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# POST-ABSORPTIVE METABOLISM OF ENERGY-YIELDING NUTRIENTS AND STARCH DIGESTIBILITY BY STEERS FED SORGHUM GRAIN FLAKED AT DIFFERENT DENSITIES

by

Oscar Germán Lozano Ascencio

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Oscar German Lozano Ascencio entitled Post-Absorptive Metabolism of Energy-Yielding Nutrients and Starch Digestibility by Steers Fed Sorghum Grain Flaked at Different Densities

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

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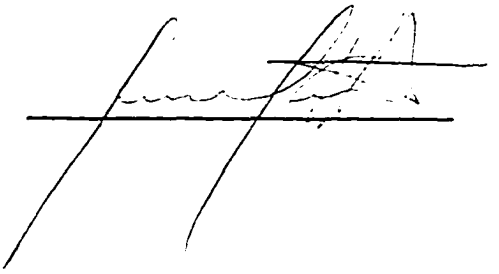
SIGNED: 

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# DEDICATION

Para;
Paty, Rodrigo, y Diego

mi familia

ya que juntos caminamos, compartimos, aprendimos, sufrimos y disfrutamos de esta aventura académica en el extranjero.

To;
Paty, Rodrigo, and Diego

my family

because together we traveled, shared, learned, suffered, and enjoyed this academic adventure far from home.

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## ABSTRACT

Objectives were to determine the effects of feeding dry-rolled (DR) vs steam-flaked (SF) sorghum grain and degree of processing (flake density, FD) of corn and sorghum grain on site and extent of starch digestion and post-absorptive metabolism of energy-yielding nutrients in steers fed 77% grain. The design for each trial was a randomized block. Seven steers (400 kg) with duodenal and ileal cannulas were used to determine corn and sorghum starch digestibilities (Cr ratio, 3-d collection). Steers fed SF versus DR sorghum increased starch digestibility in the rumen (23%; $P < .01$), total tract (2.3%; $P < .01$), and in the small intestine (6%;, $P < .01$, as percentage of starch entering duodenum). Decreasing flake density of SF sorghum grain increased linearly ($P < .05$) starch digestion (percentage of intake) in the rumen and total tract, and diminished linearly ($P < .05$) starch digestibilities post-ruminally and in the small intestine. Similar responses in starch digestibilities occurred by lowering FD of SF corn. Percent dietary corn or sorghum starch digestibility in the large intestine was less than 2% of intake. Feeding SF compared to DR sorghum did not alter net absorption and uptake or release of energy-yielding nutrient across SPL tissues. As expected, net absorption of glucose across

portal-drained viscera (PDV) was negative (-.60 mol/d). Incrementally decreasing FD of SF sorghum linearly increased net PDV absorption of lactate ($P = .04$), glucose synthesis by the liver ($P = .03$), and SPL output of glucose ($P < .01$) and L-lactate ($P = .03$). Net propionate PDV absorption ($P = .18$), hepatic uptake ($P = .21$), and SPL output ($P = .15$) tended to be increased with lower FD. Increasing degree of grain processing, by incrementally decreasing FD, linearly increased ruminal and total tract starch digestibilities and net absorption of glucose precursors (propionate and L-lactate), resulting in increased hepatic synthesis and greater output of glucose from the gut and liver to the rest of the body. Based on these changes, the optimum FD for SF sorghum grain was 283 g/L (SF22).

# CHAPTER I

## INTRODUCTION

Today grains are the principal source of energy (75 to 80% of diet) in the feedlot industry because of the unit cost of metabolizable energy and the availability of the grains. Starch is the principal structure of the grains since it comprises 50 to 80% of the kernel. Starch is organized in granules, which are embedded in a protein-rich matrix. This protein structure provides resistance to water solubility and enzymatic hydrolysis to the starch granules. Amylose and amylopectin are the two major starch molecules, which consist of a long linear chain of D-glucopyranose residues linked by $\alpha$-1,4 and by $\alpha$-1,4 and $\alpha$-1,6 bonds, respectively.

