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IMPACTS OF SMALL INTESTINAL ENZYME ACTIVITY AND
VARYING CORN GRAIN PROCESSING TYPES ON FEEDING
BEHAVIOR, AND GROWTH PERFORMANCE OF FINISHING BEEF
STEERS

BY

WYATT SMITH

A Thesis submitted in partial fulfillment of the requirements for

Masters of Science

Major Animal Science

South Dakota State University

2019

IMPACTS OF SMALL INTESTINAL ENZYME ACTIVITY AND
VARYING CORN GRAIN PROCESSING TYPES ON FEEDING
BEHAVIOR, AND GROWTH PERFORMANCE OF FINISHING BEEF
STEERS

WYATT SMITH

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

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ACKNOWLEDGEMENTS

I would like to thank my advisors Dr. Joe Cassady and Dr. Kirstin Hales for all their support and help. Their patience in teaching me the process of scientific writing is truly amazing. Along with my advisors I would like to thank Dr. Andrew Foote and Dr. Derek Brake for their help with research and writing. I would also like to thank Dr. Wes Gentry, Dr. Ethan Blom, Dr. Zachary Smith and Grady Ruble for their friendship, and mentorship. Graduate school would not have been as fun or educational without them around. Thank you to my family and friends for their continued support. Finally, I would like to thank my wife Emily Smith for all you sacrifice for me to continue my education. There is no way I would have made it through my masters without your unwavering support.

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ABBREVIATIONS

ADG	Average daily gain
BF	Backfat
BHBA	β -hydroxybutyrate
BLD	Blended corn-based diet containing 50:50 whole shelled corn and high moisture corn
BW	Body weight
DM	Dry matter
DMD	Dry matter digestibility
DMI	Dry matter intake
DOF	Days on feed
DP	Dressing percentage
DRC	Dry-rolled corn
DVI	Daily variation in dry matter intake
EBF	Empty body fat
EID	Electronic identification tag
eNDF	Effective neutral detergent fiber
G:F	Feed efficiency
HCW	Hot carcass weight
HMC	High-moisture corn
KPH	Kidney heart and pelvic fat
MARB	Marbling score
ME	Metabolizable energy
MGAM	Maltase-glucoamylase
N	Nitrogen
NDF	Neutral detergent fiber
NEFA	Non-esterified fatty acids
OM	Organic matter
PUN	Plasma urea-nitrogen

<i>q</i> PCR	real-time polymerase chain reaction
RDG	Residual daily gain
REA	Ribeye area
RFI	Residual feed intake
RFID	Radio frequency identification
SEM	Standard error of the mean
VFA	Volatile fatty acids
WSC	Whole-shelled corn
YG	Yield grade

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ABSTRACT

IMPACTS OF SMALL INTESTINAL ENZYME ACTIVITY AND VARYING CORN
GRAIN PROCESSING TYPES ON FEEDING BEHAVIOR, AND GROWTH
PERFORMANCE OF FINISHING BEEF STEERS

WYATT SMITH

2019

The objective of this study was to quantify the differences in activity of jejunal maltase and isomaltase between 2 groups of steers with average dry matter intake (DMI) and differing average daily gain (ADG). Dry matter intake and ADG were measured in crossbred steers ($n = 69$). Jejunal mucosal samples were collected from 8 steers with the greatest (high) or least (low) ADG and average DMI (± 0.55 standard deviation). Homogenates of jejunal mucosa were incubated with increasing amounts of maltose and isomaltose to determine the disaccharidase kinetics. Neither the K_m of isomaltase ($P = 0.15$) or maltase ($P = 0.43$) differed between group. The isomaltase V_{max} expressed per gram of protein ($P = 0.11$) or tissue ($P = 0.18$), respectively, did not differ between groups of steers. While previous studies have indicated that disaccharidase expression is associated with differences in ADG, data presented here indicate that differences in enzyme activity at the end of a feeding period are minimal. The objective of the second study was to evaluate the impact of corn-grain processing on feeding behavior and growth performance. There were 3 diets fed which differed in grain processing; whole-shelled corn-based diet (WSC); a blended corn-based diet containing a 50:50 whole-shelled corn and high-moisture corn (BLD); and a high-moisture corn-based diet (HMC).

Meal duration, average meal size, and number of meals differed across treatments ($P \leq 0.01$). For meal duration, HMC was greater ($P \leq 0.01$) than WSC and BLD which did not differ ($P \geq 0.13$). The average meal size was greatest for WSC which tended to differ ($P = 0.07$) from BLD, and differed ($P \leq 0.01$) from HMC which had the least kg of intake at each meal. The HMC treatment consumed the greatest number of meals and differed from WSC and BLD ($P \leq 0.01$); whereas, WSC had the least number of meals and tended to differ from BLD ($P = 0.09$). Though the growth performance resembled previous work, no differences in steer growth performance or DMI were detected in the current experiment.

CHAPTER 1: LITERATURE REVIEW

FEED EFFICIENCY

It has been estimated that feed-related costs are 55 to 75% of the total costs associated with beef cattle production (NRC, 2000). The primary feed inputs used in the United States (U.S.) feedlot industry are harvested feedstuffs, such as corn. The U.S. feedlot industry first evolved when energy and grain sources were relatively inexpensive; however, these conditions have changed. With corn being the primary component of feedlot finishing diets, grain prices have influenced cost of gain and profitability. Feedlots have suffered financial losses due to cyclical high-priced corn market (Ahola and Hill, 2012), and the recent demand for corn supply by the ethanol industry. Competition for corn and land resources could lead to a reduction in the amount of meat produced by the beef industry, resulting in decreased sustainability of beef production (Hill, 2012). Furthermore, because of increased cost of gain and narrowing profit margins, conversion efficiency of harvested crops to beef reiterating the need for improved feed efficiency (G:F) of beef cattle.

Dry matter intake (DMI) is directly correlated with production outputs such as G:F and average daily gain (ADG). The measure of G:F is a simple ratio of production outputs in relation to feed inputs over a certain period of time, where output is measured as weight gain of growing animals and input is measured as DMI. Thus, a higher value indicates an animal is more feed efficient (Dickerson, 1978). To accurately measure G:F, 2 essential pieces of data must be collected: 1) DMI and 2) ADG. The combination of G:F, ADG and DMI allow for the computation of different measures of feed efficiency, such as residual daily gain (RDG). Residual daily gain was first introduced by Koch et al. (1963) as a way to quantify the efficiency of growth. Koch et al. (1963) collected data on 1,324 individually fed bull and heifer calves from Nebraska and Oklahoma, in order to

evaluate heritability of feed efficiency and its genetic relationship with other measurable traits such as feed intake and ADG. The RDG of a growing animal is defined as a residual term from the regression of ADG on DMI. Higher (positive) phenotypes of RDG are desirable, indicating that animals are gaining more weight than expected based on their DMI. Residual daily gain is considered more of a growth trait than a true efficiency trait, but its concept does parallel that of residual feed intake (RFI). Residual daily gain can be problematic due to its correlation with ADG and thus, is confounded by its relationship with many other performance traits (Crews and Carstens, 2012). The measure of RFI was also first proposed by Koch et al. (1963). Residual feed intake is the difference between actual feed intake and that predicted based on the requirement for products such as body weight (BW) gain. The greater negative the RFI value, the more feed efficient the animal (Koch et al, 1963). Kennedy et al. (1993) reported that variation in RFI reflects differences in efficiency with which animals use the feed for gain or maintenance of BW. Kennedy et al. (1993) also reported that the heritability of RFI based on genotypic regression was close to zero; and indicated that measurement of DMI provides little additional genetic information than the measurement of ADG.

ENZYME ACTIVITY

The ruminant digestive system provides an exceptional advantage over monogastric digestive systems, with the ability to digest structural (fiber) and non-structural (starch, etc.) carbohydrates. The ruminant ability to digest fiber is accredited to the microbial population within the rumen (Hungate, 1966). The microbes digest the fiber and starch; and as a result, they produce volatile fatty acids (VFA) as an end-product. Volatile fatty acids are produced when glycolytic bonds of carbohydrates are broken down in to glucose and further metabolized. The products of the energy yield

pathways, acetyl CoA and lactate are further metabolized, acetyl CoA is metabolized to acetate and butyrate while lactate forms propionate (Van Soest, 1994). The total VFA concentration in the rumen of beef cattle is normally between 70 and 130 mM, (France and Siddons, 1993). Furthermore, the ratio of the three most prominent ruminal VFA, acetate, propionate, butyrate, is 50:40:10 in finishing feedlot diets, respectively (Bevans et al., 2005). The host (animal) uses VFA as an energy source for ruminal and intestinal epithelium (Owens et al., 1998). Harmon and McLeod (2001) stated 13 to 18% of gross energy intake in cattle can be lost during pregastric fermentation. Energetically, the small intestine is more efficient at capturing energy from the breakdown of starch via enzymatic digestion. Though the small intestine of ruminants is more energetically efficient at starch degradation there are still limiting-steps in this process. It has been hypothesized that enzyme activity is the rate-limiting step in starch degradation within the small intestine (Owens et al., 1986).

α -Amylase

Small intestinal starch assimilation starts within the lumen of the small intestine with the secretion of pancreatic α -amylase. α -Amylase is endoglycosic, meaning it can hydrolyze internal α -1-4 glucosidic bonds and doesn't need the terminal ends of the amylose to be active. Previous reports have correlated similarity between non-ruminant and ruminant α -amylase (Kreikemeier et al., 1990; Walker and Harmon, 1995). The products of this initial hydrolyzation step include maltose, maltotriose and various limit dextrans (Harmon, 1993). The concentrations of α -amylase in the small intestine increase with animal age and can vary depending on the type of diet. At birth, calves have low

concentrations of pancreatic α -amylase (Siddons, 1968), but the concentration of pancreatic α -amylase increases with age (Morrill et al., 1970).

Several previous studies compared concentrate and forage-based diets in order to evaluate the impact of diet on pancreatic enzyme concentrations. Clary et al. (1969) allowed steers to graze forage or fed an all-concentrate diet for 126 days before harvest. The steers fed the all-concentrate diet had a 40% greater pancreatic α -amylase activity compared to the steers fed forage. Janes et al. (1985) reported a similar tendency in lambs that were fed either dried grass hay, or a dry-rolled corn (DRC) based diet for 4 wk with a 34% increase in pancreatic α -amylase activity of lambs that consumed the DRC diet.

