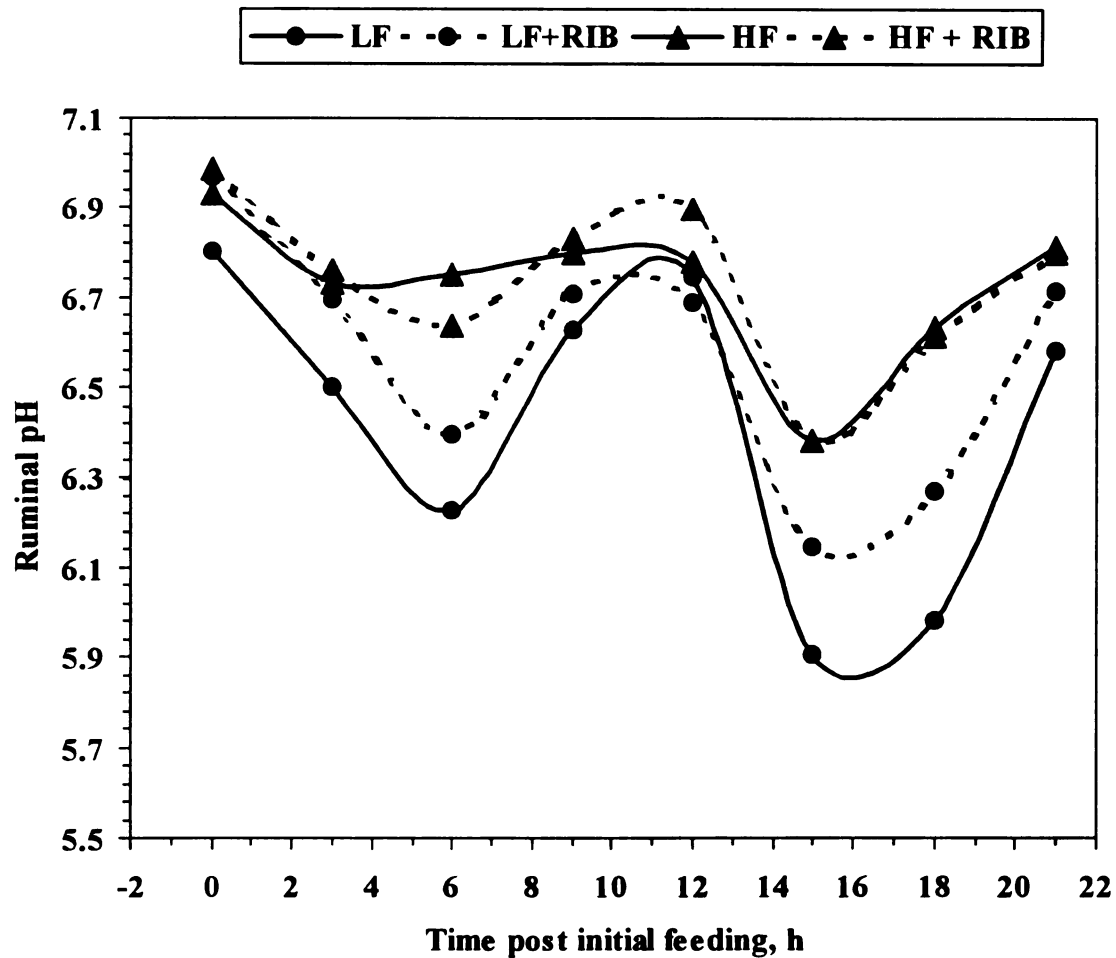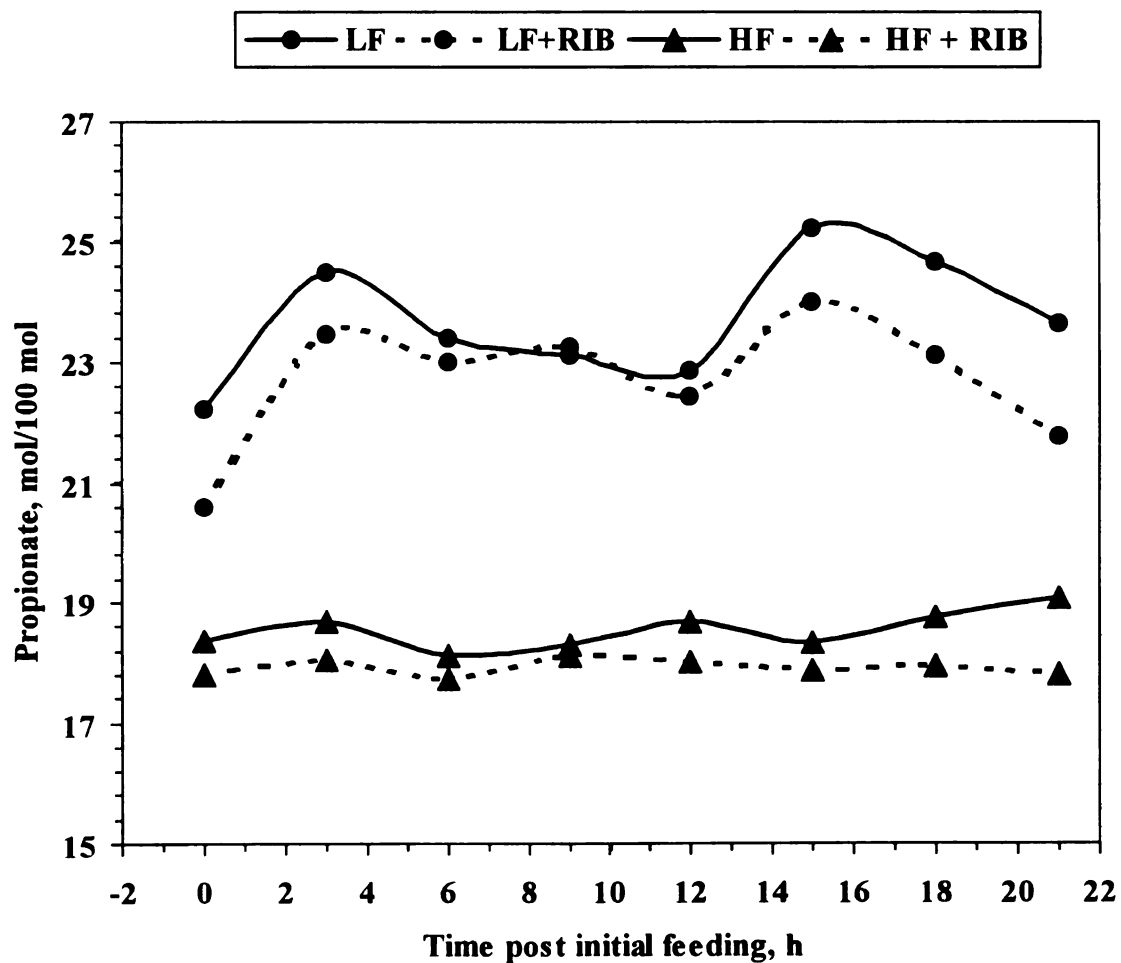
Figure 3-2. Effects of feeding a normal corn hybrid (low-fiber; **LF**) or its male-sterile counterpart (high-fiber; **HF**), without or with rumen inert bulk (**RIB**) on molar percentage of propionate over time. Feed offered at 0, 12 h. Time × fiber level interaction ($P <$ 0.0001). SEM = 0.61.

Literature Cited

Aitchison, E. M., M. Gill, M. S. Dhanoa, and D. F. Osbourn. 1986. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. Br. J. Nutr. 56:463-476.

Allen, M. S. 2000. Effects of diet on short-term regulation of feed intake by lactating dairy cows. J. Dairy Sci. 83:1598-1625.

AOAC. 1990. Official Methods of Analysis. 15th ed. Association of Official Analytical Chemists, Washington, DC.

Baile, C. A., and J. M. Forbes. 1974. Control of feed intake and regulation of energy balance in ruminants. Physiol. Rev. 54:160-214.

Bruning, C. L., and M. T. Yokoyama. 1988. Characteristics of live and killed brewer's yeast slurries and intoxication by intraruminal administration to cattle. J. Anim. Sci. 66:585-591.

Campling, R. C., and C. C. Balch. 1961. Factors affecting the voluntary intake of food by cows. I. Preliminary observations of the effect, on the voluntary of hay, of changes in the amount of the reticulo-ruminal contents. Br. J. Nutr. 15:523-530.

Carr, S. B., and D. R. Jacobson. 1967. Intraruminal addition of mass or removal of rumen contents on voluntary intake of the bovine. J. Dairy Sci. 50:1814-1818.

Dado, R. G. 1993. Voluntary intake and feeding behavior of dairy cows in response to rumen fill from forage fiber. Ph. D. dissertation, Michigan State University, East Lansing.

Dado, R. G., and M. S. Allen. 1995. Intake limitations, feeding behavior, and rumen function of cows challenged with rumen fill from dietary fiber or inert bulk. J. Dairy Sci. 78:118-133.

Dado, R. G., and M. S. Allen. 1996. Enhanced intake and production of cows offered ensiled alfalfa with higher neutral detergent fiber digestibility. J. Dairy Sci. 79:418-428.

Egan, A. R. 1972. Nutritional status and intake regulation in sheep. VII. Control of voluntary intake of three diets and the responses to intraruminal feeding. Austrailan Journal of Agricultural Resources. 23:347-361.

Fisher, L. J., and N. A. Fairey. 1979. Factors influencing the utilization by ruminants of corn silage in marginal growing areas. Can. J. Anim. Sci. 59:427-439.

Forbes, J. M. 1996. Integration of regulatory signals controlling forage intake in ruminants. J. Anim. Sci. 74:3029-3035.

Forbes, J. M., and F. D. Provenza. 2000. Integration of learning and metabolic signals into a theory of dietary choice and food intake. In: P. B. Cronje (ed.) Ruminant Physiology - Digestion, Metabolism, Growth and Reproduction. p 3-19. CABI Publishing, New York, New York.

Grant, R. J., and D. R. Mertens. 1992a. Development of buffer systems for pH control and evaluation of pH effects on fiber digestion in vitro. J. Dairy Sci. 75:1581-1587.

Grant, R. J., and D. R. Mertens. 1992b. Influence of buffer pH and raw corn starch addition on in vitro fiber digestion kinetics. J. Dairy Sci. 75:2762-2768.

Illius, A. W., and N. S. Jessop. 1996. Metabolic constraints on voluntary intake in ruminants. J. Anim. Sci. 74:3052-3062.

Johnson, T. R., and D. K. Combs. 1991. Effects of prepartum diet, inert rumen bulk, and dietary polyethylene glycol on dry matter intake of lactating dairy cows. J. Dairy Sci. 74:933-944.

Johnson, T. R., and D. K. Combs. 1992. Effects of inert rumen bulk of dry matter intake in early and midlactation cows fed diets differing in forage content. J. Dairy Sci. 75:508-519.

Karkalas, J. 1985. An improved enzymatic method for the determination of native and modified starch. J. Sci. Food Agric. 36:1019-1027.

Kaske, M., and A. Midasch. 1997. Effects of experimentally-impaired reticular contractions on digesta passage in sheep. Br. J. Nutr. 78:97-110.

Leek, B. F. 1969. Reticulo-ruminal mechanoreceptors in sheep. J. Physiol. (Lond.). 202:585-609.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76:1216-1231.

Llamas-Lamas, G., and D. K. Combs. 1991. Effect of forage to concentrate ratio and intake level on utilization of early vegetative alfalfa silage by dairy cows. J. Dairy Sci. 74:526-536.

Mowat, D. N. 1963. Factors affecting rumen capacity and the physical inhabition of feed intake. Ph.D. dissertation, Cornell University, Ithaca, NY.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. National Academy Press, Washington, DC.

Oba, M., and M. S. Allen. 2000. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 1. Feeding behavior and nutrient utilization. J. Dairy Sci. 83:1333-1341.

Orskov, E. R., G. W. Reid, and M. Kay. 1988. Prediction of intake by cattle from degradation characteristics of roughages. Anim. Prod. 46:29-34.