Starch is principally digested in the rumen by microbial fermentation. Volatile fatty acids (VFA) are the primary end products of this fermentation, and they constitute about 75% of the energy from this digested starch. The rest of the energy is used for the maintenance and growth of the ruminal microorganisms, and (or) it is lost as hydrogen and methane (Bergman, 1989). In the small intestine, the starch, which was not fermented in the rumen, is digested by enzymes from the animal. Pancreatic amylase

and the disaccharidase from the intestinal epithelium are the enzymes that digest the starch to form the final product, glucose. The amount of starch which flows to the duodenum varies according to the kind of grain (sorghum > corn > barley) and the type of processing.

In order to improve starch digestion of grains, several methods for processing the grains have been developed. The principle of these processes is to apply sufficient steam, heat and pressure to disorganize the starch granule structure. This change in starch organization facilitates water and enzyme penetration and enzymatic hydrolysis (Rooney and Plugfelder, 1986). Processing of grain by steam-flaking is a conventional method, in which grains are steamed for 30 to 50 min; then these grains are passed through a large roller mill to produce grain flakes of specific density.

Steam-flaked (SF) corn and sorghum grain increases ruminal starch digestion more those less intensive processes--dry-rolled (DR) or cracked (Theurer, 1986). Because of this increase, less starch flows to the duodenum, and consequently, the amount of starch digested in the small intestine decreases. However, the starch digested in the intestine, as a percentage of starch flow to duodenum, increases as a result of the steam-flaking process.

Starch digestion in the small intestine and,

consequently, glucose absorption from the intestinal lumen traditionally has been considered more efficient than ruminal starch digestion because the latter implies an extra metabolic energy expenditure in the synthesis of glucose in the liver. Owens et al. (1986), using data from performance trials with growing steers and digestibility data from other trials, pointed out that starch digestion in the small intestine is 42% more efficient than ruminal starch digestion. According to this statement, the SF grain is inefficient because of the reduction of the amount of starch digested in the small intestine. In contrast, reviews of Theurer (1986) and Theurer et al., (1996a) clearly demonstrate that steam-flaking, which reduces starch digestion in the small intestine consistently improves feed efficiency by feedlot cattle.

Despite the capacity for starch digestion in the small intestine, several authors (Huntington and Eisemann, 1988, Reynolds and Huntington, 1988a, Theurer et al. 1990), using permanent catheters in an artery and the portal vein, have reported that net glucose absorption from the lumen to the portal vein is consistently negative or close to zero. Positive net glucose absorption by steer fed high-concentrate diets has been reported from mesenteric (intestinal) tissues (Theurer et al., 1990; Reynolds and Huntington, 1988; Huntington et al., 1996). However, the

greater net uptake of glucose by the stomach region (rumen, abomasum, spleen) results in negative or low net glucose absorption across the portal-drained viscera (PDV) .

In contrast to glucose, the end products of ruminal starch digestion (VFA and lactate) are broadly absorbed across the PDV. The liver transforms the metabolites released by the PDV into glucose and other nutrients and partition these nutrients to the rest of the body. Glucose, acetate, ß-hydroxybutyrate, and ketone bodies are the primary energetic hepatic substrates. Propionate, L-lactate, and α-amino-acids are the principal glucose precursors.

The objectives of the present study are: 1) determine starch digestibility at different sites of the digestive tract by steers fed high-grain diets with DR and SF sorghum or corn flaked at different densities; and 2) detect the effect of DR and SF sorghum grain flaked at different densities on net absorption of energetic nutrients and hepatic metabolism of these metabolites by growing steers fed the same high-grain diets.

# CHAPTER 2

# LITERATURE REVIEW

## Structure and Composition of Grain Starch

Starch is the principal component of the grains because it constitutes 55 to 80 % of the kernel. Grain starch is in the endosperm, which with the pericarp and the embryo, are the three basic structures of the grain. The biological function of the first two components is to provide nutrients and protection to the embryo during germination and early growth. Recognizing the factors that affect the enzymatic hydrolysis of starch is the challenge in analyzing the starch structure and composition in grains, principally in corn and sorghum.