One of the first studies that evaluated the effects of energy intake on postruminal digestive enzymes was conducted by Russell et al. (1981) where steers were fed alfalfa hay or a whole-shell corn (WSC) and corn silage-based diets to meet maintenance energy requirements. Later in the study, they were also fed the same diet at 2 or 3 multiples of maintenance. At an isocaloric intake, the pancreatic concentrations of α -amylase in the steers fed the WSC and corn silage diet were slightly lower than the steers fed the alfalfa diet (Russell et al., 1981). However, increasing the caloric intake of WSC and corn silage diets from 1 to 2 multiples of maintenance increased α -amylase concentrations in the pancreases two-fold (Russell et al., 1981). When energy intake increased to 3-times maintenance no further increase in pancreatic α -amylase concentration was observed. These results suggest that pancreatic α -amylase does respond to differing levels of caloric intake; however, this response was not observed at energy intake greater than 3-times maintenance (Russell et al., 1981). In work conducted by Kreikemeier et al. (1990), calves were fed 90% forage (alfalfa hay) or a 90% wheat-sorghum grain blend diet at 1 or

2 multiples of maintenance for 140 d. They reported that regardless of diet as energy intake increased, the pancreatic concentration of α -amylase also increased by 55% and the total mg of α -amylase within the pancreas increased by 140% (Kreikemeier et al., 1990). However, when intake energy level is constant across both diets the pancreatic concentration of α -amylase and total mg of α -amylase in the pancreas was decreased in calves consuming the 90% grain diet compared to those fed the forage diet. α -amylase concentrations in the small intestinal digesta and total mg of α -amylase in the small intestinal digesta were 34 and 50% higher, respectively, in the calves fed forage-based diets. This indicates greater secretion of α -amylase from the pancreas when forages vs. concentrates are fed. These results of decreases in pancreatic α -amylase concentration with increased starch intake are in contrast to others (Clary et al., 1969; Janes et al., 1985), who reported increased pancreatic α -amylase concentrations with greater starch intakes. The results of Kreikemeier et al. (1990) coincided with those of Russell et al. (1981), who compared forage and grain were compared at a maintenance energy intake. Cumulatively, all studies that observed increases of pancreatic α -amylase concentrations with increased starch intake also had increases in total energy intake, thus suggesting a positive correlation between energy intake and α -amylase concentrations.

As discussed previously, concentration and secretion of pancreatic α -amylase can be manipulated nutritionally. Therefore, an understanding of how specific mechanisms of pancreatic α -amylase are regulated is lacking. Interest in specific mechanisms of pancreatic α -amylase regulation began with Chittenden et al. (1984); when they duodenally infused 200 g/d of glucose, maltose, or starch into wethers for 23 d while monitoring pancreatic α -amylase secretion. The glucose increased pancreatic α -amylase

secretion from 0 d to 16 d. thus, there was no difference in secretion from 16 d to 23 d (Chittenden et al., 1984). Pancreatic α -amylase secretion did not differ for wethers receiving maltose infusions from 0 d to 23 d. However, in those wethers receiving starch infusions, pancreatic α -amylase secretion decreased from 0 d to 23 d. To further evaluate the relationship between post-ruminal non-structural carbohydrate supply and pancreatic enzyme secretion, Walker and Harmon (1995) infused steers either ruminally or abomasally with partially hydrolyzed starch or a control (water). Cattle infused with partially hydrolyzed starch into the abomasum had a 60% decrease of pancreatic α -amylase secretion compared to controls. Though secretion of pancreatic α -amylase decreases, pancreatic fluid secretion was increased by 19% (Walker and Harmon, 1995). Thus, providing substantial evidence that increases in post-ruminal starch concentrations can decrease pancreatic α -amylase secretions. The increased carbohydrate concentration may cause these negative feedback mechanisms of α -amylase secretions in the lumen of the small intestine. Swanson et al. (2002) infused glucose and partially hydrolyzed starch into the abdomen of steers fitted with pancreatic cannulas. Results were similar to that of Walker and Harmon (1995), where both carbohydrate sources had an inverse effect of pancreatic α -amylase secretion. The conclusion of these experiments may indicate that DMI may not be the sole regulation mechanism for secretion of pancreatic α -amylase, as starch entering the small intestine may play a role in pancreatic α -amylase regulation as well. Nonetheless, feeding starch-based diets (Kreikemeier et al., 1990) or infusing non-structured carbohydrates post-ruminally into cattle (Swanson et al., 2002; Walker and Harmon, 1995) has consistently reduced pancreatic α -amylase concentration and secretion.

Mucosal Enzymes

Within non-ruminant small intestinal mucosa there are 2 enzymes responsible for carbohydrase activity, or the breakdown of starch sucrose-isomaltase and maltase-glucoamylase. Within humans approximately 80% of mucosal maltase is hydrolyzed by sucrose-isomaltase, while the remaining 20% is thought to be hydrolyzed by maltase-glucoamylase (Galand, 1989). Work conducted in humans and porcine have reported that maltase-glucoamylase is the primary disaccharidase at low substrate concentrations (Quezada-Calvillo et al., 2007a). As substrate concentration increases, maltase-glucoamylase becomes saturated and sucrose-isomaltase becomes the primary disaccharidase. Further studies were conducted to evaluate the importance of maltase-glucoamylase activity in humans (Quezada-Calvillo et al., 2008), and found removing the maltase-glucoamylase decreased the intestinal starch assimilation capacity by 40% (Quezada-Calvillo et al., 2008). Coombe and Siddons (1973) reported maltase activity involves the protein maltase-glucoamylase. Though the characteristics of these proteins in ruminants are not fully understood, more research is needed to understand the limitations of post-ruminal carbohydrate hydrolyzation.

Some published data that evaluated starch or energy intake impacts the total concentration of small intestinal brush border enzymes of cattle and sheep include (Russell et al., 1981; Janes et al., 1985; Kreikemeier et al., 1990). These studies provide evidence of the limited capacity diet has on the alteration of disaccharidases activity within the small intestine of cattle. Conversely, the work reported by Mcneill et al. (1974) report dramatic changes in small intestinal maltase activity, where they duodenally infused wethers fed alfalfa hay with increased concentrations of glucose (60, 120, and

180 g/d). As glucose increased from 0 to 180 g/d for 2 d, small intestinal maltase activity increased 28-fold but then decreased to a stable level by 5 d. Bauer et al. (2001b) abomasally infused sheep with 144 g/day of partially hydrolyzed starch for 7 d, which resulted in a decrease of jejunal maltase activity. However, within the same experiment, jejunal maltase activity decreased when 960 g/day of partially hydrolyzed starch was infused into the abomasum of cattle for 7 d (Bauer et al., 2001a). Rodriguez et al. (2004) post-ruminally infused glucose or partially hydrolyzed starch into steers for 40 d and reported increases of maltase activity for both treatments. In a more recent study, Foote et al. (2017) evaluated natural variation of small intestinal disaccharidases expression in the jejunum of steers with divergent ADG. Cattle with higher ADG had an increase in the gene expression of maltase-glucoamylase (MGAM) a brush border disaccharidase (Foote et al., 2017). After reviewing the literature in this section of small intestinal enzyme activity one may suggest that ruminant small intestinal mucosal enzymes are highly variable and have a small response to dietary manipulation. Further research should be conducted on the natural variation of small intestinal mucosal enzyme activity of ruminants to gain a better understanding of post-ruminal starch digestion limitations.

GRAIN PROCESSING

Events of grain processing were first recorded in the 1840s when the corn sheller and hammer mill were invented. Since this time, advancement in technology has furthered the processing methods used in the feedlot industry (Matsushima, 2006). Methods such as grinding, crimping, pelleting, extruding, popping, micronizing, roasting, soaking, cooking, steam-rolling, steam flaking, high moisture ensiling, pressure cooker-roll, reconstitution, and exploding have been researched for decades (Matsushima, 2006). Grain processing is used to increase energy or starch availability in a cost-effective

manner (Hale, 1973; Owens et al., 1997). The increase in energy availability is established by reducing grain particle size, thus increasing the surface area available for microbial attachment and colonization, which increases the rate and extent of starch digestibility (Rooney and Pflugfelder, 1986). Grain processing increases starch availability by destroying the pericarp or the outer protective layer of the grain kernel (Hale, 1973). This multilayer pericarp contains high concentrations of lignin and waxy esters which act a barrier from microbial colonization and water uptake (McAllister et al., 2006). Once the pericarp is destroyed, microbes can easily penetrate the endosperm cell wall and begin digesting starch granules located within the endosperm. However, in corn and sorghum grains the starch of the endosperm is tightly packed in a protein matrix, which is difficult for microbes to digest. Therefore, grain processing also breaks down the protein matrix through denaturation of amino acid complexes within matrix. (McAllister et al., 1994). Ørskov (1976) reported that grain processing is a balance between an optimal increase of digestibility and a manageable rate of fermentation. Grain processing is widely used within the feedlot industry today. In a recent survey of consulting feedlot nutritionist, 73% of respondents used some processed grain, primarily corn, in their finishing diets (Samuelson et al., 2016).

In a 6-trial series of studies Tonroy et al. (1974) evaluated the growth performance and feed intake of different corn grain processes, WSC, DRC, and high moisture corn (HMC) in cattle. The ADG did not differ between processing techniques for 5 of the 6 studies. In experiment 2 the HMC fed cattle had 10% lower ADG, this was accredited to the moisture content of the grain (72.2% DM). The depression was likely due to the increased rate of starch digestibility and bouts of subclinical acidosis. Yet,

Tonroy et al. (1974) reported a 9 to 25% increase in G:F for cattle fed HMC compared to WSC or DRC for 5 study's and in experiment 2 the G:F did not differ across processing type. Others have reported a 5% increase in G:F for HMC compared to WSC and DRC when fed to cattle (Macleod et al., 1976; Wagner et al., 1976).

In a 3-trial series of studies Stock et al. (1987) evaluated growth performance differences in feedlot cattle fed different proportions of HMC and WSC. Diets consisted of 80% grain, 10% corn-silage, and 10% supplement. The 3 trials led to the conclusion that feeding HMC and WSC together during the step-up to finishing diet phase may improve ADG and G:F compared to steers feed only 1 grain processing type. Thus, using HMC and WSC together was beneficial. Also, improvements in ADG and G:F within the step-up phase can translate to improvement in ADG and G:F over the entire feeding period.

There has been debate over the advantages and disadvantages of feeding WSC compared to processed corn grains. In an extensive review, DRC did not improve starch digestibility over WSC (Owens et al., 1986) or cattle growth performance (Owens et al., 1997). Some trials report ADG and G:F did not differ for cattle consuming WSC diets compared to processed grain diets (Vance et al., 1972; Ørskov et al., 1974; Owens et al., 1997). The discrepancy of these earlier results compared to more recent trials (Stock et al., 1987; Swingle et al., 1999) is likely because of differences in bunk management. Advancement in feeding strategies to reduce acidosis have likely increased the ADG and G:F advantages commonly reported when feeding processed grains.

Whole-shelled corn is not typically used in large-scale commercial feedlot settings. Samuelson et al. (2016) reported that only 4.35% of respondents did not utilize

corn processing throughout the entire feeding phase. Ørskov (1986) suggested that the main reason for not feeding WSC is the number of whole kernels found in feces, which infers decreased digestibility of WSC. Many of the studies reporting a greater starch digestibility in DRC versus WSC have used yearling cattle and not calves (Ørskov et al., 1974; Galyean et al., 1979; Turgeon et al., 1983). Conversely, those who used calves (Loerch and Fluharty, 1998) have often reported no differences in growth performance between WSC and DRC. The difference in cattle age may be accredited to the differing results of these experiments as mastication capacity is greater in younger cattle than older cattle (Mathison, 1996). The digestibility of WSC is increased through extensive chewing, increased surface area and increasing microbial attachment to starch particles (McAllister et al., 1994).