Orskov, E. R., G. W. Reid, and M. Kay. 1991. Influence of straw quality and level of concentrate in a completely mixed diet on intake and growth rate in steers. Anim. Prod. 52:461-464.

Perry, T. W., and D. M. Caldwell. 1969. Comparative nutritive value of silages made from high-sugar male sterile hybrid corn and regular starchy corn. J. Dairy Sci. 52:1119-1121.

Reid, G. W., E. R. Orskov, and M. Kay. 1988. A note on the effect of variety, type of straw and ammonia treatment on digestibility and on growth rate in steers. Anim. Prod. 47:157-160.

Ritchie, H., R. Black, A. Booren, L. Copeland, J. Ferris, J. Lloyd, T. Louden, H. Person, and S. Rust. 1992. Type of Farming Systems Study: Beef feedlot survey. Agric. Exp. Station Res. Rep. 522. Michigan State University, East Lansing, MI.

Schettini, M. A., E. C. Prigge, and E. L. Nestor. 1999. Influence of mass and volume of ruminal contents on voluntary intake and digesta passage of a forage diet in steers. J. Anim. Sci. 77:1896-1904.

Stake, P. E., M. J. Owens, D. J. Schingoethe, and H. H. Voelker. 1973. Comparative feeding value of high-sugar male sterile and regular dent corn silages. J. Dairy Sci. 56:1430-1444.

Tjardes, K. E., D. D. Buskirk, M. S. Allen, N. K. Ames, L. D. Bourquin, and S. R. Rust. 2000. Brown midrib-3 corn silage improves digestion but not performance of growing beef steers. J. Anim. Sci. 78:2957-2965.

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods of dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74:3583-3597.

Waybright, T. R., and G. A. Varga. 1991. Effect of water-filled bags in the rumen of wethers on ruminal digesta kinetics and total tract nutrient digestibility. J. Anim. Sci. 69:2157-2167.

Woodford, J. A., N. A. Jorgensen, and G. P. Barrington. 1986. Impact of dietary fiber and physical form on performance of lactating dairy cows. J. Dairy Sci. 69:1035-1047.

CHAPTER 4

Neutral Detergent Fiber Concentration in Corn Silage Influences Dry Matter Intake, Diet Digestibility, and Performance of Angus and Holstein Steers

Abstract

Twelve Angus (237 ± 13 kg) and twelve Holstein (235 ± 15 kg) steers were used to determine if a corn silage-based diet high in NDF depresses DMI as steers increase in body weight and to determine if a diet high in NDF has the same influence on Angus and Holstein steers. Steers were randomly assigned to individual slatted-floor pens and used in a crossover design consisting of six 14-d periods. Experimental diets contained corn silage from a normal hybrid (low-fiber; **LF**) and its male-sterile counterpart (high-fiber; **HF**) and were alternated each period. The LF and HF diets contained 33.8 and 50.8% NDF, respectively. The HF diet decreased overall steer mean DMI 14.0% relative to LF ($P < 0.001$), with mean differences increasing as steers increased in body weight ($P < 0.001$). Feeding HF also reduced ADG by an average of 13.8% relative to LF ($P < 0.001$). Holstein steers consumed 14.4% more DM, and gained 14.3% faster than Angus steers ($P < 0.001$). There was a fiber level × breed-type interaction ($P = 0.08$) for efficiency of gain. Angus steers receiving HF had greater efficiency of gain than Angus steers consuming LF; however, Holstein steers consuming LF had greater efficiency of gain than those receiving HF. The HF treatment reduced total-tract digestibility of DM and GE by 4.6 and 4.5%, respectively ($P < 0.001$) and decreased DE intake 20.5% ($P < 0.001$), but increased apparent total-tract digestibility of NDF and ADF (9.4 and 8.4%, respectively; $P < 0.001$). Holstein steers had similar digestibility of DM and GE ($P > 0.10$), but had greater DE intake ($P < 0.01$) when compared to Angus steers. There were

fiber level × breed-type interactions for total-tract digestibility of NDF and ADF ($P \leq$

0.06). Difference in DM digestibility was negatively associated with difference in DMI (r^2

= 0.23; P < 0.001) for LF minus HF within Angus steers, but not within Holstein steers (P

= 0.42). Total-tract digestibility of NDF and ADF was 4.1 and 3.4% lower for HF, but

was only 1.1 and 0.6% lower for LF when fed to Holsteins compared to Angus. Results

from this trial demonstrate that high NDF corn silage-based diets reduced intake of both

Angus and Holstein steers, and this reduction in DMI continues as steers increase in body

weight from 235 to 330 kg.

Introduction

Many cattle receive a growing diet before being placed on a high-concentrate

finishing diet. Growing diets often contain high levels of corn silage in upper Midwest

beef cattle feeding systems (Ritchie et al., 1992). Concentration of NDF in corn silage can

vary greatly (46.0 ± 6.5% NDF, $\bar{x}$ ± SD; NRC, 1996). In a previous study, corn silage

high in NDF fed to light-weight steers (198 ± 13 kg) depressed DMI (Tjardes et al.,

2001). A review of several studies indicates that depression in intake, as a result of

physical fill in the form of inert bulk, was greatest for animals with relatively lighter body

weight within a species, and for animals in physiological states with higher nutrient

requirements (Dado, 1993). It is uncertain whether the filling effect of a high-fiber corn

silage-based diet continues to limit DMI as steers increase in body weight.

In addition to dietary effects, DMI may be influenced by steer breed-type.

Holstein and Holstein crossbred steers have DMI that is 4.2 to 17.0% greater compared to

other breeds (Garrett, 1971; Fox and Black, 1984). Due to differences in DMI, it was our

hypothesis that physical fill in the rumen may depress DMI to a lesser extent for Holsteins compared to steers of beef breeding. Therefore, our objectives were to determine if a high NDF corn silage-based diet depresses DMI as steers increased in body weight and to determine if the depression in DMI was different for Holstein compared to Angus steers.

Materials And Methods

A corn hybrid (5456, UAP Dyna-Gro, East Lansing, MI) and its male-sterile isogenic counterpart were planted in separate fields on the same day to achieve a population of approximately 66,700 plants/ha. The male-sterile hybrid was isolated from all other corn hybrids to prevent pollination. As the corn approached maturity, DM for each hybrid was determined every third day to estimate the desired time of harvest. The normal and male-sterile corn hybrids were harvested with a three-row silage chopper (Model 900, New Holland North America Inc., New Holland, PA) set at 1.3 cm theoretical cut length, and ensiled separately in adjacent 2.4-m dia. plastic silage bags (Ag Bag International, Warrenton, OR) at the Michigan State University Beef Cattle Teaching and Research Center. Before feeding, forages were analyzed for DM, NDF, CP, pH, and VFA. Post-ensiled nutrient composition and fermentation characteristics of the silages are presented in Table 4-1.

Animal handling and experimental procedures in this trial were conducted according to those approved by the Michigan State University All University Committee on Animal Use and Care (AUF No. 07/99-089-00).

Twelve Angus (237 ± 13 kg) and twelve Holstein (235 ± 15 kg) steers were randomly assigned to individual 2.1× 1.8 m slotted-floor metabolism pens for a 10-d

acclimation period. Steers had ad libitum access to water and a common corn silage-based diet (Table 4-2). Corn silage was the primary dietary ingredient, with soybean meal and supplement added to meet or exceed requirements for metabolizable protein, minerals, and vitamins (NRC, 1996). After acclimation, diets were formulated using either the male-sterile (low-fiber diet; **LF**) or normal (high-fiber diet; **HF**) corn hybrids resulting in LF and HF containing 33.8% and 50.8% dietary NDF, respectively (Table 4-2). Steer diets were mixed once daily and offered at 0730 and 1930 to allow steers ad libitum access ($\geq 10\%$ orts) to the total mixed ration. Amounts fed and refused were weighed daily for each steer. Representative samples of the complete mixed diets, individual ingredients, and orts were taken twice weekly. Samples were dried immediately at 57°C in a forced-air oven for 72 h to determine DM. A crossover design, consisting of six 14-d periods (five crossovers), was used to determine the effect of dietary NDF concentration on diet digestion and steer performance as steers increased in body weight. Dietary treatments were switched on d 14 of each period.

Steer weights were the average of full weights taken on two consecutive days at d 0, 1, 13, and 14 of each period throughout the trial. Steers were implanted with 200 mg of progesterone and 20 mg of estradiol benzoate (IMPLUS-S, Upjohn Co., Kalamazoo, MI) before acclimation. Fecal grab samples were collected at 1900 on d 12, 0700 and 1900 on d 13, and 0700 on d 14 and immediately frozen at -20°C. Fecal samples were later dried at 57°C in a forced-air oven for 72 h to determine DM.

Sample Analysis

Diets, individual ingredients, and fecal samples were ground through a Wiley mill

(Arthur H. Thomas, Philadelphia, PA) equipped with a 1-mm screen. Samples of diets

and individual ingredients were then composited for each stage, and fecal samples were

composited by animal for each stage. Diet, individual ingredient, and fecal samples were

then analyzed for percentages of NDF, ADF, ADL, indigestible NDF, and ash. Neutral

detergent fiber, ADF, and ADL were analyzed according to procedures of Van Soest et al.

(1991; method A for NDF) and corrected for ash. Ash content was determined after 5 h

of oxidation at 500°C in a muffle furnace. Diets and individual ingredients were analyzed

for CP by the combustion method (AOAC, 1990; Model FP-2000, LECO, St. Joseph,

MI). Free glucose in the diets and feed ingredients were measured by an enzymatic

method (Karkalas, 1985; glucose kit #510-A, Sigma Diagnostics Inc., St. Louis, MO)

using a microplate reader (Spectra Max 190, Molecular Device Corp., Sunnyvale, CA)

after samples were extracted with deionized water. Starch in the diets, feed ingredients,

and feces were measured by an enzymatic method (Karkalas, 1985; glucose kit #510-A)

after samples were gelatinized with sodium hydroxide and digested with amylase

(CRYSTALZYME 40 L, Vally Research Inc., South Bend, IN). Fecal output and

apparent total-tract digestibility of dietary nutrients were calculated using indigestible

NDF as an internal marker (Cochran et al., 1986). Indigestible NDF residues in feed and

feces were quantified as NDF content of samples following in vitro fermentation in

buffered rumen media (Goering and Van Soest, 1970) for 120-h without addition of

pepsin. Gross energy was determined for both feed and fecal samples by bomb

calorimetry (AOAC, 1990; Model 1241 Adiabatic Calorimeter, Parr Instruments, Moline,

IL). Digestible energy was determined as the difference between intake of dietary gross energy and output of fecal gross energy. Concentration of ME, NE_m, NE_g in the diets were calculated from DE using published equations (NRC, 1996). The concentrations of all nutrients were expressed as percentage of DM determined from drying at 57°C.

Statistical Analysis

Intake, performance, and digestibility data were analyzed based on a mixed effect model using the MIXED procedure of SAS (SAS Inst. Inc., Cary, N.C.). The model contained animal nested within breed-type as a random effect, and period, fiber level, breed-type, and fiber level × breed-type as fixed effects. Using the Schwarz Bayesian criterion (Littell et al., 1998), a first-order compound symmetry error structure was determined as the most appropriate residual covariance structure for repeated measures over period within animals. Main effects were considered significant at $P < 0.05$, and two-way interactions were considered significant at $P < 0.10$.

Difference in DMI, DMI as a percentage of BW, DMI as a percentage of $BW^{0.75}$, DE intake, DE intake as a percentage of BW, DE intake as a percentage of $BW^{0.75}$, and apparent total-tract DM digestibility between the two treatments were calculated by subtracting the high-fiber diet from the low-fiber diet (LF-HF) data for each steer within each of the five crossovers. Relationships between the factors were then determined using the simple linear regression procedure of SAS (PROC REG). Slopes of regression lines for Angus and Holstein steers were tested using dummy variables to set the Holstein slope equal to zero and determine if the Angus slope was different from zero. Slopes of the regressions lines were considered significantly different at $P < 0.10$.