Amylose and amylopectin are the two major molecules of the starch. In most of the grains, 20-30% of the starch is amylose which consists of a long linear chain of 900-3000 D-glucopyranose residues linked by α-1,4 bonds. Amylopectin comprises 70 to 80% of the starch; the latter is a highly branched polymer of linear chains of α-1,4 linked D-glucose with α-1,6 branch point every 20 to 25 glucose units.

Starch is organized in granules, which are distributed in the endosperm in two different areas, the peripheral or corneous endosperm and the floury endosperm. In the corneous area, the starch granules are embedded in a protein-rich

matrix and surrounded by protein storage bodies. These protein structures cause corneous starch to resist water solubility and enzymatic hydrolysis. On the other hand, the floury endosperm has less of this protein matrix than corneous, but has a major concentration of starch granules; therefore, this endosperm region is more susceptible to enzymatic action (Kotarski et al., 1992).

The variation in extent and rate of enzymatic digestion of starch among species or varieties of grains is the result of the different proportions of the corneous or floury areas in the endosperm. To illustrate: the grains have been described as waxy, vitreous, non-waxy, and opaque according to the endosperm regions. In general, waxy grains have more amylopectin and floury endosperm; therefore, these grain have faster rate of digestion than the heterogenous or non-waxy genotypes (Rooney and Plugfelder, 1986; Huntington, 1997). However, there are differences in starch digestion among the floury endosperm of the grains due to the protein structures present in this endosperm (Kotarski et al., 1992).

Waxy grains have more starch digestion in vitro and in vivo than hetero-waxy or non-waxy grains (Street et al., 1990, Wester et al. 1992). These results have motivated studies of several varieties of waxy grain principally in sorghum (Cobert et al., 1996, Holtaus et al., 1996).

However, Rooney and Plugfelder (1986) pointed out that the waxy sorghum tends to have poor agronomic performance--inadequate seedling emergence, low vigor, and rapid deterioration before harvest--as compared to hetero-waxy hybrids of sorghum grain.

The pore size in the endosperm of the grains is a physical factor that affects the starch hydrolysis. Small pores reduce water penetration into the grain and prevent contact between the enzyme and the starch granules (Fannon et al. 1992).

Starch grains with intact pericarp are not soluble in cold water since the grain possess physical and chemical proprieties to prevent hydrolysis degradation. When hot water, steam, or pressure is applied to grains, the corneous endosperm is disrupted, and water can move inside of the starch granules; consequently, the grains swell. This process take place, principally, in the corneous region where the endosperm irreversibly loses its original structure. This changes in endosperm structure, which facilitates enzymatic degradation, is known as gelatinization.

The classical procedure for improving starch digestion is by processing the grains. This has been a common practice in human history for facilitating the digestion of cereals for food. Several cultures have developed their own

empirical methods for processing. Today, the animal industry has developed several methods for processing grains: grinding, dry rolling, popping, extruding, micronizing, pelleting, early harvesting, and steam-flaking.

The principle for processing grain is to "damage" the structure of the grain in order to help the amylose enzyme to reach the starch granules. The process of steam-flaking process consists of applying steam for 40 to 50 min to the grain, then flaking the grain to a specific density by passing the heated grain through large rolles. The effect on the grain of this process is the disruption of the protein matrix (Hale, 1976; Theurer, 1986).

Processing grains, such as by steam-flaking, increase the rate and the amount of starch digestion in rumen. When the rate of degradation is too rapid it may cause acidotic problem due to pH reduction as a result of abnormal increases of lactate production (Huntington, 1989). For that reason, some techniques--birefringence, viscosity, and enzymatic susceptibility-- have been developed to establish the optimal processing level of the grain. Rooney and Plugfelder, (1986) pointed out that the first two measurements are subject to a great deal of variability; whereas, enzymatic susceptibility is a more secure technique, which together with measurement of bulk density at the flaking site are two easy and practical methods for

measuring the degree of the steam-flaking process.