Owens et al. (1997) reviewed data from 164 studies and cattle feeder's day reports with different varieties of grain sources, processing methods, roughage sources, and roughage levels being reported. The mean metabolizable energy (ME) was reported for WSC (3.56 Mcal/kg) and DRC (3.26 Mcal/kg). There was no difference in ADG between cattle fed WSC and DRC. However, DMI was greater for cattle fed DRC while G:F was greater for cattle fed WSC. Owens et al. (1997) outlined 4 factors that may have attributed for WSC having a higher ME. The first factor is roughage inclusion in the diet; the WSC diet typically had a lower percentage of roughage compared to processed diets. Another factor was greater chewing or rumination of the WSC because of increased particle size or effective neutral detergent fiber (eNDF). The increase in eNDF would stimulate greater amounts of salivation and increase buffering capacity to neutralize acid production in the rumen. Increased salivation and subsequent buffering capacity could

reduce the incidence of subclinical acidosis, which would improve feed efficiency and DMI (Stock et al., 1995). Another reason is thought to be changes in site of starch digestion from the rumen to the small intestine, as the coarser particle size (WSC) is expected to improve energetic efficiency if total tract digestion is not depressed (Owens et al., 1986). Thus, the conclusion was that there was little difference between WSC and DRC in feedlot cattle diets; however, those results should be interpreted with caution as they were derived from back-calculated ME values (based on growth-performance) and starch digestibility was not directly measured.

Gorocica-Buenfil and Loerch (2005) reported 3 experiments evaluating the effects of cattle age and dietary forage level when WSC or DRC-based diets were fed to feedlot cattle. The first experiment used 16 steers in a 2×2 factorial arrangement of age (weanling or yearlings) and grain processing (WSC or DRC). Cattle age and corn processing did not affect DM or starch digestibility, and no interaction between cattle age and corn processing was detected. The absence of an interaction between cattle age and corn processing fails to support the previous idea that younger cattle have greater chewing capacity. Though, it has been reported that younger cattle have greater chewing capacity than older cattle (Nicholson et al., 1971). However, Gorocica-Buenfil and Loerch (2005) suggested weanlings and yearlings may not have enough variation in age to detect differences in chewing capacities, and thus the effects on ADG and G:F may be negligible. Chewing or mastication becomes important when WSC is fed because the disruption of the cuticle of the corn kernel allows for the initiation of rumen fermentation of starch (Kotarski et al., 1992). The disruption of the cuticle can be achieved either

through mechanical (grain processing) or chewing (McAllister et al., 1994; Beauchemin et al., 2003).

In experiment 2, reported by Gorocica-Buenfil and Loerch (2005) effects of forage level and corn grain processing was evaluated using 180 steers allotted to 24 pens. There were 6 treatments: 1) high-forage (18.2% corn silage) 2) cracked corn high-forage and 3) WSC; high-forage shifting corn (whole corn for the first half of trial, then cracked corn until harvest; 4) low-forage (5.2% corn silage) cracked corn; 5) low-forage and WSC; 6) low-forage shifting corn (whole corn for the first half of trial, then cracked corn until harvest. Within the high-forage diets, steers fed DRC had 7% greater DMI compared to WSC; however, in the low-forage diets, grain processing did not affect DMI. In addition, no interaction between forage level and corn processing were found for ADG and G:F. When days on feed (DOF) was evaluated, cattle with fewer DOF grew faster and had greater G:F when fed DRC. Cattle with extended DOF had greater ADG and G:F when WSC was fed. The increased ADG and G:F for steers fed WSC with greater DOF may be accredited to decreased bouts of subclinical acidosis.

FEEDING BEHAVIOR

Research conducted in the mid to late 1980s found that feedlot steers exhibit a diurnal feeding behavior pattern in which corresponds to sunrise, sunset and feeding delivery (Stricklin, 1986). Hicks et al. (1989) observed 93 steers at 30-minute intervals for 24 hours on day 40 of a 138-day feeding trial to examine the diurnal patterns of feed consumed. Steers were fed 80% cracked corn, 11% chopped alfalfa, 3.9% cane molasses and 5.1% pelleted supplement Dry-matter basis (DMB) ad libitum. Hicks et al., (1989) reported steers spent 6.6, 15.5 and 54.4% of their time eating, ruminating, and laying,

respectively. Peak eating times occurred at 0650 (47.3% steers eating) and 1700 (36.8% steers eating), and these times correspond to delivery of fresh feed. There was an additional peak at 2100 (17.9% steers eating), which did not correspond with feed deliveries, but rather sunset. Reports of 3 major peaks in feed consumption by Hicks et al., (1989) are similar to previous work. Gonyou and Stricklin (1981); (1984) reported cattle fed ad libitum a 55% or 65% concentrate diet exhibited 3 major periods of eating activity during a 24-hour day. Major periods of eating activity were 0200, 0900, and 1900 h. The 0900 h may be in response to the morning feeding, while the 1900 h eating activity is 3 h following the evening feeding but is at the time of sunset. Night feeding at 0200 h cannot be explained. Further research in the area of feeding behavior may provide answers about night feeding.

In order to quantify number of visits to the bunk and time spent eating Laudert (1990) used a Pinpointer 4000 feeding system and reported that steers ate 13.5 times per day for a total of 80 min during a 12 to 14-hour daily observation, when fed a high-concentrate diet with either monensin or monensin plus tylosin. Laudert (1990) also reports cattle on a high concentrate diet with monensin plus tylosin had 15 meals each day vs. 12 meals each day with just monensin alone. Chirase et al. (1992) used similar methods Pinpointer 4000 feeding system and reported when cattle were fed a 95% concentrate diet that contained monensin steers visited the bunk 17 times each day while heifers visited the bunk 16 times each day. However, steers spent more time eating (38 vs. 30 minutes each day) than heifers.

Advancements in radio frequency identification (RFID)-based technologies have made it easier to objectively measure feeding behavior traits in larger groups of animals.

These advancements in technology were used by Sowell et al. (1998) to measure feeding behavior and health of steers entering the feedlot. Sowell et al. (1998) used 108 steers with initial BW of 139 kg for the first 32 d of the feeding period. The experiment was conducted in a commercial feedlot and used a GrowSafe System™. The system collected the exact time and duration of each bunk visit by each animal during the feeding period. Results from Sowell et al. (1998) suggested healthy cattle spent 66 minutes per day at the bunk during the 32 d while the morbid cattle spent 46 minutes at the bunk.

Schwartzkopf-Genswein et al. (2002) also used the GrowSafe System technology along with a video camera to quantify the interaction between bunk attendance and growth performance of steers and heifers. They reported heifers had 17.7 visits each day with a duration of 130 min each day at the bunk while steers averaged 15.4 visits each day with a duration of 102 min each day at the bunk. The frequency of bunk visits was not related to DMI, which led to the conclusion that duration at the bunk was a better indicator of DMI than the frequency of attendance, which is not intuitive.

Furthermore, Schwartzkopf-Genswein et al. (2011) evaluated the feeding behavior and animal growth performance in a 2-year study. Barley-based diets were fed to 274 steers across 2 years; year 1 (n = 115) with an initial BW of 293 kg, year 2 (n = 159) with an initial BW of 349. They reported cattle with more variable feeding behavior such as daily variation in DMI (DVI) had a greater ADG, and a tendency for increased G:F. The results provide evidence that cattle with sporadic eating patterns of greater variability have greater ADG, and this conclusion is contrary to industry perception.

In more recent work using an insentec roughage intake control feeding system Davis et al. (2014) evaluated the influence of DMI, dry matter digestibility (DMD) and

feeding behavior on BW gain of beef steers. One hundred and forty-three steers were used in the study with an initial BW of 338 kg. Steers were fed ad libitum with fresh feed being delivered twice daily at 0800 and 1500 h. The DMI accounted for the greatest variation with ADG, and DMI was positively correlated to the number of meals the steers consumed, meal size and the initial BW of the animal. These results differ from the observation of Schwartzkopf-Genswein et al. (2011) who reported variation in DMI was positively correlated with ADG. Results from Davis et al. (2014) suggested that DMD and passage rate (measured with titanium) does not account for much of the variation in ADG when steers are fed a common high-concentrate diet.

In order to gain a better understanding of accuracy for evaluating ADG and DMI in beef cattle using the Insentec Roughage Intake Control Feeding System, Ahlberg et al. (2018) performed a regression analysis using increasing days of the study (7, 14, 21, 28, 35, 42, 56, 63, and 70 d) in 1 week intervals, in order to evaluate the optimal study length in relation to accuracy for the differing variables (ADG and DMI). In order to relate the accuracy of the test to the duration of the study a Pearson and Spearman correlation was computed from each shortened test period and for the full 70-d test. Minimum test duration was determined when the Pearson correlation was greater than 0.95 for each trait. The results suggested a minimum test duration for DMI and ADG were 42 and 70 d, respectively. These results will help in the design of feeding trials using these systems in the future.

Many studies have evaluated the different effects of feeding behavior on animal performance. Also, there have been numerous studies evaluating the factors affecting DMI patterns in cattle including temperament (Voisinet et al., 1997) weather (Hahn,

1995), bunk space (McKinnon, 2001), and bunk management-strategies (Pritchard and Bruns, 2003). However, there has been little research on the effects of grain processing and feeding behavior patterns of feedlot cattle fed high-concentrate diets.

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CHAPER 2: ASSOCIATIONS OF MUCOSAL DISACCHARIDASE KINETICS AND
EXPRESSION IN THE JEJUNUM AND OF STEERS WITH DIVERGENT AVERAGE
DAILY GAIN

ABSTRACT

The objective of this study was to quantify differences in activity of jejunal maltase and isomaltase between 2 groups of steers with average dry matter intake (DMI) and differing average daily gain (ADG). Dry matter intake and ADG were measured in crossbred steers ($n = 69$) consuming a finishing diet containing 67.8% dry-rolled corn, 20.0% wet distillers grains with solubles, 8.0% alfalfa hay, and 4.2% vitamin/mineral supplement on a dry matter basis for 84 days. Blood samples were collected at 3 time points to evaluate metabolic differences related to ADG. Jejunal mucosal samples were collected from 8 steers with greatest (high) or least (low) ADG and average DMI (± 0.55 standard deviation). Homogenates of jejunal mucosa were incubated with increasing amounts of maltose and isomaltose to determine the disaccharidase kinetics. Neither the K_m of isomaltase ($P = 0.15$) or maltase ($P = 0.43$) differed between group. Isomaltase V_{max} expressed per gram of protein ($P = 0.11$) or tissue ($P = 0.18$), respectively, did not differ between groups of steers. Similarly, neither the maltase V_{max} expressed per gram of protein ($P = 0.33$) or tissue ($P = 0.45$), differed between groups. Protein concentration ($P = 0.45$) of the mucosa and small intestinal weights ($P = 0.69$) did not differ between groups. Relatively few metabolic differences were observed between the 2 groups of cattle through the feeding period as plasma urea nitrogen, triglycerides, β -hydroxybutyrate, non-esterified fatty acids, cholesterol, and lactate did not differ between groups ($P > 0.11$). There was a group \times day interaction for plasma glucose ($P < 0.01$), indicating that the high-ADG group was higher than the low-ADG on day 42. While previous studies have indicated that disaccharidase expression is associated with differences in ADG, data presented here can be interpreted that differences in enzyme activity at the end of a feeding period were minimal.