Results And Discussion

The normal and male-sterile corn silages in the current study were the same as those used in Tjardes et al. (2001). Since the male-sterile corn silage contained greater concentration of ethanol (7.0%), steers receiving HF would have consumed up to 550 mL of ethanol over the entire day. No adverse signs related to ethanol ingestion were observed among steers.

The HF diet decreased steer DMI 14.6% when summarized over the entire trial (Table 4-3; $P < 0.001$). This reduction in DMI agrees with Tjardes et al. (2001), who reported a 14.0% reduction in DMI when a similar diet was fed to cannulated steers. There was a period × fiber level interaction for DMI ($P < 0.001$; Figure 4-1a), and DMI as a percentage of BW ($P < 0.001$; Figure 4-1b). In addition, there was a positive relationship between average steer BW for each crossover and the difference in steer DMI for LF minus HF, ($r^2 = 0.24$; $P < 0.001$; Figure 4-2). There was also a positive relationship ($P < 0.001$) between average steer BW for each crossover and difference in DMI whether DMI was expressed as a percentage of BW (y = -0.319 • 0.002x; $r^2 = 0.13$) or expressed as a percentage of $BW^{0.75}$ (y = -1.678 • 0.011x; $r^2 = 0.18$). These data suggest that when steers increased in body weight, the HF diets became more limiting to DMI as compared to LF. In addition to the reduction in DMI, feeding HF also reduced ADG by an average of 13.8% ($P < 0.001$; Table 4-3). In contrast to the current study, Stake et al. (1973) reported that steers consumed similar intakes of male-sterile or normal corn silage when they were receiving 1.81 kg/d of a protein/grain supplement and there was no difference in the crude fiber value between the normal and male-sterile hybrids.

The researchers also reported no difference in steer ADG due to treatment (Stake et al., 1973).

Holstein steers consumed 14.4% more DM, and gained 14.3% faster than Angus steers ($P < 0.001$; Table 4-3). Previous researcher has indicated that Holstein and Holstein crossbred steers have 4.2 to 17.0% greater DMI when compared to British steers (Garrett, 1971; Dean et al., 1976; Thonney et al., 1981; Fox and Black, 1984). The influence of breed-type on ADG in previous studies has been variable. Garrett (1971) reported no difference in ADG between Holstein and Hereford steers when they were fed either 70% sorghum or 44% barley diets. Dean et al. (1976) found a reduction in ADG of 0.2 to 0.4 lb/d for Holstein crossbred steers compared to British steers when they received a 65% sorghum diet. In contrast, Thonney et al. (1981) reported that Holstein steers gained 0.4 lb/d faster that small-framed Angus calves when they were fed either corn- or silage-based diets.

There was no breed-type × fiber level × period interaction ($P = 0.88$) for DMI and the slope of the relationship between average steer body weight for each crossover and the difference in steer DMI for LF minus HF were not different for the two breeds ($P = 0.18$). This suggests that the diet high in NDF had the same influence over DMI for both breed types.

The HF treatment reduced total-tract digestibility of DM and gross energy (**GE**) by 4.6 and 4.5%, respectively ($P < 0.001$), but increased apparent total-tract digestibility of NDF and ADF (9.4 and 8.4%, respectively; $P < 0.001$) compared to LF. Since steers receiving HF consumed less DM and had lower digestibility of GE, digestible energy intake was reduced by 20.5% ($P < 0.001$). Similar results were reported by

Tjardes et al. (2001), where feeding HF compared to LF increased digestibility of NDF and ADF (11.0 and 9.3%, respectively), but decreased digestibility of DM and GE (4.5 and 4.7%, respectively), and reduced digestible energy intake 23.4%.

Holstein steers had similar digestibility of DM and GE ($P > 0.10$), but had greater digestible energy intake ($P = 0.002$) when compared to Angus steers. There were fiber level × breed-type interactions for total-tract digestibility of NDF and ADF ($P \leq 0.06$). Within the HF diet, total-tract digestibility of NDF and ADF was 1.1 and 0.6% lower, respectively, for Holstein compared to Angus steers. When steers received the LF treatment, total-tract digestibility of NDF and ADF was 4.1 and 3.4% lower, respectively, for Holstein compared to Angus steers. The decline in fiber digestibility for Holstein steers receiving LF could be due to a greater amount of starch fermented in the rumen (Grant and Mertens, 1992) and(or) an increased passage rate resulting in more potentially digestible fiber escaping ruminal degradation (Oba and Allen, 2000).

There was a negative relationship between difference in apparent total-tract DM digestibility and difference in DMI (LF-HF) for Angus steers ($r^2 = 0.23$; $P < 0.001$; Figure 4-3a). There was also a negative relationship ($P < 0.001$) when DMI was expressed as a percentage of $BW^{0.75}$ (y = 13.82 • -7.30x; $r^2 = 0.25$). These data suggest that when there was no difference in DMI due to fiber level, LF had a higher total-tract DM digestibility. However, when steers consumed greater levels of LF as compared to HF, the total-tract DM digestibility of LF was reduced. The reduction in DM digestibility may have been because of an increase in passage rate for LF in association with the higher DMI. Similar responses were reported by Oba and Allen (1999, 2000) when they compared diets fed to early lactation dairy cows containing corn hybrids with different digestibilities of NDF.

113

No relationship was reported between difference in apparent total-tract DM digestibility and difference in DMI for Holstein steers ($P = 0.42$; Figure 4-3b) or when DMI was expressed as a percentage of $BW^{0.75}$ ($P = 0.45$). Reasons for the different relationship for Holstein steers compared to Angus steers might be because of differences between the breeds in ruminal retention time of digesta for the two diets.

There was no relationship between difference in DE intake and difference in DMI for Angus steers ($P = 0.57$; Figure 4-4a). This was due to the negative relationship between difference in DM digestibility and difference in DMI. In contrast, there was a positive relationship between difference in DE intake and difference in DMI for Holstein steers ($r^2 = 0.23$; $P < 0.001$; Figure 4-4b). The relationship between differences in DE intake and DMI were consistent with difference in ADG for each breed type. Within the Angus steers, there was no relationship between differences in DE intake and DMI which corresponded to only a 0.1 kg/d difference in ADG between the LF and HF diets. However, for the Holstein steers, there was positive relationship between differences in DE intake and DMI, and the Holstein steers receiving LF gained 0.2 kg/d faster than those receiving HF.

There was a fiber level × breed-type interaction for efficiency of gain ($P = 0.08$; Table 4-3). Angus steers receiving HF had greater efficiency of gain than Angus steers consuming LF. The reduction in efficiency of gain for the Angus steers receiving LF is consistent with the negative relationship between difference in DM digestibility and difference in DMI. In contrast, the Holstein steers consuming LF had greater efficiency of gain than those receiving HF. Previous research has reported that Holstein and Holstein crossbred steers range from having greater efficiency of gain (Thonney et al., 1981) to

114

having lower efficiency of gain (Dean et al., 1976; Wyatt et al., 1977) when compared to British steers.

Implications

Corn silage high in fiber has the potential to limit intake of light-weight steers. As steers increased in body weight, intake of the high-fiber corn silage diet was depressed to a greater extent compared to the lower-fiber diet. The two breeds responded differently to the different fiber levels. Although the Holstein steers consumed more dry matter and gained faster than the Angus steers, the increased fiber concentration appeared to be more detrimental to performance of the Holstein steers as compared to the Angus steers. Further research is needed to more clearly define the factors controlling intake of corn-silage based diets and the determination of ruminal digesta kinetics of both breed-types would be beneficial to determine the reasons for the breed difference between the two fiber levels.

Tables and Figures

Table 4-1. Post-ensiled nutrient composition and fermentation characteristics of normal and male-sterile corn hybrids

Item	Corn hybrid	
	Normal	Male-sterile
Nutrient composition, % in silage DM[a]		
DM	36.7	31.0
CP	6.91	6.18
NDF[b]	38.6	56.7
ADF[b]	22.7	32.3
Starch	32.0	3.3
Fermentation		
pH	3.61	3.46
Acetate, g/100 g DM	0.80	1.42
Propionate, g/100 g DM	–	0.30
Ethanol, g/100 g DM	0.52	7.57
Lactate, g/100 g DM	5.67	7.88

[a]During trial analysis.
[b]Corrected for ash.
[c]Pre-trial analysis.

Table 4-2. Ingredient and nutrient composition of normal (Low-fiber) and male-sterile (High-fiber) corn silage-based diets

Item	Low-fiber	High-fiber
Ingredient composition, % in diet DM		
Normal corn silage	87.72	–
Male-sterile corn silage	–	85.76
Soybean meal, 44% CP	9.04	11.07
Ground shelled corn	0.21	0.20
Trace mineralized salt[a]	0.62	0.61
Urea	0.46	0.45
Potassium chloride	0.34	0.34
Selenium 90[b]	0.07	0.06
Vitamin A[c]	0.01	0.01
Rumensin 80[d]	0.02	0.02
Dicalcium phosphate	0.13	0.13
Calcium carbonate	1.37	1.34
Nutrient composition		
DM, %	39.3	30.3
CP, % DM	11.4	11.2
NDF, % DM[e]	33.8	50.8
indigestible NDF, % NDF	43.2	36.0
ADF, % DM[e]	20.3	30.1
ADL, % DM[e]	2.07	2.72
ADL, % NDF	6.12	5.35
Starch, % DM	29.1	4.2
Free glucose, % DM	0.12	0.05

[a]Composition (%): NaCl, 96-98.5; Zn, > 0.35; Mn, > 0.2; Fe, > 0.2; Cu, > 0.03; I, > 0.007; Co, > 0.005.
[b]Composition (%): Ca, > 28.5; Se, 0.02.
[c]Contains 30,000 IU of vitamin A per gram.
[d]Contains 176 g of monensin per kg.
[e]Corrected for ash.

Table 4-3. Dry matter intake, average daily gain, apparent total tract digestibility, and energy concentration of low-fiber (LF) and high-fiber (HF) corn silage-based diets fed to growing Angus and Holstein steers

| | Angus | | Holstein | | | Effect[b], P-value | | |
Item	LF	HF	LF	HF	SEM[a]	Fiber	Breed	F × B
DMI, kg/d	5.98	5.05	6.76	5.85	0.13	<0.001	<0.001	0.85
DMI, % BW	2.19	1.86	2.44	2.11	0.05	<0.001	0.006	0.18
NDF intake, kg/d	2.10	2.51	2.37	2.91	0.05	<0.001	<0.001	0.004
ADG, kg/d	1.05	0.95	1.25	1.03	0.05	0.002	0.006	0.18
Gain:Feed	0.173	0.188	0.186	0.174	0.008	0.97	0.80	0.08
Apparent total tract digestibility								
DM, %	63.3	60.0	62.1	59.6	0.61	<0.001	0.26	0.43
NDF, % DM	47.4	55.3	43.3	54.2	0.83	<0.001	0.009	0.05
ADF, % DM	48.5	55.2	45.1	54.6	0.82	<0.001	0.04	0.06
Starch, % DM	94.2	96.5	94.5	96.9	0.69	<0.001	0.69	0.13
GE digestibility, %	63.3	60.3	62.1	59.5	0.59	<0.001	0.11	0.66
DE intake, Mcal/d	14.8	11.5	16.4	13.3	0.35	<0.001	0.002	0.81
Energy concentration of diets[c]								
ME, Mcal/kg DM	2.03	1.88	1.99	1.85	0.02	<0.001	0.11	0.65
NE_m, Mcal/kg DM	1.18	1.03	1.14	1.01	0.02	<0.001	0.13	0.65
NE_g, Mcal/kg DM	0.61	0.48	0.58	0.46	0.02	<0.001	0.13	0.65

[a]Standard error of the least squares mean.

[b]Fiber = Fiber level main effect; Breed = steer breed-type main effect; F × B = fiber level × steer breed-type interaction.