## Rumen Fermentation of Starch

The rumen is the place where the major digestion of starch in cattle occurs. This digestion is a fermentation by anaerobic microorganisms which live in symbiosis with the ruminant animal. These ruminal microorganisms are capable of fermenting both structural (cellulose and hemicellulose) and non-structural (starch, sugar, pectin) carbohydrates. Ruminants utilize as nutrients the waste (end-products) of this anaerobic fermentation and the bodies of these microbial fermenters.

Bacteria, protozoa, and fungi are the principal microorganisms in the rumen. Bacterial population is about $10^{10}$ to $10^{11}$ cells/g and protozoal numbers are $10^{5}$ to $10^{6}$ cells/ml of ruminal contents. The environmental conditions of the rumen--dark, anaerobic, moist, warm, and full of food--are adequate for growing anaerobic microorganism. All these ruminal microorganisms live in a small universe: the rumen, where they developed among the species, complex interactions: commensalism, competition, mutualism, and predation. Each microorganism must develop its own niche in order to survive. Therefore, in the rumen, the microbial populations coexist in constant agitation, but they maintain a dynamic equilibrium (Yokoyama and Johnson, 1989).

It is commonly accepted that the reduction of the ruminal pH, related to increased levels of starch in the diet, alters the microbial population and decreases neutral detergent fiber (NDF) digestion. However, Murphy (1989 cited by Mertens, 1993) pointed out that the low pH and resultant reduction of cellulolytic bacterial fermentation have a causal relationship, because the ruminal bacteria possess an internal regulation that inhibit the production of unneeded enzyme for cellulose digestion when starch is present in the rumen. In addition, Mertens (1993) pointed out that, in high-concentrate diet, the reduction of NDF digestion is due to the high affinity of the bacterial enzyme for a specific substrate. Therefore, this reduction of NDF digestion, when is available starch in the rumen, is more related to internal propensity and repression in the cellulolytic enzyme production inside the microorganism than a reduction of the ruminal pH.

Kotarski et al. (1992) reported the presence of 15 ruminal species of bacteria capable of using only starch as a substrate. These microorganisms are from six genuses: Bacteroides, Bifibacterium, Butyrivibrio, Streptococcus, Succinimonas, and Ruminobacter. These bacteria synthesize endo or exo amylose enzymes, and some of them have the ability to attach to starch granules. Kotarski also described nine amylolytic enzymes which are produced by

these bacteria. In addition, these authors suggested that some proteolytic enzymes for starch digestion must be involved in order to degrade the protein structures in the endosperm. Because of the difficulty in isolating and cultivating these anaerobic bacteria in a laboratory, Kotarki et al. (1992) opined that only a small part of the bacterial population that participates during the ruminal starch digestion is known.

Ruminal protozoa make a partial contribution to ruminal starch digestion. Mendonza et al., (1993) have demonstrated that defaunated ruminants exhibited more starch digestion than the undefaunates. However, several authors (Bergman, 1991; Kotarski et al., 1992; and Yokoyama and Johnson, 1989) have pointed out that protozoa have an important role in the high-grain diet because of their capacity to store starch, and, therefore, they can provide a more uniform starch fermentation.

The end products of starch fermentation are the VFA and the gases: carbon dioxide and methane. The VFA represent about 75% of the energy of the starch, the rest of energy is used by the microorganisms for growing, or lost as hydrogen and methane (Bergman, 1990). After starch is digested to glucose by the amylose and maltase enzymes, glucose is metabolized to pyruvate through the glycolysis pathway in the bacteria yielding acetate, propionate, and butyrate.

Acetate and butyrate arise from acetyl-CoA via oxidation of pyruvate. These two VFAs can be inter-convertible. Propionate is obtained from two pathways; one involves the formation of oxaloacetate and succinate, and the other includes acrylate formation. Both pathways operate equally (Owen and Goestch, 1988).