INTRODUCTION

The increasing cost of resources such as land, feed, and labor has raised the interest in feed efficiency or traits that impact feed efficiency in beef cattle. Feed-related cost can be 55 to 75% of the total production cost (NRC, 2000). Thus, maximizing the utilization of nutrients from the diet could have positive economic impacts on beef production.

Footo et al. (2017), reported differences in small intestinal expression of maltase-glucoamylase (*MGAM*) between 2 groups of cattle with average dry matter intake (DMI) and either low-average daily body weight gain (ADG) or high-ADG groups. Maltase-glucoamylase is a disaccharide bound to the luminal surface of enterocytes that hydrolyzes non-reducing terminal α -1,4 glycosidic bonds (Quezada-Calvillo et al., 2007b). Given that the small intestine of beef cattle is estimated to be 33 to 42% more energetically efficient at the digestion of starch than the rumen when cattle are fed a high-concentrate diet (Black, 1971; Owens et al., 1986), it is possible that increased mucosal enzyme activity could have a positive effect on feed efficiency. Though there is an increase in efficiency of starch degradation in the small intestine compared to the rumen, small intestinal starch digestion appears to be significantly less thorough than in other species (Owens et al., 1986). It has been suggested that disaccharidase activity limits starch digestion in the small intestine (Huntington, 1997). However, other studies have indicated that other steps of starch assimilation may be more limiting than disaccharidase activity (Russell et al., 1981; Sanford, 1982). Several studies have reported that disaccharidase expression and activity is not altered as cattle age (Siddons, 1968; Coombe and Siddons, 1973) or in response to dietary starch and energy concentration (Russell et al., 1981; Janes et al., 1985; Kreikemeier et al., 1990). Additionally, it appears

that several aspects of small intestinal function, including enzyme activity (Wang et al., 1998), morphology (Meyer et al., 2014), and gene expression (Lindholm-Perry et al., 2016) could contribute to differences in feed efficiency. Therefore, the objective of this experiment was to determine the difference of jejunal disaccharidase activity and expression in finishing beef steers with average DMI and differing ADG. The hypothesis was that steers with greater ADG have greater disaccharidase activity.

MATERIALS AND METHODS

All animal protocols were reviewed and approved by the U.S. Meat Animal Research Center Institutional Animal Care and Use Committee (protocol no. 43.2).

Animals

Steers ($n = 69$ total) used in this experiment were part of a larger study evaluating feed efficiency and were the result of breeding commercial cows to Charolais, Red Angus, and Simmental bulls that were in current use on ranches. The number of steers included from each sire-breed were 16, 24, and 29 for Charolais, Red Angus, and Simmental, respectively. Cattle were housed and managed as described previously (Foote et al., 2014) with the exception of steers receiving a Revalor S implant (Merck Animal Health, Madison, NJ) on day 0 of the experiment. Cattle received a ration that consisted of (dry matter basis) 67.75% dry-rolled corn, 20% wet distillers grains with solubles, 8% chopped alfalfa hay, and 4.25% supplement beginning 21 days prior to initiation of measurement of feed intake and growth. Feed intake, growth and performance were evaluated for 83 days using methods previously described by Foote et al. (2014, 2015). Blood samples (9 mL) were collected on day 0, 42, and 83 via jugular venipuncture into

tubes containing EDTA and placed on ice immediately. Plasma was collected by centrifuging blood at $3,000 \times g$ for 25 min at 4°C and stored in multiple aliquots at -80°C .

Immediately following the feed intake and growth evaluation, 8 cattle with the greatest or least ADG and average DMI (± 0.55 standard deviations) were selected for slaughter as described previously (Reynolds et al., 2017).

Tissue Collection

Beginning 4 days after measures of feed intake and growth, 2 steers (1 from each group) were slaughtered each day for a period of 2 weeks. A 10 cm segment of jejunum was taken at approximately 3 meters proximal to the ileo-cecal fold, cut open longitudinally along the mesentery line and rinsed free of digesta with phosphate-buffered saline. A razor blade was used to scrape the mucosa and samples were placed in liquid nitrogen for transport and then stored at -80°C . The remainder of the small intestine was separated from the mesenteric fat, the digesta was removed, and small intestine weighed.

Mucosal Enzyme Analysis

Analyses of mucosal enzymes were based on procedures described by Dahlqvist (1964) and Kreikemeier et al. (1990). A subsample of frozen mucosa was combined with ice-cold isotonic saline (1:4 ratio of tissue to saline) in a 40 mL Dounce Tissue Grinder (Wheaton, Millville, NJ). Homogenates were centrifuged at $800 \times g$ for 10 min at 4°C and supernatant was transferred to a new tube and kept on ice throughout the experiment. A portion of the homogenate was retained for total protein analysis using a bicinchoninic

acid reagent adapted for a 96-well plate colorimetric assay (Smith et al., 1985) and another portion was used to determine enzyme kinetics for maltase or isomaltase.

Measures of maltase and isomaltase were achieved by incubating homogenates with increasing amounts of isomaltose (Tokyo Chemical Industry Co., LTD. Tokyo, Japan) and maltose (Sigma-Aldrich, St. Louis, Mo.). Maltose and isomaltose were added to a malate buffer (pH = 5.8) prior to incubation with homogenates. Final concentrations of isomaltose were 0, 1, 2.5, 5, 10, 20, 40, 60, 80 and 100 mM and concentrations of maltose were 0, 0.1, 0.5, 1, 2.5, 5, 10, 20, 30, and 40 mM and included the dilution of the added homogenate. Homogenates (50 μ L) were combined with 350 μ L of the appropriate substrate in duplicate for each substrate and concentration. Tubes were immersed in a shaking water bath at a constant temperature of 37°C for 60 min. Enzymatic reactions were terminated by adding 0.8 mL of deionized water and placing tubes in boiling water for 30 sec. Tubes were then cooled by dipping in room temperature water, placed on ice, and then centrifuged at 3,000 \times g for 30 min at 4°C. Glucose concentrations of the supernatant from the incubation were determined using the Autokit Glucose kit (Wako Diagnostics, Mountain View, CA.) adapted for use on a Gallery Automated Photometric Analyzer (Thermo Scientific, Middletown, VA.).

Plasma glucose and L-lactate were quantified using an immobilized enzyme system (YSI model 2700; YSI Inc., Yellow Spring, OH). Triglycerides and cholesterol were quantified using commercial kits (Infinity Triglycerides and Infinity Cholesterol; Thermo Scientific) using a Gallery Automated Photometric Analyzer. Non-esterified fatty acids (NEFA) were quantified using a commercial kit (Wako Diagnostics, Mountain View, CA.) adapted for the Gallery. β -Hydroxybutyrate (BHBA) was quantified using the

Gallery Analyzer and the method described by Williamson and Mellanby (1965). Plasma urea-N (PUN) was analyzed using the diacetyl method (Marsh et al., 1957) modified for a 96-well plate.

RNA Isolation

RNA from a 50 to 100 mg subsample of the jejunal mucosa was isolated with the RNeasy Plus Mini Kit columns (Qiagen, Valencia, CA). Tissue samples were added to 800 μ L of buffer containing 2-mercaptoethanol. Tissues were homogenized for 40 sec with an 6-station homogenizer. Homogenized samples were then transferred to a QiaShredder column (Qiagen) and centrifuged at $18,000 \times g$ for 3 min. For the remainder of the RNA isolation procedure, the RNeasy Plus Mini kit manufacturer's protocol was followed, except that one volume of 50% ethanol was added to elute from the gDNA column and mixed by pipetting. Total RNA was eluted from the RNeasy spin column in 100 μ L of RNase free water. The concentration of the RNA was determined with a NanoDrop 8000 spectrophotometer (Thermo Scientific). The 260:280 nm absorbance ratios were above 1.8. Complimentary DNA (cDNA) was prepared from 1 μ g of total RNA using the iScript cDNA synthesis kit (Bio-Rad Laboratories Inc. Hercules, CA). Prime PCR™ primer assays (Bio-Rad Laboratories Inc.) were used for quantitative real-time PCR (*qPCR*) of the following genes: *sucrase-isomaltase (SI)* with a unique assay ID: qBtaCID0003816, *maltase-glucoamylase (MGAM)* with a unique assay ID: qBTaCID0003708, and the reference gene used was *glyceraldehyde 3-phosphate dehydrogenase (G3PDH)*, assay ID: qBtaCID0013312. Real-time PCR was performed in triplicate with a final concentration of 1X SsoAdvancedUniversal SYBR Green Supermix (Bio-Rad Laboratories Inc.), 1X *qPCR* Prime assay or *qPCR* Prime reference control

assay, and 5 ng cDNA template adjusted to a final volume of 10 μ L. The *q*PCR reactions were performed on a CFX384 thermal cycler (Bio-Rad Laboratories Inc.) at 95°C for 2 min followed by 40 cycles at 95°C for 5 s, 60°C for 30 s, with a final melting curve from 65 to 95°C. A pooled control sample served as a calibrator sample. The fold change expression differences between samples were calculated with the $2^{-\Delta\Delta C_t}$ method (Livak and Schmittgen, 2001).

Calculations and statistical analysis

One unit of disaccharidase activity equals 1 hydrolyzed μ mol of substrate per minute at 37°C per gram of mucosa. Specific activity equals 1 hydrolyzed μ mol of substrate per min at 37°C per gram protein. Following the calculation of enzyme activity (tissue weight corrected) and specific activity (protein concentration corrected) for each concentration of substrate, the maximum velocity (V_{max}) and the Michaelis-Menten constant (K_m) were calculated for each animal and substrate combination by fitting the data to the Michaelis-Menten equation:

$$\text{Activity or Specific Activity} = \frac{V_{max}[S]}{(K_m + [S])}$$

Where $[S]$ is the concentration of substrate, using the nonlinear procedure of SAS 9.4 (SAS Inst. Inc., Cary, NC).

Normality of each variable was assessed using the Shapiro-Wilk test in the univariate procedure of SAS. When assumptions of normality were violated, variables were log-transformed and used for statistical analyses. Animal was the experimental unit. All data were analyzed using a completely randomized design with PROC MIXED in SAS 9.4. For the enzyme kinetic parameters, the model included ADG group as the fixed

effect. Blood metabolites were analyzed as repeated measures in time; the models included fixed effects of group, day, group \times day interaction. An autoregressive covariance structure resulted in the smallest Akaike and Schwarz Bayesian information criteria and was considered the most appropriate for analysis. Effects were considered statistically significant when $P \leq 0.05$ and tendencies were declared when $0.05 \leq P \leq 0.15$

RESULTS AND DISCUSSION

Feed intake and performance

Initial body weight (BW), DMI, and residual feed intake (RFI) were not different between the high-ADG and low-ADG groups ($P < 0.01$; Table 2.1). As designed, ADG ($P < 0.01$) and G:F ($P < 0.01$) were greater in the high-ADG group.

Enzyme activity and expression

Foote et al. (2017) reported differences in *MGAM* expression in cattle with divergent ADG, and concluded that differences in disaccharidase expression could contribute to greater feed efficiency through increased enzymatic hydrolyzation of starch in the small intestine. In order to further examine the conclusions of Foote et al. (2017), the goal of this experiment was to evaluate potential biological processes of the small intestine such as enzyme activity that could influence natural variation in growth and efficiency of cattle.