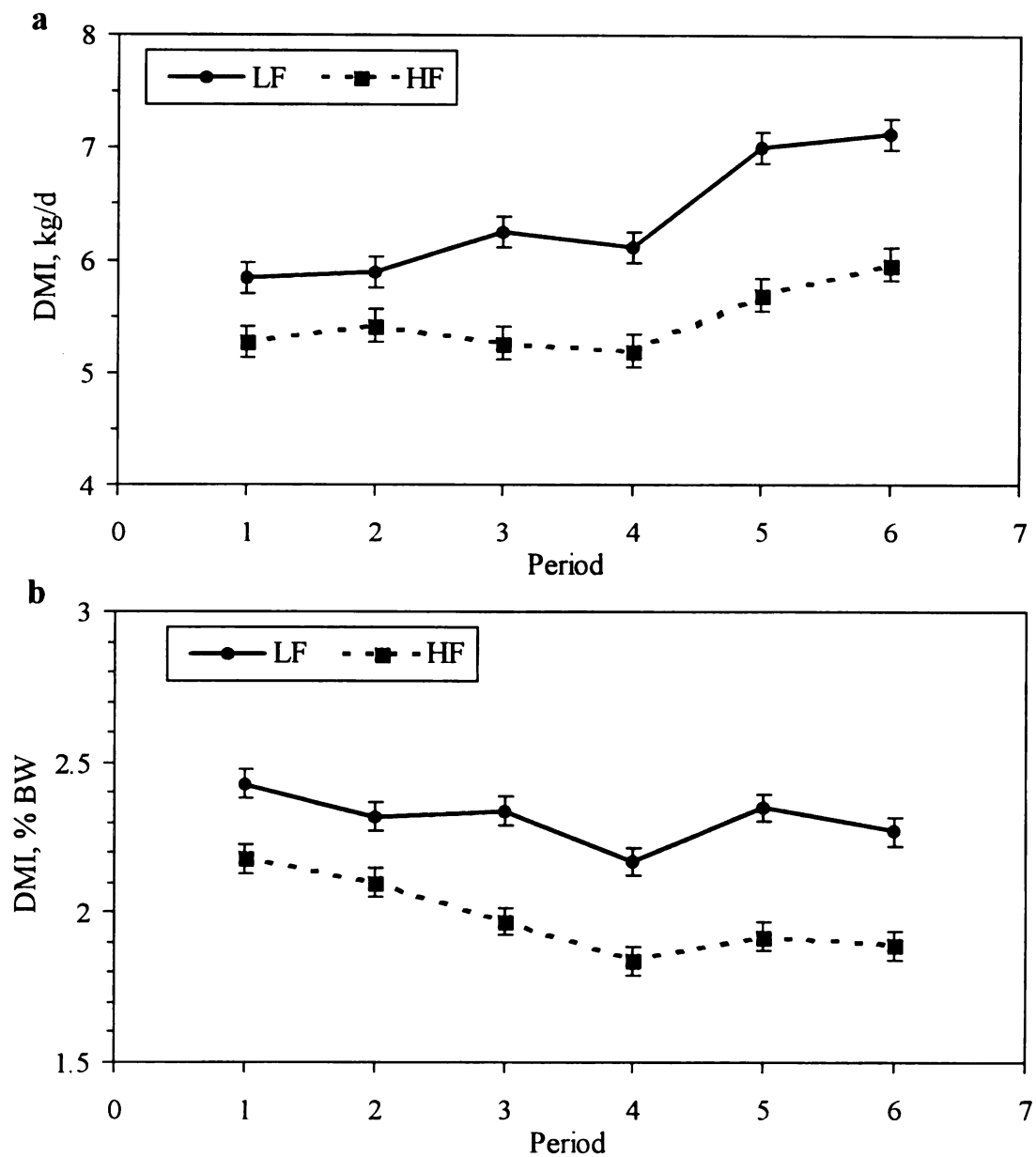[c]Calculated from DE using NRC (1996) equations.

Figure 4-1. Effects of feeding low-fiber (LF) and high-fiber (HF) corn silage-based diets on growing steer a) dry matter intake least squares mean (DMI) over period and b) dry matter intake as a percentage of body weigh least squares mean (DMI, % BW) over period. Period × fiber level interactions ($P < 0.0001$).
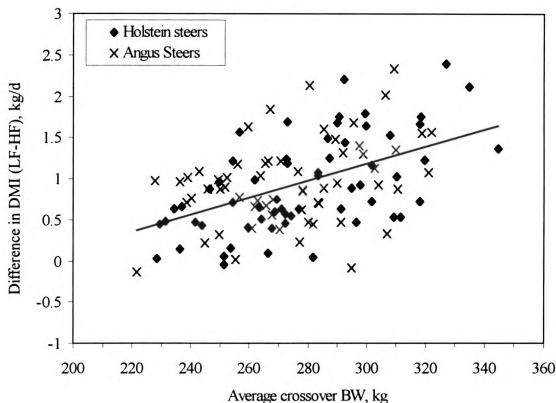
Figure 4-2. Relationship between difference in DMI for low-fiber (LF) minus high-fiber (HF) and average crossover body weight of Angus and Holstein steers. Difference in DMI (LF - HF) = -1.856 + 0.011 × average crossover body weight (r^2 = 0.24; P < 0.001).
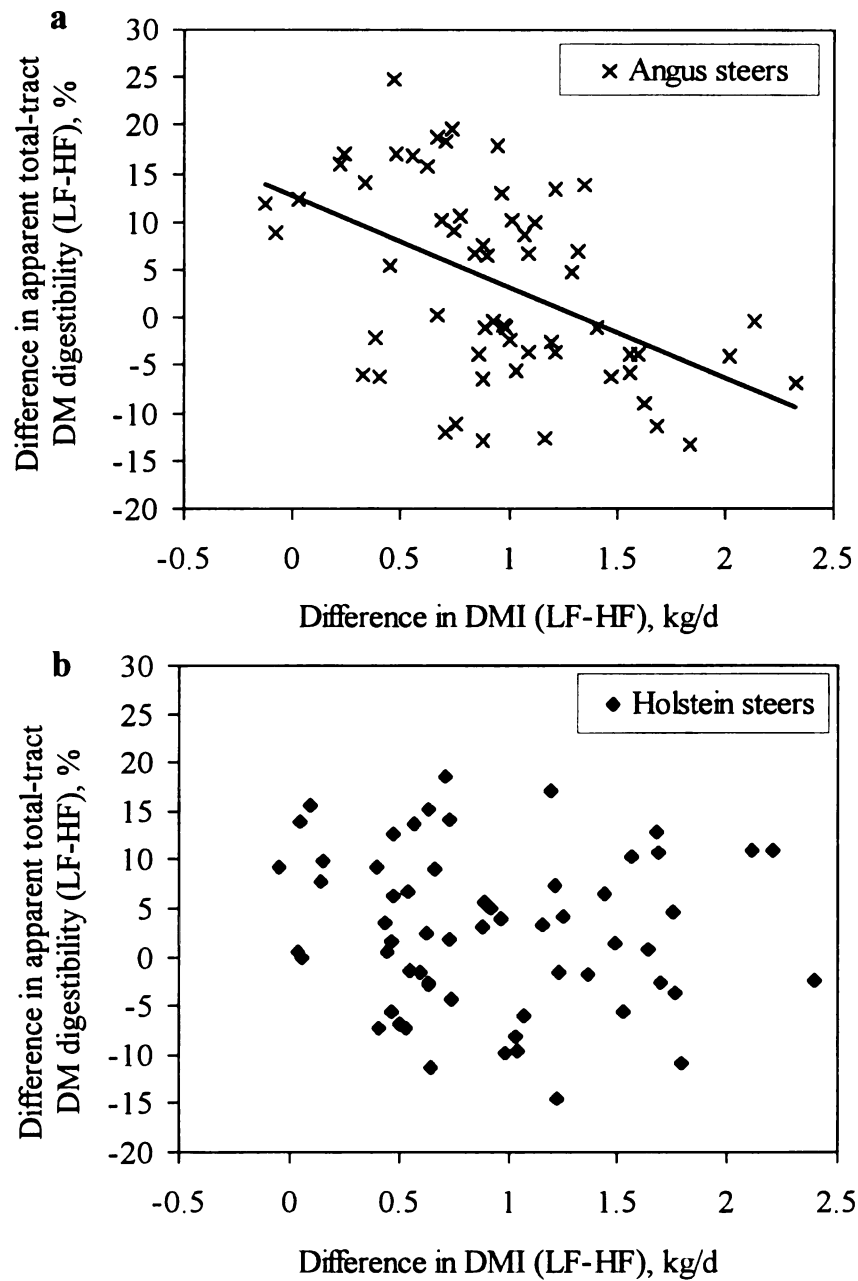
Figure 4-3. Relationship between difference in apparent total-tract DM digestibility and difference in DMI for low-fiber (LF) minus high-fiber (HF) within a) Angus steers ($r^2 = 0.23$; $P < 0.001$) and b) Holstein steers ($r^2 = 0.01$; $P = 0.42$). Difference in apparent total-tract digestibility (LF - HF) of Angus steers = 12.54 - 9.45 × difference in Angus steer DMI.
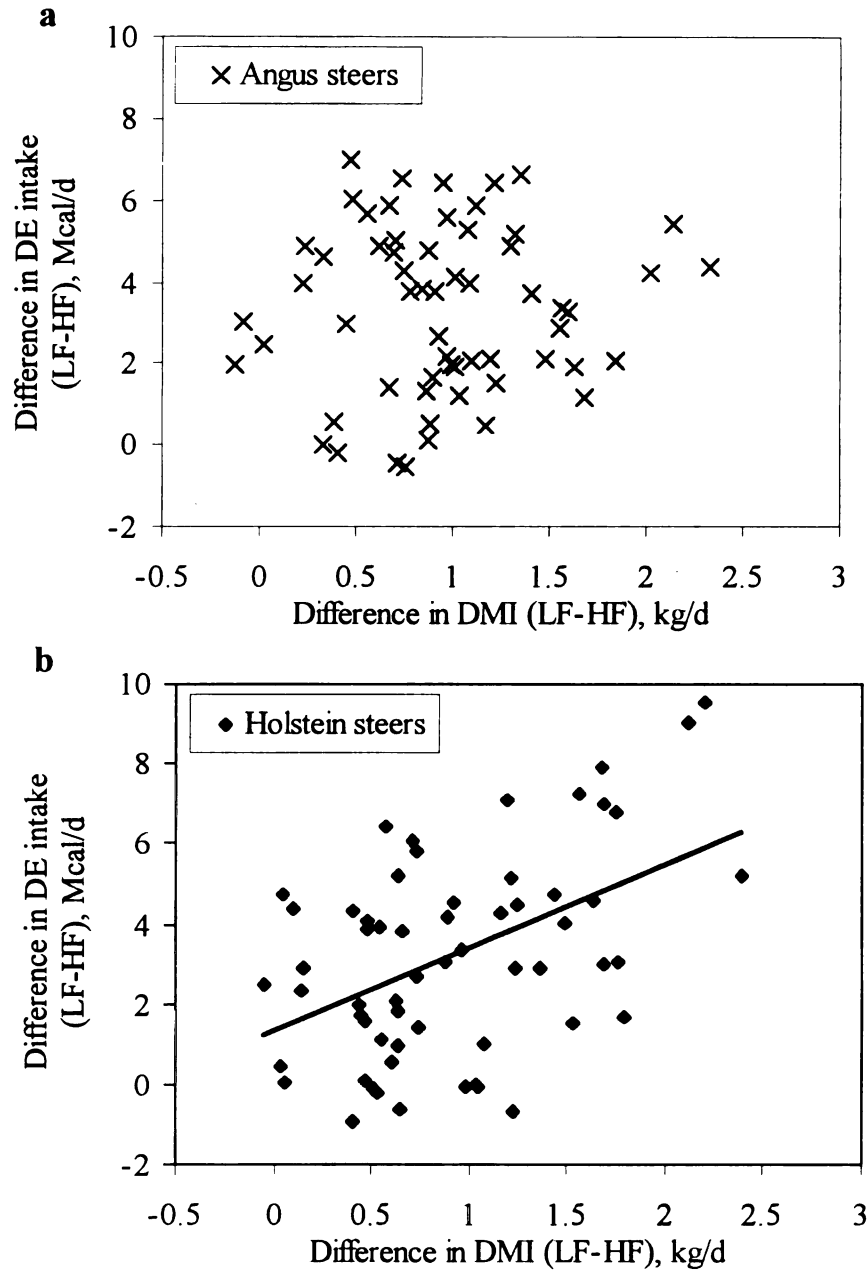
Figure 4-4. Relationship between difference in DE intake and difference in DMI for low-fiber (LF) minus high-fiber (HF) within a) Angus steers ($r^2 = 0.01$; $P = 0.57$) and b) Holstein steers ($r^2 = 0.23$; $P < 0.001$). Difference in DE intake (LF - HF) of Holstein steers = 1.294 + 2.080 × difference in Holstein steer DMI.
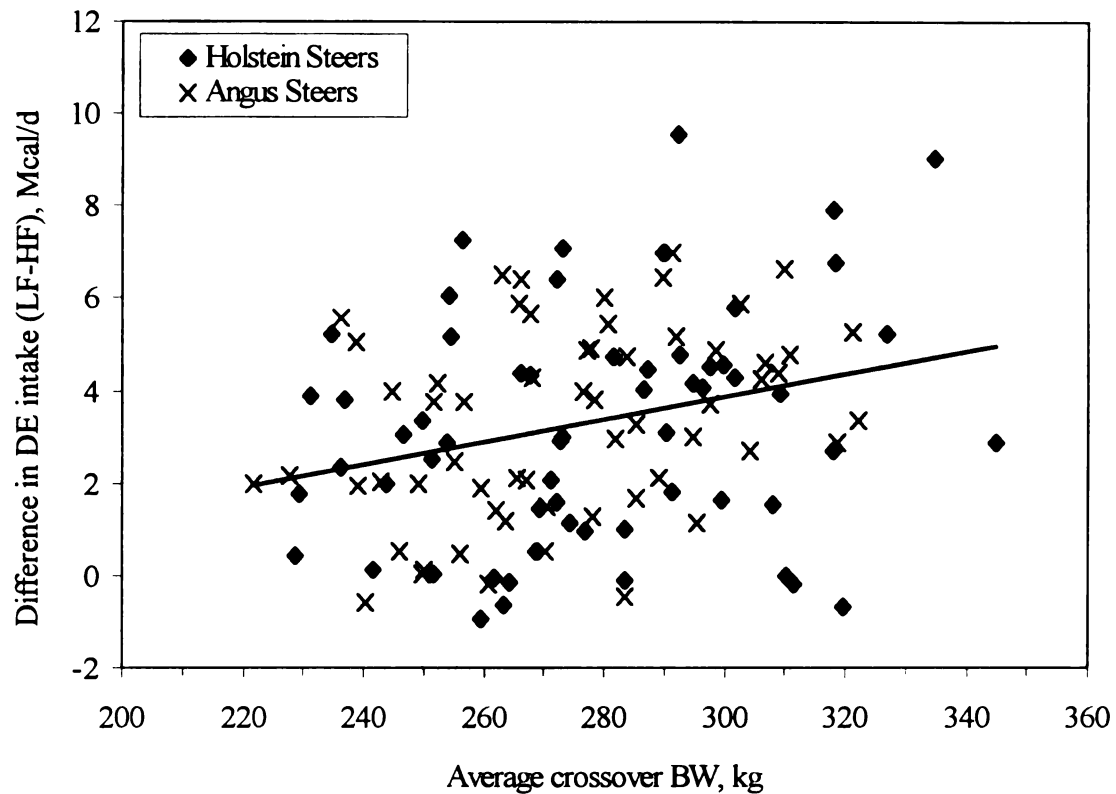
Figure 4-5. Relationship between difference in DE intake for low-fiber (LF) minus high-fiber (HF) and average crossover body weight of Angus and Holstein steers. Difference in DE intake (LF - HF) = -3.499 + 0.025 × average crossover body weight (r^2 = 0.08; P < 0.01).