Lactate is another byproduct of starch fermentation. The principal lactate producers are the lactobacillus, which grow in low pH ruminal environments. Lactate is not an important intermediate for VFA production, and it can be absorbed in the rumen wall or passed to the abomasum (Bergman 1990).

The VFA concentration in the rumen is highly variable, from 60 to 150 mmol/L. An elevated value like 200 mmol can occur 2 h after a sheep consume a diet rich in grain (Bergman, 1990). The molar proportion of individual VFA in a concentrate diet is about 50:40:10 for acetate, propionate, and butyrate, respectively. The reduction of the ratio acetate:propionate in high-concentrate diets is due more to changes in propionate production than in acetate production (Reynolds et al. 1994b). This increased in propionate is the result of increased in numbers of microbial propionate producers.

A higher carbohydrate digestion in the rumen gives more available energy for bacterial activities: reproduction and

protein synthesis of enzymes. Some theoretical models try to predict microbial protein synthesis according to the amount of organic matter digested (INRA, 1982; NRC, 1996, Russell et al., 1992). According to these models, there is a positive relation between the amount of organic matter digested and the extent of microbial protein synthesized. Furthermore, there is a tendency to increase microbial protein flow to the abomasum when ruminal starch digestion increases. Theurer et al., (1996a,b) reported a 10% increase in this flow by growing steers and lactating cows when ruminal starch digestion increased.

A summary of previous starch digestion studies by steers fed high-grain diets with DR or SF of corn and sorghum, at different sites of the digestive system, are presented in Table 1. Only trials with steers cannulated in both the duodenum and ileum have been included in summarizing ruminal, small intestinal, large intestinal, and total digestion. Corn, either DR or SF, had more ruminal starch digestion than sorghum grain. In both corn and sorghum, the SF grains increased ruminal starch digestion; however, this improvement was greater for sorghum grain than corn: 19% vs 8% percentage units, respectively. The SF corn and sorghum grain consistently reduced the variability (SEM) in the starch digestion, probably due to the gelatinization, which provides a more uniform digestion.

The extent in the SF process in corn and sorghum grain increases the ruminal starch digestion. The reduction of the flake density of these grains increases the starch digestion in both grains (Table 2).

## Starch Digestion in the Small Intestine

The small intestine, an important organ of the splanchnic bed, has several important functions, including absorption of nutrients and secretion of enzymes, mucus, and immunoglobulins. A coordinate system of neural and hormonal signals regulates these activities. The largest endocrine gland is the gastrointestinal tract where at least 20 hormones and their receptors have been identified (Uvnas-Moberg, 1992; cited by Birth et al., 1996). The immuno-protection in the small intestine is provided by a large amount of immuno-components, which constitute approximately 25% of the mucosal mass of this organ (Saxena et al., 1993). In order to maintain these activities, the small intestine has the fastest cell renewal and replacement system in the body, and; therefore, it has a considerable demand for energy and nutrients.

In the small intestine starch is hydrolyzed by α-amylase, which is secreted by the pancreas. This enzyme hydrolyses the α-1,4 glucosic linkage, and the final products for this digestion are the oligosaccharides:

maltose, maltriose, and branched oligosaccharides with α-1,6 linkage. This first starch digestion occurs in the initial part of the small intestine (Gray, 1992).

The α-amylase represents only 2% of the pancreatic secretion (Keller et al., 1958; cited by Croom et al., 1992). The regulation of this secretion in ruminants differs from simple-stomach animals, which have two steps during the pancreatic secretion: the cephalic and the gastric phases. Ruminants do not have these two phases of regulation because of the continuous flow of digesta to the abomasum. When the level of starch increases in the diet, amylase secretion is also greater. However, this increase in enzyme secretion is more a result of greater metabolizable energy intake rather than level of starch intake (Harmon, 1992) .