Isomaltase activity (V_{\max}) as a proportion of wet-tissue weight did not differ between groups ($P = 0.18$; Table 2.2). However, isomaltase activity (V_{\max}) on a protein basis tended ($P = 0.11$) to be 29.6% greater in jejunum from high-ADG steers compared to mucosa harvested from low-ADG steers, but isomaltase affinity for isomaltose (K_m) did not differ between groups ($P = 0.15$). Maltase activity (V_{\max}) on a protein and tissue

basis did not differ between groups ($P > 0.45$) and maltase affinity for maltose (K_m) did not differ between groups ($P = 0.43$).

While increases in enzyme activity did not differ in the current experiment, the results could help expand the understanding of disaccharidase activity in small intestinal starch digestion of ruminants. The final step in the assimilation of starch is completed by surface oligosaccharidases. Within the nonruminant small intestine, it has been reported that approximately 80% of mucosal maltase activity can be accredited to sucrase-isomaltase and 20% to maltase-glucoamylase (Galand, 1989). Others report a change in primary hydrolyzing enzyme based on substrate concentration in nonruminants (Quezada-Calvillo et al., 2007b). Quezada-Calvillo et al. (2007b) reported that maltase-glucoamylase is the primary disaccharidase at low substrate concentrations; however, as substrate concentrations increase, maltase-glucoamylase becomes saturated with substrate thus accounting for a lesser proportion of the total amount of polymerized glucose that is subsequently hydrolyzed. In turn allowing sucrase-isomaltase to become the predominate disaccharidase. Given the K_m for maltose (6 mM) and isomaltose (3 mM) measured in the present experiment, it is apparent that isomaltase activity will be saturated as luminal disaccharide concentrations increase, where maltase activity will continue to increase. However, both disaccharidases are critical in the complete hydrolyzation of starch to glucose as maltase is predominantly thought to cleave released maltose, and isomaltase to cleave the branch points of amylopectin.

Small intestine weight did not differ between groups ($P = 0.69$) in the present experiment. Protein concentration of the jejunum did not differ between high and low ADG groups ($P = 0.45$). Similar to our results, Wang et al. (1998), noted no difference in

protein concentration across groups with differing ADG.

As a result of the differential expression of maltase and isomaltase in the jejunum of steers differing in ADG by Foote et al. (2017) we used qPCR to quantify enzyme expression between the two groups of steers in the current experiment. Use of qPCR along with enzyme activity data allows for a more complete understanding of the link between gene expression and enzyme activity. The qPCR showed no difference between groups for both isomaltase ($P = 0.96$) and maltase ($P = 0.95$) (Table 2.4). These results were not expected and perhaps explains the lack of significance presented in the enzyme activity data (Table 2.3).

Metabolic differences between feed efficiency groups

A group \times day interaction was detected for plasma glucose concentration ($P < 0.01$; Table 2.3; Figure 2.1). Initial glucose concentrations did not differ between the 2 groups ($P \geq 0.37$); however, the low-ADG group decreased from 0 d to 42 d ($P < 0.01$) and again to 83 d ($P = 0.05$). The high-ADG group did not change from 0 d to 42 d ($P > 0.1$) but did decrease by 83 d ($P \leq 0.01$). Results of the current study are similar to those of Richardson et al. (2004), who did not detect a difference in plasma glucose levels between two groups of steers with differing ADG.

A group \times day interaction was detected for plasma triglyceride concentration ($P < 0.05$; Table 2.3; Figure 2.2). The interaction for triglyceride concentrations was due to directional changes from d 0 to d 42 and from d 42 to d 83. The low-ADG group decreased initially (d 0 to d 42) and then increased (d 42 to d 83), while the high-ADG group increased (d 0 to d 42) and then decreased (d 42 to d 83). An interaction of plasma triglyceride concentration was not expected as triglycerides are energy reserves storied in

adipocytes (Cameron, 1992; Vernon and Houseknecht, 2000), and cattle were fed ad lib finishing diets. β -hydroxybutyrate was less ($P = 0.03$; Table 2.3) on day 0 than day 42 or 83; however, there was no difference between low and high ADG groups ($P = 0.45$). The NEFA concentration did not differ among group ($P = 0.24$; Table 2.3) or across day ($P = 0.50$; Table 2.3). This was expected because cattle were fed above maintenance and mobilization of fat depots was not expected. There was no effect of day or difference between groups for L.Lactate ($P = 0.99$; Table 2.3).

No difference in PUN was noted between ADG groups ($P = 0.45$, Table 2.3), yet there was a difference in PUN concentration over time ($P < 0.01$) as both groups increased in PUN concentration from day 0 to 83. Overfeeding of protein may have caused the increase in PUN. As cattle mature, protein accretion rate begins to slow, therefore the metabolizable protein requirements for growth decrease at an increasing rate (NASEM, 2016). Cholesterol concentrations increased over time ($P < 0.01$; Table 2.3) with a tendency to differ between groups ($P = 0.11$) with the low-ADG group being 13.5% greater than high-ADG. The difference in cholesterol between the two groups may indicate an increased energy status in the low-ADG due to increased lipoprotein transport. In conclusion, the results of the metabolites evaluated in the present study suggest differences in feed efficiency was not attributed to differences in metabolites.

In summary, data present here can be interpreted that finishing beef cattle with similar DMI and divergent ADG tend to have differences in isomaltase specific activity. Plasma glucose differed between the high and low ADG groups at the mid-point sample collection. Results from this study can help in the understanding of physiological mechanisms that contribute to differences in feed efficiency. Further research is needed

on how enzymatic activity contributes to feed efficiency at varying time points within the beef cattle growing and finishing phases. While previous studies have indicated that disaccharidase expression is associated with differences in ADG, data presented here indicate that differences in enzyme activity are minimal.

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Table 2.1 Feed intake and growth performance of two groups (High-ADG and Low-ADG) of steers (n=16) with divergent average daily gain (ADG) fed a finishing diet for 105 d.

Variable	Group		SEM ¹	P- value
	Low-ADG	High-ADG		
Initial BW ² , kg	467	446	16.4	0.37
DMI ³ , kg/d	11.8	12.0	0.14	0.27
ADG, kg/d	1.85	2.39	0.060	<0.01
G:F ⁴ , kg/kg	0.16	0.20	0.006	<0.01
RFI ⁵ , kg/d	-0.04	-0.11	0.230	0.83

¹Standard error of the mean (n= 8 steers/groups)

²BW= Body weight,

³DMI= Dry matter intake

⁴G:F = Gain to feed ratio

⁵RFI = Residual feed intake

Table 2.2 Isomaltase and maltase: V_{\max}^1 and K_m^2 , protein concentration and small intestinal weight of two groups (High-ADG and Low-ADG) of steers (n=16) with divergent average daily gain (ADG) fed a finishing diet for 105d.

Substrate	Group		SEM ³	P-value
	Low-ADG	High-ADG		
Isomaltase				
K_m , mmol/L	2.29	3.34	0.683	0.15
Specific-Activity				
Log V_{\max}^4 , $\mu\text{mol min}^{-1}\text{g protein}^{-1}$	1.43	1.57	0.086	0.11
V_{\max} , $\mu\text{mol min}^{-1}\text{g protein}^{-1}$	26.2	37.2	-	-
Activity				
Log V_{\max}^4 , $\mu\text{mol min}^{-1}\text{g tissue}^{-1}$	0.32	0.45	0.062	0.18
V_{\max} , $\mu\text{mol min}^{-1}\text{g tissue}^{-1}$	2.10	2.80	-	-
Maltase				
K_m , mmol/L	4.45	4.69	0.296	0.43
Specific-Activity				
Log V_{\max}^4 , $\mu\text{mol min}^{-1}\text{g protein}^{-1}$	1.05	1.15	0.098	0.33
V_{\max} , $\mu\text{mol min}^{-1}\text{g protein}^{-1}$	11.20	14.10	-	-
Activity				
Log V_{\max}^4 , $\mu\text{mol min}^{-1}\text{g tissue}^{-1}$	-0.05	0.02	0.069	0.45
V_{\max} , $\mu\text{mol min}^{-1}\text{g tissue}^{-1}$	0.89	1.05	-	-
Protein, mg/g tissue	78.80	75.3	4.461	0.47
Small Intestine, kg	9.26	8.98	0.679	0.69

¹ V_{\max} = Maximum velocity

² K_m = Michaelis-menten constant

³Standard error of the mean (n=8 steers/group)

⁴Variable were log10 transformed to achieve a normal distribution. Means \pm the SEM of the log transformed data are presented as well as the non-transformed in the row immediately below the transformed data

Table 2.3 Blood plasma metabolites related to average daily gain (ADG) between two groups (High-ADG and Low-ADG) of steers (n=16) fed a finishing diet for 83d.

Variable	Group			Day				P- value		
	Low-ADG	High-ADG	SEM ²	0	42	83	SEM ²	Group	Day	Group x Day
Glucose, mM	5.06	5.16	0.121	5.34	5.14	4.83	0.098	0.58	<0.01	0.01
Triglycerides, mg ⁻¹ L	239	220	17.8	227	226	235	14.8	0.48	0.77	0.04
BHBA ³ , mM	1.02	0.98	0.034	0.93	1.03	1.05	0.035	0.45	0.03	0.31
Log NEFA ^{1,4} , μ Eq ⁻¹ L	2.15	2.05	0.061	2.05	2.08	2.16	0.068	0.24	0.50	0.36
NEFA ⁴ , μ E	181	124	-	137	146	175	-	-	-	-
Log Lactate ¹ , mM	0.21	0.21	0.040	0.19	0.21	0.23	0.039	0.99	0.73	0.16
Lactate, mM	1.62	1.62	-	1.54	1.63	1.69	-	-	-	-
Urea N, mM	7.31	6.98	0.309	6.36	7.29	7.78	0.259	0.45	<0.01	0.34
Cholesterol, mM	4.15	3.59	0.235	3.22	3.87	4.51	0.181	0.11	<0.01	0.52

¹Some variable were log10 transformed to achieve a normal distribution. Means \pm the SEM of the log transformed data are presented as well as the non-transformed in the row immediately below the transformed data.

²Standard error of the mean ($n = 8$ steers/group), ($n = 83$ days)

³BHBA = β -hydroxybutyrate

⁴NEFA = Non-esterified Fatty Acids

Table 2.4 Quantitative reverse transcriptase polymerase chain reaction (qRT-PCR) data for expression of sucrase-isomaltase (*SI*) and maltase-glucoamylase (*MGAM*) of two groups of steers with divergent average daily gain.

Gene symbol ¹ , arbitrary unit	Group		SEM ²	P-value
	Low-ADG	High-ADG		
<i>Sucrase-isomaltase (SI)</i>	-0.10	-0.10	0.096	0.96
<i>Maltase-glucoamylase (MGAM)</i>	-0.18	-0.17	0.098	0.95

¹The fold change ($2^{-\Delta\Delta CT}$) was transformed to achieve a normal distribution, means \pm the SEM of the log transformed data are presented.

²Standard error of the mean ($n= 8$ steers/groups).