Literature Cited

AOAC. 1990. Official Methods of Analysis. 15th ed. Association of Official Analytical Chemists, Washington, DC.

Cochran, R. C., D. C. Adams, J. D. Wallace, and M. L. Galyean. 1986. Predicting digestibility of different diets with internal markers: Evaluation of four potential markers. J. Anim. Sci. 63:1476-1483.

Dado, R. G. 1993. Voluntary intake and feeding behavior of dairy cows in response to rumen fill from forage fiber. Ph. D. dissertation, Michigan State University, East Lansing.

Dean, R. A., J. W. Holloway, J. V. Whiteman, D. F. Stephens, and R. Totusek. 1976. Feedlot performance of progeny of Hereford, Hereford x Holstein and Holstein cows. J. Anim. Sci. 42:1290-1296.

Fox, D. G., and J. R. Black. 1984. A system for predicting body composition and performance of growing cattle. J. Anim. Sci. 58:725-739.

Garrett, W. N. 1971. Energetic efficiency of beef and dairy steers. J. Anim. Sci. 32:451-456.

Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agric. Handbook No. 379. ARS-USDA, Washington, DC.

Grant, R. J., and D. R. Mertens. 1992. Influence of buffer pH and raw corn starch addition on in vitro fiber digestion kinetics. J. Dairy Sci. 75:2762-2768.

Karkalas, J. 1985. An improved enzymatic method for the determination of native and modified starch. J. Sci. Food Agric. 36:1019-1027.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76:1216-1231.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. National Academy Press, Washington, DC.

Oba, M., and M. S. Allen. 1999. Effects of brown midrib 3 mutation in corn silage on dry matter intake and productivity of high yielding dairy cows. J. Dairy Sci. 82:135-142.

Oba, M., and M. S. Allen. 2000. Effects of brown midrib 3 mutation in corn silage on productivity of dairy cows fed two concentrations of dietary neutral detergent fiber: 3. Digestibility and microbial efficiency. J. Dairy Sci. 83:1350-1358.

124

Ritchie, H., R. Black, A. Booren, L. Copeland, J. Ferris, J. Lloyd, T. Louden, H. Person, and S. Rust. 1992. Type of Farming Systems Study: Beef feedlot survey. Agric. Exp. Station Res. Rep. 522. Michigan State University, East Lansing, MI.

Stake, P. E., M. J. Owens, D. J. Schingoethe, and H. H. Voelker. 1973. Comparative feeding value of high-sugar male sterile and regular dent corn silages. J. Dairy Sci. 56:1430-1444.

Thonney, M. L., E. K. Heide, D. J. Duhaime, A. Y. M. Nour, and P. A. Oltenacu. 1981. Growth and feed efficiency of cattle of different mature sizes. J. Anim. Sci. 53:354-362.

Tjardes, K. E., D. D. Buskirk, M. S. Allen, N. K. Ames, and S. R. Rust. 2001. Neutral detergent fiber concentration of corn silage and rumen inert bulk influences dry matter intake and ruminal digesta kinetics of growing steers. J. Anim. Sci. (submitted).

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods of dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74:3583-3597.

Wyatt, R. D., K. S. Lusby, M. B. Gould, L. E. Walters, J. V. Whiteman, and R. Totusek. 1977. Feedlot performance and carcass traits of progeny of Hereford, Hereford X Holstein and Holstein cows. J. Anim. Sci. 45:1131-1137.

CHAPTER 5

Interpretive Summary

Fiber digestibility

The overall hypothesis of the research described in this dissertation is that corn silage high in fiber potentially limits intake and performance of light-weight steers by ruminal distension. Therefore, improving fiber digestibility or decreasing fiber concentration in corn silage should reduce ruminal distension and increase intake and performance. In Experiment 1, feeding BMCS compared to Control improved NDF digestibility and increased DMI but did not improve steer ADG. Reasons for the lack of improvements in ADG are unclear.

In Experiment 1, the brown midrib-3 and its isogenic control corn hybrids were planted to achieve similar populations, but the bm_3 resulted in a 19% reduction in as-is silage yield per hectare (Table 5-1). In addition, the bm_3 seed typically costs $100 more per bag when compared to its isogenic normal counterpart. Assuming the normal corn silage would cost $27.60/t of wet silage delivered to the bunk, the bm_3 corn silage would cost an additional $7.36/t of wet silage as a result of the higher seed cost and yield reduction (Table 5-1). During the performance trial, feeding BMCS increased steer DMI, but had no effect on ADG and resulted in poorer feed efficiency. The higher DMI and cost of silage production would have resulted in a $9.16/steer increase in feed cost for steers receiving BMCS compare to Control (Table 5-4). Total operating costs (excluding animal purchase price) would have been $9.53/steer greater for BMCS, resulting in the cost of gain (excluding animal purchase price) being increased from $0.87/kg for Control,

to $0.97/kg for BMCS. Assuming steers were purchased at $1.82/kg ($82.40/cwt)[1] and

sold after the 112-d growing period at $1.67/kg ($75.60/cwt)[2], feeding BMCS would

have reduced the return to labor and management by $12.14/steer when compared to

Control (Table 5-4). Finally, kilograms of gain per hectare of corn was reduced 11% for

BMCS when compared to Control as a result of the reduction in silage yield, with no

improvements in steer ADG (2,850 vs 2,530 kg/ha for Control and BMCS, respectively).

Fiber concentration

In Experiment 2, feeding HF compared to LF reduced DMI, and the addition of

RIB to both diets depressed DMI. These data appear to agree with the hypothesis that

increasing fiber concentration in corn silage reduces voluntary DMI by ruminal distension.

Digesta volume was also similar between LF and HF, suggesting that animals were eating

to maintain a similar digesta volume further suggesting that ruminal distension may be

regulating DMI. However, when RIB was added at 25% of pre-trial ruminal volume, total

ruminal volume was increased by approximately 25% for both LF and HF treatments.

These data suggest that steers with the RIB adapted to additional fill in an attempt to

minimize the discomfort from satiety as well as hunger. The RIB addition was expected

to distend the rumen and increase the stimulation of tension receptors in the rumen. The

tension receptors would have sent nerve impulses to the brain via the vagus nerve that

would have contributed to satiety. However, the reduction in DMI due to ruminal

distension would have reduced the amount of absorbed metabolic fuels, resulting in

---

[1]CATTLE-FAX 10-year average (1990-2000) for 250 kg feeder calves during October.

[2]CATTLE-FAX 10-year average (1990-2000) for 363 kg feeder calves during February.

stimulation of hunger. The steers would have integrated the competing signals of discomfort from hunger and satiety. The steers might have then adjusted the threshold for the tension receptors to signal discomfort in attempt to consume enough DM in order to reduce the stimulus of hunger. Feeding behavior and blood metabolite data collected simultaneous would be necessary to confirm this hypothesis.

In Experiment 3, the HF treatment when compared to LF, reduced DMI of both the Angus and Holstein steers. As the steers increased in body weight, differences in DMI and DE intake between LF and HF became greater and it appears that the HF diet became more limiting to DMI as compared to LF. The reason for this difference in DMI as steers increase in BW is unclear. A possible explanation might be that the balance between hunger and satiety may have become different between the two treatments as the steers increased in BW. Ruminal distension was potentially the major constraint regulating DMI of both treatments when the steers were of lighter BW. However, the energy concentration of the HF diet was lower than that of the LF diet. This would have resulted in a reduction of absorbed metabolic fuels and may have increased the discomfort due to hunger for the steers receiving HF as compared to those receiving LF. Therefore, when the steers had lighter BW, hunger may have been the predominant factor controlling DMI of HF, but DMI of LF may have been regulated to a greater extent by satiety. As the steers increased in BW, they consumed more DM. This increase in DMI might have provided more absorbed metabolic fuels, potentially reducing the discomfort due to hunger. The reduction in hunger would have potentially switched the balance of intake regulation towards those signals producing satiety. Since the HF diet contained greater NDF concentrations, it would have potentially increased ruminal distension to a greater

extent when compared to the LF diet. Therefore, at the heavier BW, ruminal distension might have became a greater factor regulating DMI for steers receiving HF when compared to those receiving LF.