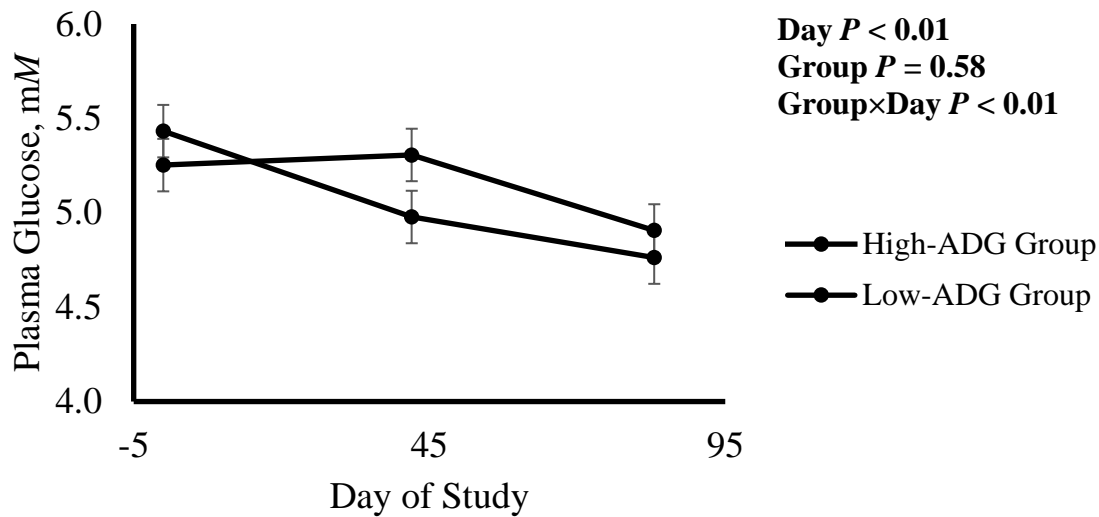


Figure 2.1 Means \pm standard error of the mean (SEM) of plasma glucose concentration between two groups ($n = 8$) of steers (High-ADG, Low-ADG) with divergent average daily gain (ADG) receiving a finishing diet.

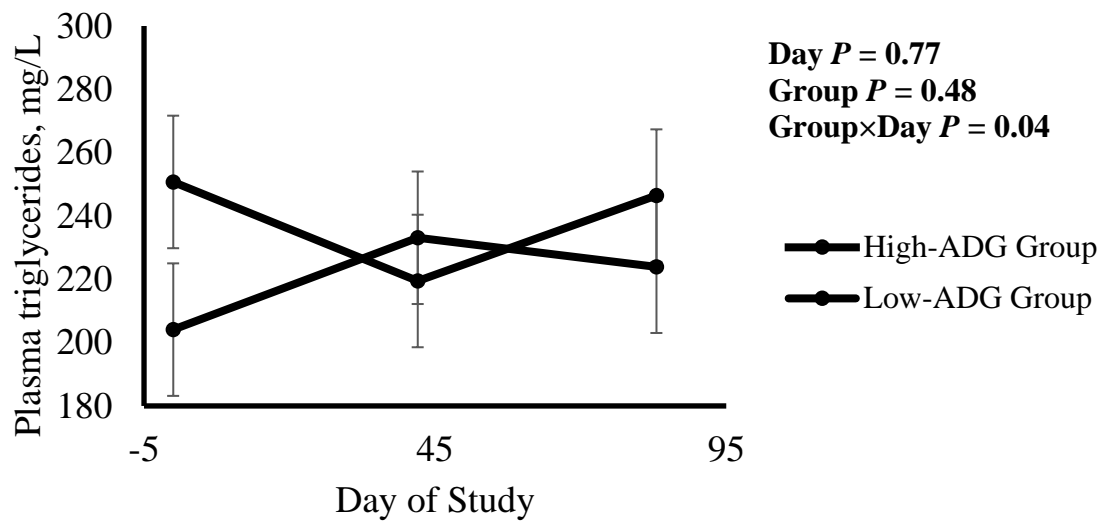


Figure 2.2 Means \pm standard error of the mean (SEM) of plasma triglyceride concentration between two groups (n=8) of steers (High-ADG, Low-ADG) with divergent average daily gain (ADG) receiving a finishing diet.

CHAPTER 3: IMPACTS OF CORN-GRAIN PROCESSING ON FEEDING
BEHAVIOR, GROWTH PERFORMANCE, AND CARCASS CHARACTERISTICS
OF FINISHING BEEF STEERS

ABSTRACT

The objective of this study was to evaluate the impact of differences in corn-grain processing on feeding behavior and growth performance. Twenty-seven Simmental × Angus steers were blocked by initial body weight (BW) into 3 groups: heavy BW, medium BW, and light BW (initial BW 482 ± 14.8 kg). There were 3 diets fed that differed in grain processing type: whole-shelled corn-based diet (WSC), a blended corn-based diet containing a 50:50 whole-shelled corn and high-moisture corn (BLD), and a high-moisture corn-based diet (HMC). Each of these diets contained 73% corn, 12% alfalfa hay, 8% soybean meal and 7% supplement. All data were analyzed with steer as the experimental unit, treatment included as a fixed effect, and BW block as a random effect. Day was the subject of repeated the repeated measure for the feeding behavior data. Meal duration, average meal size and number of meals consumed differed across treatments ($P \leq 0.01$). For meal duration, HMC was greater ($P \leq 0.01$) than WSC and BLD, which did not differ ($P \geq 0.13$). Average meal size was greatest for WSC which tended to differ ($P = 0.07$) from BLD, and differed ($P \leq 0.01$) from HMC which had the least kg of intake at each meal. The HMC treatment consumed the greatest number of meals and differed from WSC and BLD ($P \leq 0.01$); whereas, WSC had the least number of meals and tended to differ from BLD ($P = 0.09$). For animal growth performance, initial BW did not differ ($P = 0.31$). Additionally, in the first interim period of d 1 to 28 BW, average daily gain (ADG), dry matter intake (DMI), and gain:feed (G:F) did not differ ($P \geq 0.33$) across treatment. However, in the second interim period of d 29 to 56, ADG was greater for the BLD than the WSC or HMC treatments ($P = 0.04$). For the period from d 57 to 84, BW did not differ among treatments ($P = 0.73$); whereas, ADG tended to differ ($P = 0.10$), in that WSC had the greatest ADG, BLD had the least, with

HMC was intermediate. Dry matter intake tended ($P = 0.09$) to be greater for WSC and lesser for HMC with BLD being not different for both. Gain:feed did not differ ($P = 0.16$) among treatments from d 57 to 84. Cumulative ADG, DMI, and G:F were not different among treatments ($P \geq 0.42$). Carcass characteristics and estimated empty body fat did not differ between treatments ($P \geq 0.36$). Though the growth performance resembled previous work, no differences in steer growth performance or DMI were detected in the current experiment.

INTRODUCTION

An important goal in cattle feeding is to maximize the efficiency of nutrient utilization. One approach to increase intake energy is to increase the energy density of the diet by feeding more fermentable grains. Owens et al. (1997) summarized studies that evaluated the impact of differing grain processing methods on growth performance and feed efficiency. They concluded that grain processing could improve feed efficiency (G:F), if bunks are managed properly and rumen health was not compromised with acidosis. This increase in G:F may be accredited to increases in ruminal degradation of starch leading to the increase of volatile fatty acid (VFA) production while also enhancing the flow of microbial protein to the small intestine (Owens et al., 1986; Huntington, 1997). An important aspect of dietary intake energy capture is site of digestion and absorption of nutrients. Several reviews have concluded that grain processing as a positive effect on ruminal degradation of starch (Ørskov, 1976; Owens et al., 1986; Huntington, 1997). However, in work conducted by Stock et al. (1987), results could be interpreted that feeding combinations of processed and non-processed grains can have a greater increase in G:F and average daily gain (ADG) than feeding a single processed grain. Feeding a combination of processed grain's impacts on growth performance and G:F have been extensively studied (Sharp et al., 1982; Stock et al., 1987; Stock et al., 1991); however, the impacts of these combinations on feeding behavior has not been evaluated. The objective of this study was to evaluate the effects of feeding behavior and growth performance when finishing beef steers were fed WSC and HMC alone or in combination.

MATERIAL AND METHODS

All procedures that involved the use of animals in this project were approved by the South Dakota State University Institutional Animal Care and Use Committee (#A3958-01).

Experimental Design and Treatments

Twenty-seven Simmental \times Angus steers were blocked by initial body weight (BW) into 3 groups: heavy BW, medium BW, and light BW (initial BW 482 ± 14.8 kg). Steers were used in a randomized complete block design to determine factors that contribute to variation of feeding behavior based on differences in corn grain processing. Three diets were fed that differed in grain processing type (Table 3.1) whole-shelled corn-based diet (WSC); a blended corn-based diet containing a 50:50 whole-shelled corn and high-moisture corn (BLD); and a high-moisture corn-based diet (HMC). Initially there were 9 animals in each treatment; however, a situation unrelated to treatment caused 1 of the WSC steers to be removed from the study. The steers were housed in a (106.4 m²) monoslope barn with an open-lot pen (1540.3 m²) connected to the barn. The feeding facility was equipped with an Insentec Roughage Intake Control Feeding System (Insentec B.V., Marknesse, The Netherlands). Three steers on a common treatment diet were assigned to each bunk, and each dietary treatment was replicated across 3 bunks. The feed bunks have the ability to evaluate individual DMI. Feeders and automatic waters were located inside the monoslope with an opening to the south. The barn was equipped with lights that were on at night. Steers were acclimated to the pen, feeding system, and diets during a 28-d adaptation period, where inclusion of concentrate grain

was increased in each diet. The adaptation period was followed by an 84-d finishing period in which feeding behavior and growth performance were evaluated.

Feeding Behavior Analysis

Steers had *ad libitum* access to feed and water; fresh feed was offered once daily at 0930 h. Diets were mixed in a stationary feed mixer (Davis HD-5, Bonner Springs, KS; Sudenga batch control system, George, IA; readability ± 0.5 kg) and conveyed into a delivery cart (Valmetal Supercart HT, Tomah, WI; readability ± 0.1 kg). The Insentec feeding system allowed for calculation of individual eating events, meal durations, meal size, and number of meals consumed each day using an electronic identification tag (EID) (Allflex halfduplex, Allflex USA Inc., DFW Airport, TX) with pneumatic load cells on each bunk to record the weight of the bunk and contents before and after an eating event. A meal was defined as a series of individual eating events that did not exceed 30 min from the last eating event. Meal duration was computed as the sum of the difference between eating event end times and start times within a day for each animal. Meal duration was equal to the total number of minutes each day spent in eating-related activities at the bunk. Meal size was defined as the quantity of feed consumed within a meal. Meal number is a sum of meals within a 24-hr period.

Animal Production Data

Individual BW measurements were taken before feed delivery (0730 h) on d 1, 28, 56 and 84. The interim period live growth performance was also tabulated and analyzed by applying a 4% shrink to initial BW, d 28, d 56, and d 84. Cumulative performance was calculated using d 1 BW with a shrink 4% as the initial BW, and then

by assigning a 4% shrink to final BW on d 84. The ADG and G:F were calculated on a live BW and carcass-adjusted basis. Carcass-adjusted variables were standardized to common dressing percent of 59.7%, which was the average dressing percent of all the steers ($n = 27$). Gain-to-feed was computed as the quotient of ADG divided by daily DMI.