Holstein steers consumed more DM than Angus steers. The higher DMI may have been a result of Holstein steers having larger skeletal size, larger rumen capacity, and(or) higher energy requirements as compared to Angus steers. The skeletal sizes of the two breeds were not measured, but visually the Holsteins appeared to be roughly two frame score sizes larger than the Angus. There was a negative relationship between the difference in apparent total-tract DM digestibility and the difference in DMI for LF minus HF with Angus steers. When there was no difference in DMI due to fiber concentration, LF had a greater total-tract DM digestibility. When the Angus steers consumed greater amounts of LF as compared to HF, total-tract DM digestibility of LF was reduced. This reduction in DM digestibility may have been due to increased passage rate for LF in association with greater DMI, resulting in more potentially digestible DM escaping fermentation. In contrast, no relationship was observed for Holstein steers. The reasons for the breed differences are not clear, but might be because of differences between breeds in ruminal retention time of digesta for the two diets. Further studies using cannulated steers of both breeds would be helpful in determining if digestion kinetics and efficiency of metabolite utilization are different between the two breeds.

Recommendation

When determining if a hybrid has economic potential for use in growing diets, one must first determine if there will be any added production costs associated with the hybrid.

129

Higher seed costs and yield reductions are two of the major factors associated with added production costs. Improvements in ADG and feed efficiency can also have great impacts on profitability. Average daily gain impacts the number of days on feed to reach a certain final weight and influences the cost of yardage, feed, and interest of money borrowed to purchase cattle and feed. Feed costs and interest on feed also are affected by feed efficiency. An analysis of returns to labor and management as a result of altering ADG and gain to feed ratio is presented in Figure 5-1. This analysis was based on the partial budget and assumptions for steers receiving the isogenic normal (Control) diet in Experiment 1, and assumes that there is no added production cost for different hybrids. An improvement in feed efficiency of 0.01, with no change in ADG, increased returns to labor and management by $6.55/steer. A 0.09 kg/d improvement in ADG, with no change on feed efficiency, resulted in a $4.03/steer increase in returns. Therefore, selecting hybrids that would increase or decrease ADG and(or) feed efficiency slightly can have dramatic effects on profitability.

Feeding the brown midrib-3 corn silage during the 112-d growing period in Experiment 1 did not change ADG, but resulted in poorer feed efficiency. Ignoring the higher productions costs, this reduction in gain:feed of 0.01 would have reduced returns to labor and management by $7.52/steer. Therefore, it may not be economical to feed corn silage with higher fiber digestibility in diets that contain less than 40% NDF, unless increases in ADG can offset the potential decreases in feed efficiency. In Experiment 3, feeding the corn silage diet that contained greater than 50% NDF did not affect feed efficiency, but reduced ADG by 0.32 kg/d. This reduction in ADG would have reduced returns by greater than $10.39. Therefore, selecting corn hybrids that contain less than

50% NDF should be beneficial in improving profitability unless declines in feed efficiency offset the improvements in ADG. Further research needs to be performed to determine if improvements in fiber digestibility of corn silage diets that contain greater than 50% NDF are economical for light-weight steers.

Tables and Figures

Table 5-1. Beef growing phase partial budget for steers receiving brown midrib-3 (BMCS) and isogenic normal (Control) corn silage based diets (Based on Experiment 1)

Item	Corn silage diet	
	Control	BMCS
Production		
Seed cost, $/bag	80.00	180.00
Corn silage DM, %	29.8	35.2
Corn silage as-is yield, t/ha	57.6	45.8
Corn silage DM yield, t/ha	16.9	16.2
Partial budget		
Additional seed cost, $/t	--	2.33
Additional cost for yield reduction, $/t[b]	--	5.03
As-is silage delivered to bunk, $/t	27.60	34.96

[a]One bag is required for each 1.09 hectares at 69,200 plants per hectare.

[b]Assumes that Control costs $27.60/t wet silage delivered and harvesting cost per hectare are the same for both hybrids.

Table 5-2. Feed proportions and prices of isogenic normal (Control) corn silage based growing diet

Feed ingredient	% DM	Percentage in diet (DM basis)	kg per price unit	Price (as-fed basis)	kg/hd/day DM	kg/hd/day as-fed	Price /kg DM	Cost in diet DM
Corn	88%	0.21%	25.4	$2.70	0.01	0.01	$0.121	$0.000
Corn silage	28%	86.30%	907.2	$25.00	6.08	21.70	$0.098	$0.085
Soybean meal	89%	10.38%	907.2	$250.00	0.73	0.82	$0.310	$0.032
Urea	99%	0.47%	907.2	$275.00	0.03	0.03	$0.306	$0.001
Macro-minerals	100%	1.91%	907.2	$100.00	0.13	0.13	$0.110	$0.002
Vitamins/trace-minerals	100%	0.71%	907.2	$500.00	0.05	0.05	$0.551	$0.004
Ionophore	100%	0.02%	0.45	$5.00	0.00	0.00	$11.023	$0.002

Table 5-3. Feed proportions and prices of brown midrib-3 (BMCS) corn silage based growing diet

Feed ingredient	% DM	Percentage in diet (DM basis)	kg per price unit	Price (as-fed basis)	kg/hd/day DM	kg/hd/day as-fed	Price /kg DM	Cost in diet DM
Corn	88%	0.21%	25.4	$2.70	0.02	0.02	$0.121	$0.000
Corn silage	34%	86.30%	907.2	$31.66	6.44	18.94	$0.103	$0.089
Soybean meal	89%	10.38%	907.2	$250.00	0.77	0.87	$0.310	$0.032
Urea	99%	0.47%	907.2	$275.00	0.04	0.04	$0.306	$0.001
Macro-minerals	100%	1.91%	907.2	$100.00	0.14	0.14	$0.110	$0.002
Vitamins/trace-minerals	100%	0.71%	907.2	$500.00	0.05	0.05	$0.551	$0.004
Ionophore	100%	0.02%	0.45	$5.00	0.00	0.00	$11.023	$0.002

Table 5-4. Beef growing phase partial budget for steers receiving brown midrib-3 (BMCS) and isogenic normal (Control) corn silage based diets

Item	Control	BMCS
Weights and Prices		
Purchase weight, kg	244.0	246.3
Shrunk sale weight, kg	358.3	359.3
Delivered purchase price, $/kg[a]	1.82	1.82
Purchase cost, $/steer	443.31	447.43
Sale price, $/kg[b]	1.67	1.67
Gross revenue, $/steer	597.24	598.75
Gross margin. $/steer	153.93	151.32
Performance		
Daily gain, kg	1.02	1.01
Gain:Feed, DM basis	0.145	0.135
Out shrink,%	0.00	0.00
Death loss, %	1.00	1.00
Days on feed, d	112	112
Feed costs		
Feed price, $/t DM	127.00	130.65
Feed cost, $/steer	100.00	109.16
Other operating costs		
Yardage rate, $/steer/d	0.30	0.30
Yardage amount, $/steer	33.60	33.65
Veterinary and medication, $/steer	10.00	10.00
Death loss, $/steer	4.43	4.47
Operating cost subtotal, $/steer	48.03	48.12
Interest rate	9.50	9.50
Interest on cattle, $/steer * 1.00	13.23	13.38
Interest of feed, $/steer * 0.50	1.48	1.62
Interest on other operating, $/steer * 0.50	0.64	0.65
Total interest, $/hd	15.36	15.64
Total operating cost, $/steer[c]	163.39	172.92
Return to labor and management, $/steer	(9.46)	(21.60)
Feed cost of gain, $/kg	0.87	0.97
Total cost of gain, $/kg[c]	1.43	1.53

[a]CATTLE-FAX, average (1990-2000) for 250 kg feeder calves during October.
[a]CATTLE-FAX, average (1990-2000) for 363 kg feeder calves during February.
[c]Excludes animal purchase price.

134

Difference in Gain:Feed

Difference in ADG, kg/d	-0.04	-0.03	-0.02	-0.01	0	0.01	0.02	0.03	0.04	0.05
-0.45	(79.01)	(66.68)	(56.31)	(47.49)	(39.88)	(33.25)	(27.43)	(22.27)	(17.67)	(13.55)
-0.36	(66.43)	(54.14)	(43.81)	(35.02)	(27.43)	(20.83)	(15.03)	(9.89)	(5.31)	(1.20)
-0.27	(56.94)	(44.68)	(34.38)	(25.61)	(18.05)	(11.46)	(5.68)	(0.55)	4.02	8.12
-0.18	(49.52)	(37.29)	(27.01)	(18.26)	(10.72)	(4.14)	1.63	6.74	11.30	15.40
-0.09	(43.57)	(31.36)	(21.10)	(12.36)	(4.83)	1.73	7.49	12.60	17.15	21.24
0	(38.68)	(26.49)	(16.25)	(7.52)	0.00	6.55	12.31	17.40	21.95	26.03
0.09	(34.60)	(22.42)	(12.19)	(3.48)	4.03	10.58	16.32	21.42	25.96	30.03
0.18	(31.15)	(18.98)	(8.76)	(0.05)	7.45	13.99	19.73	24.82	29.35	33.43
0.27	(28.18)	(16.02)	(5.81)	2.89	10.39	16.92	22.66	27.74	32.27	36.34
0.36	(25.60)	(13.45)	(3.25)	5.45	12.94	19.46	25.20	30.27	34.80	38.87
0.45	(23.34)	(11.20)	(1.00)	7.68	15.17	21.69	27.42	32.49	37.02	41.08

Figure 5-1. Return to labor and management ($/steer) as a result of difference in average daily gain (ADG) and feed efficiency (Gain:Feed). Based on the isogenic normal (Control) corn silage diet in Table 5-4. Assumes that cost of producing silage does not change.
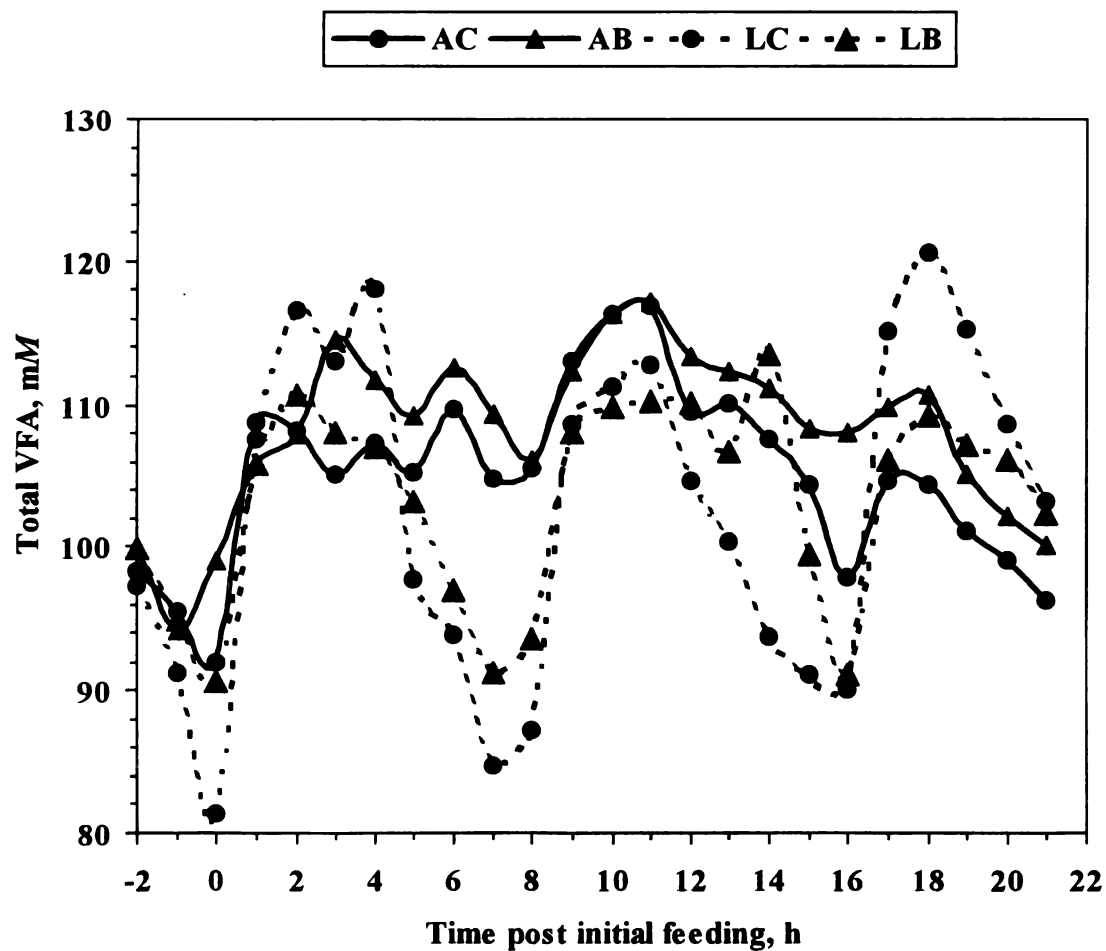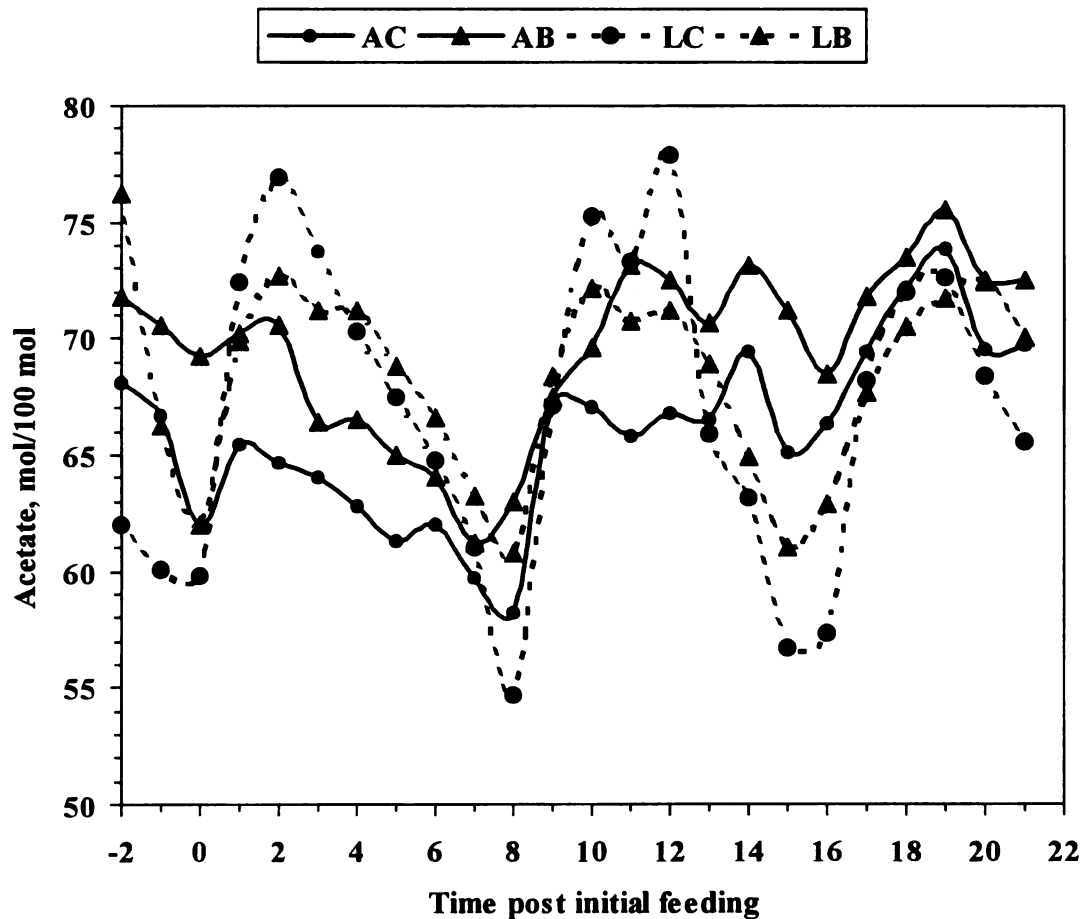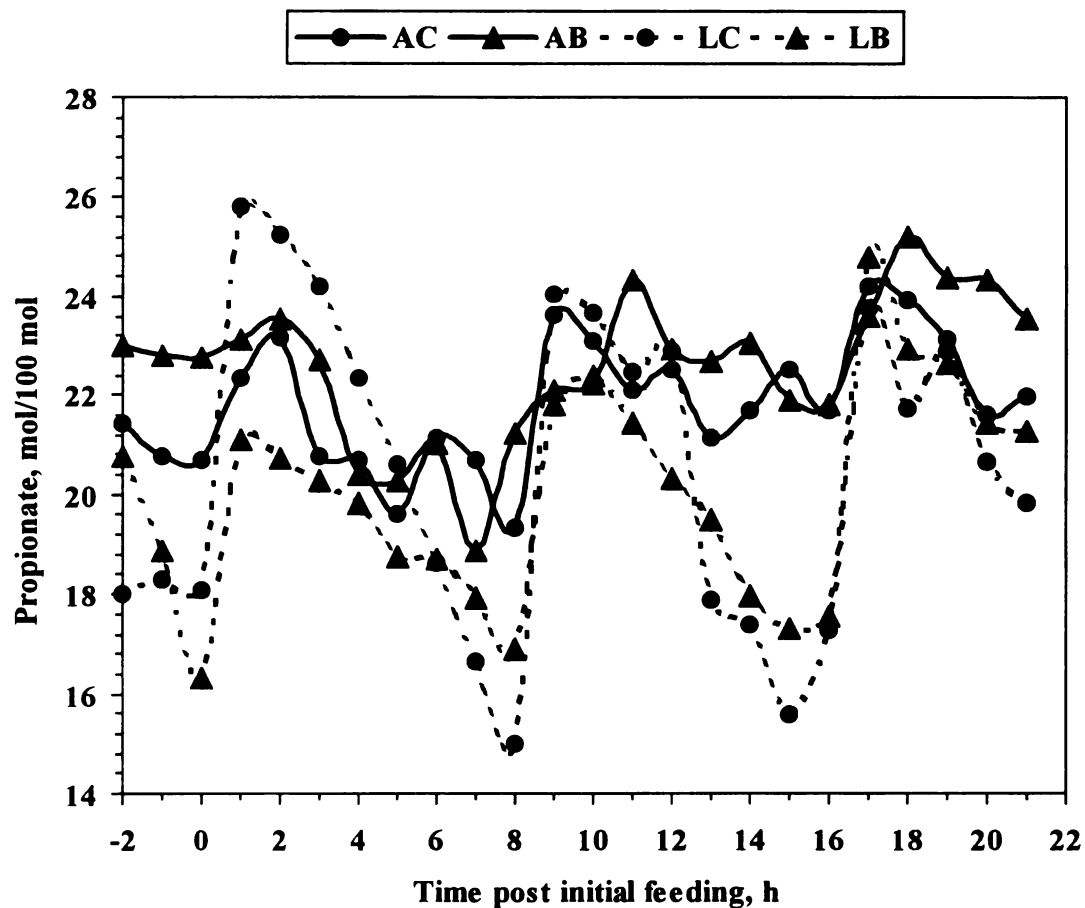
135

APPENDICES

Figure A-1. Effects of feeding ad libitum isogeneic normal control (AC), ad libitum brown midrib-3 (AB), limited isogeneic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on total ruminal VFA concentration over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × hybrid interaction ($P < 0.001$). SEM = 4.14.
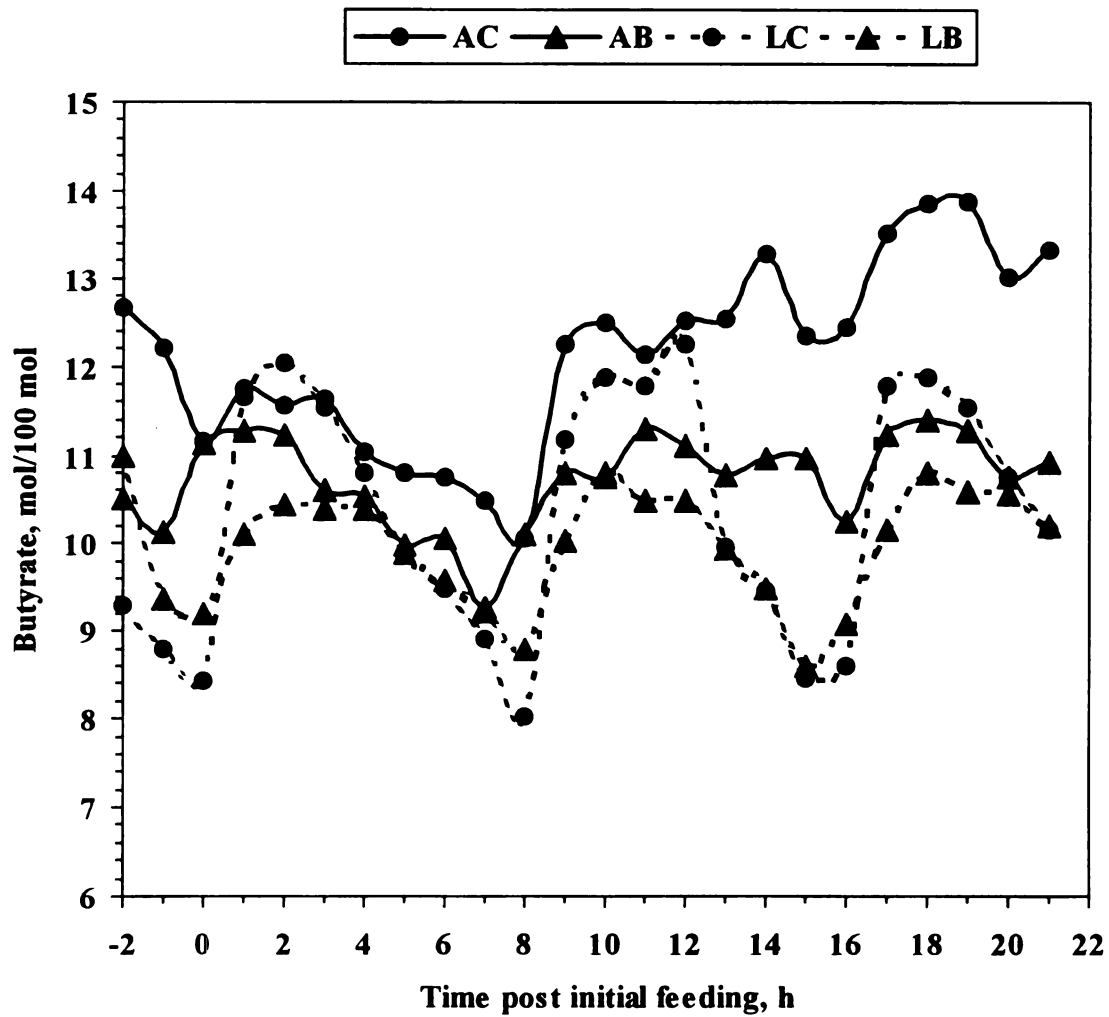
Figure A-2. Effects of feeding ad libitum isogeneic normal control (AC), ad libitum brown midrib-3 (AB), limited isogeneic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on molar percentage of acetate over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × hybrid interaction ($P < 0.001$). SEM = 2.64.

Figure A-3. Effects of feeding ad libitum isogeneic normal control (AC), ad libitum brown midrib-3 (AB), limited isogeneic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on molar percentage of propionate over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × hybrid interaction ($P < 0.001$). SEM = 1.30.

Figure A-4. Effects of feeding ad libitum isogeneic normal control (AC), ad libitum brown midrib-3 (AB), limited isogeneic normal control (LC), or limited brown midrib-3 (LB) corn silage diets on molar percentage of butyrate over time (Trial 1). Feed offered at 0, 8, and 16 h. Time × hybrid interaction ($P < 0.05$). SEM = 0.70.