When personnel estimated approximately 60% of the steers had a backfat of 1.02 cm, all cattle were transported 218 km to a commercial abattoir (Tyson Fresh Meats, Dakota Dunes, SD). Hot carcass weight (HCW) was collected by trained personnel, while USDA quality grade, USDA yield grade (YG), ribeye area (REA), marbling score (MARB), backfat (BF) and kidney heart and pelvic fat (KPH) were collected using camera data. Yield grade was calculated by using the USDA regression equation with camera collected data (USDA, 1997). Percentage of empty body fat (EBF) was estimated using the equation described by (Guiroy et al., 2001). Dressing percentage (DP) was the quotient of HCW divided by final shrunk BW. Final BW for the carcass-adjusted data was calculated from the HCW divided by the overall average dressing percent.

Laboratory Analyses

Individual samples (100 g) of dietary ingredients were collected weekly and dried at 55°C for 48 h in a forced-air oven (Despatch Industries, Minneapolis, MN). Samples were then ground in a Wiley Mill (model 4, Thomas Scientific, Swedesboro, NJ) to pass a 1-mm screen. Dietary ingredients were sampled weekly for determination of dry matter (DM). Dry matter intake (DMI) was calculated as the feed consumed within a day and multiplied by the DM composition of the feed for that week. Dry matter was determined on a weekly basis by drying ingredient samples at 105°C for 16 h in a forced-air oven

(method no. 934.01; AOAC 2012). Weekly ground samples were composited monthly for determination of nitrogen (N), neutral detergent fiber (NDF), and organic matter (OM). The N content was analyzed by the Dumas procedure (method no. 968.06; AOAC, 2012; rapid Max N exceed; Elementar, Mt. Laurel, NJ). Neutral detergent fiber was measured as described by Van Soest et al. (1991) and included additions of α -amylase and sodium sulfite (Ankom-Fiber Analyzer 200, Ankom Technology, Fairport, NY). Measures of NDF were corrected for ash content which was measured by combustion (500°C for 8 h; method no. 942.05; AOAC, 2012). Organic matter was mathematically determined by the difference using ash. Dry matter intakes, ingredient, and nutrient composition were calculated and summarized weekly using the weekly feed ingredient analyses.

Statistical Analysis

Feeding behavior, live performance, and carcass data were analyzed using a randomized complete block design and the PROC MIXED procedure of SAS 9.4 (SAS Inst. Inc., Cary, NC). Steer was used as the experimental unit for all analyses. Within the statistical model for feeding behavior, dietary treatment was considered a fixed effect, BW block was considered a random effect, and day was analyzed as a repeated measure. The covariance structure resulting in the lowest Akaike information criterion (AIC) was used for the repeated measures analyses. The statistical model for live and carcass-adjusted data included the fixed effect of dietary treatment and BW block as a random effect. Least squares means were generated using the LSMEANS statement. Data were separated and denoted to be different using the pairwise comparisons PDIFF option when a significant *F*-test was detected. To account for unbalanced data, the Kenward-Roger

denominator degrees of freedom method was used. An α level of 0.05 was used to determine significance, with tendencies discussed at P -values between 0.05 and 0.10.

RESULTS AND DISCUSSION

Diets

The chemical composition of the dietary treatments are reported in (Table 3.1). Diets were formulated to be isonitrogenous. Results were similar to values expected from the diet formulation. Energy density increased slightly with grain processing, in which the HMC-diet was greater in energy than the WSC diet. This is expected as increasing in grain processing allows for greater enzymatically available starch and rumen digestibility (McAllister et al., 1994; Owens et al., 1997).

Feeding Behavior

Feeding behavior for the steers are reported in (Table 3.2). Meal duration or the average time spent during a meal differed across treatments ($P < 0.01$). The WSC and BLD did not differ ($P = 0.13$). However, HMC differed ($P < .01$) by having a decreased meal duration compared to WSC and BLD. Average meal size was different across treatments, where WSC had the greatest kg of DMI per meal, BLD was the intermediate and HMC had the least. The WSC and BLD tended to differ ($P = 0.06$), while HMC differed ($P \leq 0.01$) from both WSC and BLD. The number of meals within a 24-hr period differed ($P < 0.01$) across treatments where WSC had the least amount of meals, BLD was intermediate, and HMC had the greatest number of meals. The WSC and BLD treatments tended to differ ($P = 0.08$) in number of meals, while HMC differed ($P \leq 0.01$) from both WSC and BLD. Feeding behavior such as meal duration, meal size, and

number of meals can be affected by variables such as pH, VFA production, metabolic fuels, and feedstuff rate of fermentation and digestibility.

The measured feeding behavior results of the current experiment are similar to previous studies (Hicks et al., 1989; Schwartzkopf-Genswein et al., 2002; Schwartzkopf-Genswein et al., 2011). Hicks et al. (1989) fed a dry-rolled corn diet to 93 yearling steers for 138 d. They observed a diurnal eating behavior with the main peak eating times being at 0650h and 1700h. These times correlated with the morning feeding and dusk. However, (Hicks et al., 1989) reported additional eating events were observed at 0900, 1100 and 2100 for a total of 5 eating events throughout the day. Number of meals reported by (Hicks et al., 1989) is consistent with results of the current experiment. In more recent publications using radio frequency tags to detect bunk attendance and feeding behavior, instead of human observation, the results of the current experiment are still similar. Schwartzkopf-Genswein et al. (2002) fed 6 continental crossbred beef steers with an initial BW of 471 ± 44 kg and 6 continental crossbred beef heifers with an initial BW of 481 ± 22 kg. Results of the average bunk attendance were 112 min per day. However, in the current experiment, the average bunk attendance was 139 min per day. The increase in bunk attendance within the current experiment may be due to the greater BW of steers. In the same experiment Schwartzkopf-Genswein et al. (2002) reported an average daily bunk attendance of 17 events/d while in the current experiment number of meals were reported, the average number of meals were 5. Schwartzkopf-Genswein et al. (2002) defined a bunk attendance as the number of visits to the feed bunk by one steer over a 24 h period; however, if a steer left the bunk and returned within a 5 min window it was still considered the same visit. In the current experiment the steer could leave the

bunk and return within a 30 min window, and the visit or meal event would be considered the same. Furthermore, results of the current experiment are similar to those of Schwartzkopf-Genswein et al. (2011). Schwartzkopf-Genswein et al. (2011) reported bunk attendance durations of 100 to 145 min through the study and daily bunk attendance frequency of 5.6 to 6.1 event/d. The criteria for bunk attendance frequency is similar to that of (Schwartzkopf-Genswein et al., 2002). Results of current experiment for meal duration, average meal size and meal number are within the range of previously published work.

It has been suggested in previous research that cattle consuming WSC will masticate to a greater extent than cattle consuming processed corn grains (McAllister et al., 1994). Not only would the increase in mastication support the results of meal duration for the WSC treatment in the present experiment; but, the biological impacts of increased mastication would influence meal size through increased salivation and pH buffer capacity. Increases in salivation and buffering capacity could decrease bouts of acidosis and increase the VFA absorption capacity of the ruminal epithelial cells. The increase in mastication coupled with increased salivation could increase the amount of sodium-bicarbonate flowing to the rumen and acting as a pH buffer (Owens et al., 1998). Indeed, if there were an increase in sodium-bicarbonate, it could potentially decrease the bouts of subclinical acidosis (Loerch and Fluharty, 1998). The decrease in subclinical acidosis over a period of time would have led to more potential VFA absorption because the ruminal papillae would be maintained in a healthy state instead of recessing. The rate of VFA absorption has been suggested to regulate meal size and frequency (Oba and Allen, 2003). When the rate of VFA absorption, particularly propionate, increases, the meal

size, and duration decreases while meal frequency increases, because of chemostatic signals of satiety (Oba and Allen, 2003; Allen et al., 2009). Propionate is absorbed through the rumen wall and transported to the liver where it is metabolized into glucose; the increase in blood glucose activates insulin secretion from the beta-cells of the pancreas. Insulin is a regulator of satiety signaling (Allen et al., 2009). Therefore, the decrease in meal duration and size and increase in meal frequency as corn-grain processing becomes more extensive in the diets indicate that mastication is greater in the WSC diet in the current experiment. This increase in mastication would have led to greater saliva production and sodium-bicarbonate flowing to the rumen for increased pH buffering capacity. The increase in pH buffer capacity would help maintain a healthy environment for the rumen papilla to increase VFA absorption while the rate of VFA production and absorption is greater in the HMC diet.

It is understood that cattle control satiety through two mechanisms: 1) stretch receptor regulation (fill), and 2) chemostatic feedback. In feedlot finishing diets chemostatic feedback is the primary regulator of satiety. Regulation of the chemostatic feedback is reviewed in Allen et al. (2009). Chemostatic regulation can be elicited through VFA concentrations. In the current experiment, differing levels of processed corn grains were fed. It has been established by previous experiments that grain processing can impact VFA production and absorption thus changing the chemostatic regulation of satiety. When steers were fed diets of 78% corn grain Galyean et al. (1976) reported an acetate:propionate ratio of 4:1 and 3:1 for dry-rolled and ground HMC diets, respectively. Sharp et al. (1982) reported an acetate:propionate of 2:1 and 1:1 in steers fed a diet containing 84% WSC or ground corn, respectively. Results of the 2 studies outlined

above support the reports of (Vance et al., 1972; White et al., 1972) that suggested increases in grain processing decrease the acetate:propionate ratio by increasing ruminal degradation of starch. The increase in ruminal degradation of starch decreases ruminal pH and increases hydrogen ion concentration within the rumen (Owens et al., 1998). The change in ruminal pH causes a shift in rumen microbial population to a higher concentration of propionate producing bacteria (Hale, 1973; Theurer, 1986; Van Soest, 1994). The increase in ruminal degradation of WSC vs. HMC may have also led to decreases in meal size and duration, but an increase in meal number. Huntington (1997) reported a 29% increase in ruminal degradation of starch going from WSC to HMC. Researchers from previous studies suggested that HMC is typically more ruminally degradable than WSC (Stock et al., 1987; Owens et al., 1997). In the current study, the HMC diet had a shorter meal duration and smaller meal size but greater meal frequency compared to WSC and BLD. The change in feeding behavior may be a result of the chemostatic regulation of satiety previously described.

Steer Growth Performance

Interim and cumulative live growth performance data for steers are reported in (Table 3.3). By design, no differences ($P = 0.31$) were detected for initial BW between treatments. In the first interim period of d 1 to 28 BW, ADG, DMI, G:F did not differ ($P \geq 0.34$). However, in the second interim period of d 29 to 56 ADG was greater for the BLD than the WSC or HMC treatments ($P = 0.04$). The increase in ADG of the BLD might have been in response to a positive associative effect of feeding rapidly digestible grain like HMC along with a slower digesting grain WSC (Stock et al., 1987). Similarly, G:F tended to ($P = 0.06$) be greater for the BLD than the WSC or HMC treatments. The

elevated G:F for the BLD may be related to the positive associative effects described previously. For the period from d 57 to 84, BW did not differ among treatments ($P = 0.73$); whereas ADG tended to differ ($P = 0.10$), WSC had the greatest ADG with BLD having the least with HMC being similar to both. The ADG for the BLD was markedly decreased from the d 29 to 56 period. Dry matter intake tended ($P = 0.09$) to be greater for WSC and lesser for HMC with BLD being similar to both. Gain:feed did not differ ($P = 0.16$) among treatments for d 57 to 84. The cumulative ADG, DMI, and G:F were not different among treatments ($P \geq 0.42$). The increase in ADG of WSC from d 57 to 84 may be related to increased DMI. The DMI was greatest for the WSC, while BLD had the intermediate DMI, and HMC had the lowest DMI. Because HMC is digested faster in vitro compared to WSC (Stock et al., 1987), steers feed HMC diet may have experienced more subacute acidosis, leading to the reduced DMI (Fulton et al., 1979).

On a carcass-adjusted basis, final BW, ADG, G:F did not differ between treatments ($P \geq 0.51$). Cattle used in the present study were sent to the abattoir at a fewer days on feed than previous studies that have reported differences in DMI, ADG, and G:F from feeding varies processed corn grain diets (Stock et al., 1987). Others have reported that feeding slowly and rapidly digestible corn grain together can improve DMI, ADG, and G:F. However, this difference was not observed in the present study, potentially because of fewer days on feed (Lee et al., 1982; Stock et al., 1987).

Positive associative effects mentioned above are elicited by 2 different mechanisms. First, the increase in the extent of fermentation, the combinations of feeding fast fermenting grains and slow fermenting grains allow for prolonged VFA production and absorption between meal events. The second mechanism that helps to

elicit the positive associative effects for feeding combinations of processed grains and non-processed grains is the shifts in nutrient digestion and absorption, by feeding WSC with HMC, proportions of the WSC will flow out of the rumen undigested into the small intestine where enzymes hydrolyze the starch into glucose to be absorbed directly into the intestinal capillary beds through the intestinal epithelial (Huntington et al., 2006; Harmon, 2009).

In a study with similar treatments as the present study, Stock et al. (1987) individually fed 12 yearling steers per treatment for 132 d; the diets contained 80% WSC, 40% WSC: 40% HMC, or 80% HMC. Stock et al. (1987) reported a magnitude of change for ADG, DMI, and G:F across levels of corn grain processing diets of -0.66% for ADG, 1.04% for DMI, and -1.69% for G:F in steers fed WSC versus BLD diets. Additionally a magnitude change of -2.03 for ADG, -6.55 for DMI, and 3.28% for G:F in steers fed WSC versus HMC diets. In the current study, the magnitude of change was similar for ADG, DMI, and G:F as reported by Stock et al. (1987). In the present experiment, calculated change was -2.03% for ADG, 0.69% for DMI, and -2.72% for G:F in WSC versus BLD diets (data not reported). Likewise, -4.23% for ADG, -4.96% for DMI and 1.34% for G:F in steers fed WSC versus HMC (data not reported). Though the biological impact of a positive associative effect of an increased ADG for the BLD vs. HMC or WSC treatments was not significant in the present study, it was observed by Stock et al. (1987). Animal-to-animal variation and low replication in the current study may have led to the lack of differences when feeding a blend of varying processed corn-grains; compared to only one proceed corn-grain type. Nonetheless, Stock et al. (1991) reported similar results to the current study, when feeding a blend of HMC and dry-rolled corn

(DRC) with no differences in DMI, ADG, or G:F; compared to feeding HMC or DRC as the sole corn-grain source. Thus, the use of processed grains alone or in combination when included in finishing diets seems to be variable in the literature (Stock et al., 1987; Stock et al., 1991).

Carcass Data

Carcass data are reported in (Table 3.4). The HCW and DP did not differ across treatments ($P \geq 0.50$). Furthermore, by design, BF did not differ as cattle were harvested at a common backfat across treatment ($P = 0.69$). Ribeye area, MARB, YG, and EBF also did not differ ($P \geq 0.36$). Our results for HCW are similar to previous studies (Stock et al., 1987; Loerch and Fluharty, 1998) who fed cattle varying types of processed-corn grains and detected no differences in HCW. The DP in the present experiment was lower than often observed in the feedlot industry; however, decreased final BW and increased accumulation tag may have influenced this decrease in DP. Field and Schoonover (1967) reported similar DP for cattle harvested in the weight range of the cattle in the present study. As planned, the BF did not differ, as steers were sent to the abattoir when their estimated average BF was 1.02 cm. Results for ribeye area of the current study are consistent to results of Stock et al. (1987) in which no difference was detected when grain processing types differed. Marbling score for the current experiment is similar to the results of (Stock et al., 1987) who fed similar dietary treatments. However, Stock et al. (1991) did report differences in marbling score when steers were fed different concentrations of HMC but stated that though the results were statistically significant; they may not be important biologically. As cattle in the present experiment were targeted to harvest at similar BF, yield grade and EBF was not expected to differ.

In conclusion, results of the feeding behavior provide evidence that cattle fed a greater NEg diet will have smaller, more frequent eating events. This change in eating behavior compared to cattle consuming a lesser NEg diet is likely because of the chemostatic regulation of satiety. Though the growth performance results trended like those of past experiments when combinations of processed corn grains were fed, we did not observe an increase in ADG or G:F in the BLD treatment. The numerical increase in ADG and G:F observed in the present study for BLD treatment may be accredited to the positive associative effect of feeding greater ruminal degradable corn grain with lesser ruminal degradable feedstuff, thus prolonging the time of VFA production and nutrient absorption between meals.

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Table 3.1 Composition and analysis of diets (dry-matter [DM] basis) fed to steers in an 84 d feeding trial to evaluate growth performance and feeding behavior.

Ingredients, %	Diets ¹		
	WSC	BLD	HMC
Whole-shelled corn	72.9	36.3	-
High-moisture corn	-	36.8	73.2
Alfalfa hay	12.1	12.0	12.0
Soybean meal	8.1	8.0	8.0
Supplement ²	6.9	6.9	6.8
Analyzed composition			
Dry matter, %	82.87	76.68	71.40
Crude protein, %	13.59	13.59	13.40
Neutral detergent fiber, %	16.74	16.28	15.85
Ash, %	9.88	9.70	9.52
Organic matter, %	90.12	90.30	90.48
NE _m ³ , Mcal/kg	1.95	1.98	2.01
NE _g ⁴ , Mcal/kg	1.30	1.33	1.35

¹WSC = diet based on whole-shelled corn based-diet; BLD = corn blend diet formulated to contain a 50:50 of high-moisture corn and whole-shelled corn; HMC = high-moisture corn-based diet

²Supplement formulated to contain 8.86% urea and 640 mg of monesin/kg of DM (Rumensin 90, Elanco Animal Health) and vitamins and minerals to meet the (NASAM, 2016) requirements in the complete mixed diet

³Net energy for maintenance

⁴Net energy for gain

Table 3.2 Feeding behavior characteristics for steers in an 84 d feeding trial

	Diets ¹			SEM	<i>P</i> -value
	WSC	BLD	HMC		
n, steers	8	9	9	-	-
Meal duration ² , min/d	34.3 ^a	30.2 ^a	21.4 ^b	1.88	<0.01
Average meal size, kg	2.70 ^a	2.33 ^a	1.83 ^b	0.189	<0.01
Meal number ³	4.4 ^a	4.8 ^a	5.7 ^b	0.22	<0.01

¹WSC = whole-shelled corn based-diet; BLD = corn blend diet formulated to contain a 50:50 of high-moisture corn and whole-shelled corn; HMC = high-moisture corn-based diet

²Meal duration is the average time spent during a meal (a meal was defined as a series of individual eating events that did not exceed 30 min from the last eating event)

³Number of meals within a 24-hr period

^{a,b} Means within a row without a common superscript differ ($P \leq 0.05$)

Table 3.3 Period and cumulative average daily gain (ADG), dry matter intake (DMI), gain to feed (G:F) on a live and carcass-adjusted basis for steers during an 84 d finishing phase to evaluate growth performance and feeding behavior¹

	Diets ²			SEM	P-value
	WSC	BLD	HMC		
n, steers	8	9	9	-	-
d 1 to 28					
Initial BW ³	423	423	441	13.1	0.31
d 28 BW ³ , kg	474	478	495	14.8	0.34
ADG, kg	1.81	1.96	1.94	0.179	0.67
DMI, kg	8.98	9.28	9.03	0.388	0.70
G:F	0.204	0.213	0.216	0.0186	0.83
d 29 to 56					
d 56 BW ³ , kg	512	527	532	16.46	0.48
ADG, kg	1.36 ^a	1.76 ^b	1.32 ^a	0.181	0.04
DMI, kg	10.18	10.34	9.81	0.493	0.52
G:F	0.133 ^a	0.172 ^b	0.134 ^a	0.0176	0.06
d 57 to 84					
d 84 BW ³ , kg	549	550	561	16.50	0.73
ADG, kg	1.28	0.81	1.02	0.208	0.10
DMI, kg	11.25	10.69	10.10	0.500	0.09
G:F	0.116	0.076	0.105	0.0209	0.16
Cumulative					
ADG, kg	1.48	1.51	1.43	0.100	0.67
DMI, kg	10.16	10.08	9.67	0.406	0.42
G:F	0.147	0.151	0.149	0.0102	0.93
Carcass Adjusted ⁴					
Final BW ³ , kg	544	550	568	21.4	0.51
ADG, kg	1.43	1.51	1.51	0.119	0.73
G:F	0.140	0.150	0.157	0.0102	0.30

¹Body weights were shrunk (4%)

²WSC = whole-shelled corn based-diet; BLD = corn blend diet formulated to contain a 50:50 of high-moisture corn and whole-shelled corn; HMC = high-moisture corn-based diet

³BW = body weight

⁴Hot carcass weight divided by overall average dressing percent of 59.7%

^{a,b} Means within a row without a common superscript differ ($P \leq 0.05$)

Table 3.4 Carcass characteristics for steers in an 84 d feeding trial to evaluate growth performance and feeding behavior

	Diets ¹			SEM	P-value
	WSC	BLD	HMC		
n, steers	8	9	9	-	-
HCW ² , kg	325	329	339	12.8	0.52
Dressing percentage ³	59.1	59.6	60.5	1.19	0.50
Back fat, cm	0.89	1.02	0.97	0.153	0.69
Ribeye area, cm ²	84.2	85.4	87.8	2.63	0.37
Marbling score ⁴	512	541	572	41.1	0.36
Yield grade	2.31	2.41	2.33	0.223	0.90
EBF ⁵ , %	26.8	27.6	27.6	1.01	0.65

¹WSC = whole-shelled corn based-diet; BLD = corn blend diet formulated to contain a 50:50 of high-moisture corn and whole-shelled corn; HMC = high-moisture corn-based diet

²HCW = hot carcass weight

³Dress percentage = ([HCW/final body weight] × 100)

⁴Small⁰ = 500

⁵EBF = empty body fat percentage; estimated according to equations described by Guiroy et al. (2001)