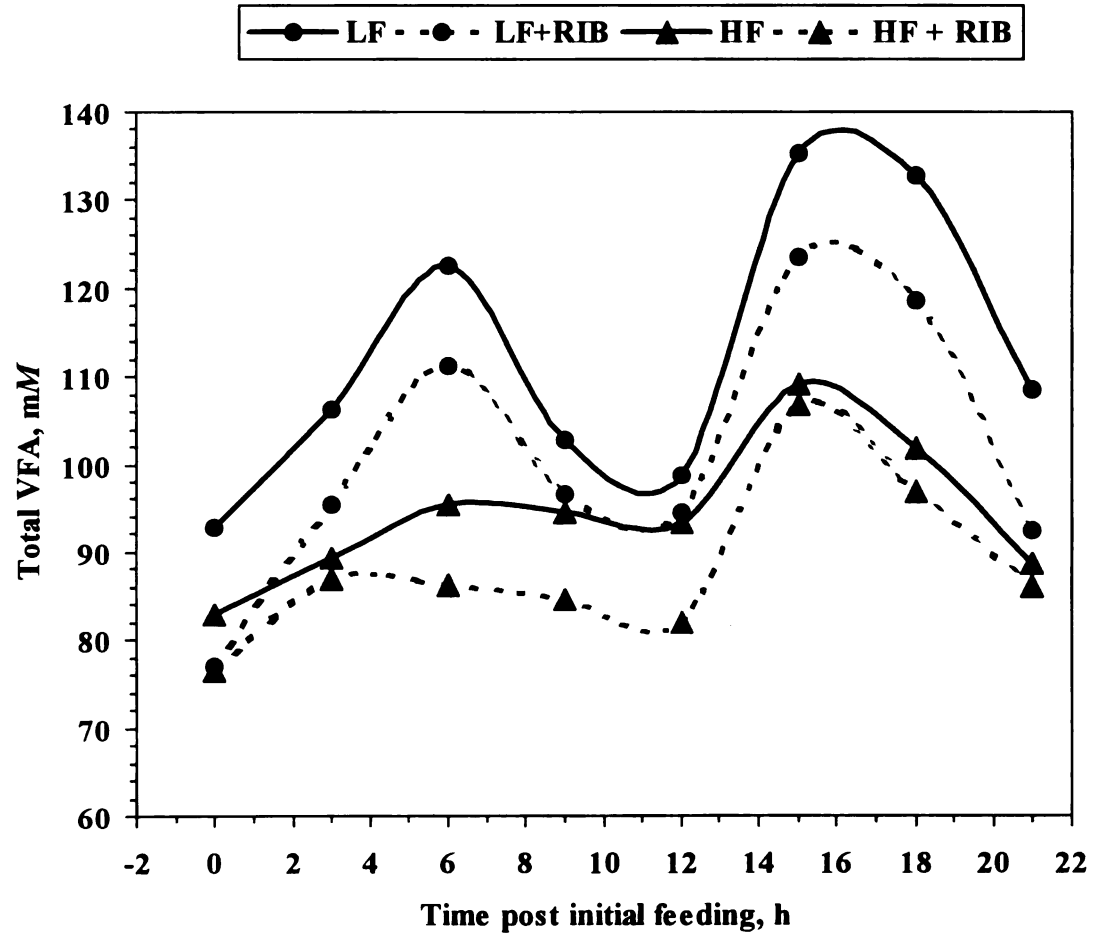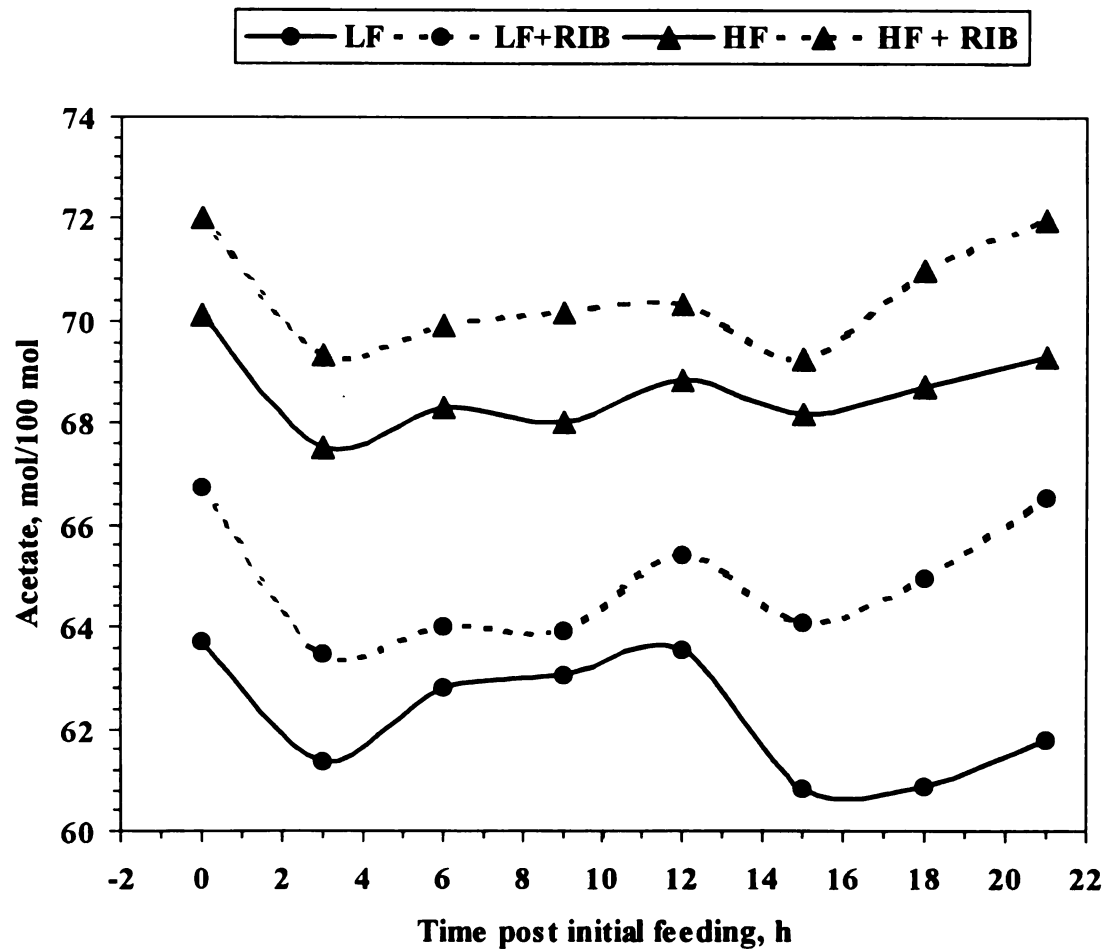Figure B-1. Effects of feeding a normal corn hybrid (low-fiber; **LF**) or its male-sterile counterpart (high-fiber; **HF**), without or with rumen inert bulk (**RIB**) on total ruminal VFA concentration over time. Feed offered at 0, 12 h. Time × fiber level interaction ($P <$ 0.0001). SEM = 4.9.

Figure B-2. Effects of feeding a normal corn hybrid (low-fiber; **LF**) or its male-sterile counterpart (high-fiber; **HF**), without or with rumen inert bulk (**RIB**) on molar percentage of acetate over time. Feed offered at 0, 12 h. Time × fiber level × bulk interaction (P < 0.01). SEM = 0.54.
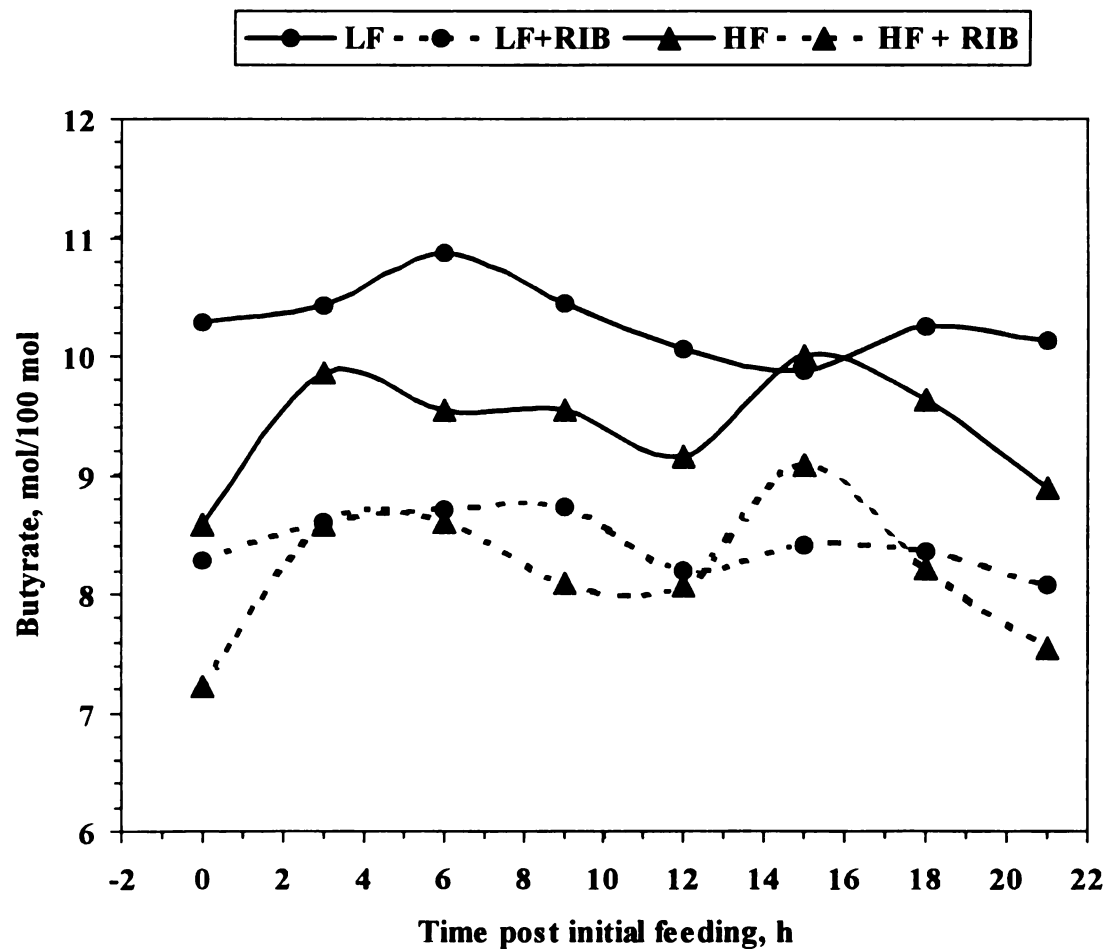
Figure B-3. Effects of feeding a normal corn hybrid (low-fiber; **LF**) or its male-sterile counterpart (high-fiber; **HF**), without or with rumen inert bulk (**RIB**) on molar percentage of butyrate over time. Feed offered at 0, 12 h. Time × fiber level interaction ($P <$ 0.0001). SEM = 0.40.

VITA

Kent Eric Tjardes was born on February 4, 1972, in Gibson City, Illinois, son of Harry and Gale Tjardes. Kent was raised on a grain and cattle farm and was a 10-year active member of the Illinois Junior Polled Hereford Association. He graduated as valedictorian from Gibson City Junior-Senior High School in 1990. In 1994, Kent received a B.S., with honor, in Animal Science from the University of Illinois, Urbana-Champaign. He continued at the University of Illinois and received a M.S., in Ruminant Nutrition, in 1996, and began work on his Ph.D. at Michigan State University in August of 1996. Kent is a member of the American Society of Animal Science, and American Dairy Science Association. He is also a member of the Gamma Sigma Delta honorary society and alumni of the Alpha Chapter of Alpha Gamma Rho social/professional fraternity. After completion of his Ph.D., Kent will become a faculty member in the Department of Animal and Range Science at South Dakota State University. Kent and his fiancé, Michelle Smiricky, will be wed on June 1, 2002.