Oligosaccharides are hydrolyzed to glucose by the disaccharidase enzymes from the brush border of the small intestine. The augmentation of these enzymes, when energy intake is increased, is the result of an indirect effect of increased the small intestine size. The disaccharidase enzymes have been characterized in simple-stomach animals; however, these enzymes are not well described in ruminants (Harmon, 1992).

Harmon (1992) concluded, using data published by Kreikemeier et al. (1991), that starch digestion in the

small intestine has a limit. They demonstrated that only 53% of the starch is digested in the small intestine when more than 900 g/d of corn starch was infused into the duodenum. However, several studies (Kartchner, 1972; Axe et al., 1987; Stock et al., 1987) have reported more than 900 g of starch digested in the small intestine by steers. Kreikemeier et al., (1991) study, they reported no limitation in glucose absorption, but incomplete starch digestion in the small intestine. These results may have been due to the low level of metabolizable energy intake (5.7 kg/d, alfalfa hay), which may not have been adequate to trigger the secretion of pancreatic juice. In the review by Owens et al. (1986) the authors pointed out that external infusion of nutrients into gastro-intestinal tract could cause alterations in the normal function of the digestive system because the additional flux exceeded the regular flux.

In the small intestine, the amount of absorbed glucose, which measured as net glucose uptake in portal blood, differs between ruminants and simple-stomach animals. Approximately, 85% of luminal glucose in simple-stomach animals is recover in portal vein (Gray, 1992). On the other hand, in beef steers, Huntington and Eisemann (1988) and Huntington (1990) demonstrated that a small or negative percentage of glucose is recover in this vein. Differences

in the digestive process between these species, where in ruminants depend upon ruminal fermentation and hepatic gluconeogenesis, may affect the physiological process for glucose uptake from small intestine.

Absorption and transport of glucose through the enterocytes are by two important strategies: active and passive systems. In active transport, a Na-dependent glucose transporter (SGLT1) participates in the absorption to the enterocyte, and a glucose transporter (GLUT2) carries the glucose to the basolateral membrane of the enterocyte. The passive transport is a paracellular diffusion related with water absorption and the laminar concentration of glucose. Because of the large differential glucose concentration between gut lumen and mesenteric blood, the contribution of this passive system to total glucose uptake is small. However, the amount of this contribution is unknown (Bird, 1996).

Gray (1992) pointed out that there are two kinetics types of SGLT1 in simple-stomach animal, low and high affinity. Wolfram et al. (1986), comparing the kinetics of this transporter in sheep and swine, reported a high affinity and low speed in enzyme kinetics for the ruminant, and the opposite for swine. When glucose in the luminal intestine is scarce, high affinity and low speed kinetics will be most important for glucose absorption; however, when

intestinal glucose is plentiful, such as for the simple-stomach animal fed high-grain diet, a low affinity and high speed kinetics should be most effective. Therefore, the type of kinetics for SGLT1 in ruminants is likely a high affinity and low speed.

The facilitated glucose diffusion in the different tissues is mediated by a family of structurally related glucose transporters. In humans and simple-stomach animals, five different types of this glucose transporter have been identified. The GLUT2 participates in glucose transport inside the enterocytes (Thorens et al. 1988). However, Zhao et al. (1993), using the complementary DNA cloning method in the bovine, reported a low amount of GLT2 in the small intestine, and a high quantity of this transporter in bovine hepatocyte in relation to the simple-stomach animals.

Gray (1992) pointed out that the efficiency of the glucose uptake from the small intestine to the portal vein by non-ruminants depends more on the transportation of the glucose inside the enterocyte to the blood rather than the glucose absorption from the lumen. In rats, Windmueller and Spaeth (1980) demonstrated that only 3% of the luminal glucose transported across the intestine was metabolized as an energy source, and arterial glutamine was the principal energetic substrate for the intestinal epithelium. However, in ruminants, Okine et al. (1995) demonstrated, using

enterocytes of dairy cows, that glucose is the principal energy source, followed by the glutamine. The proportion of the end products of glucose metabolism in the enterocytes appears to be similar between ruminants and simple-stomach animals. In human enterocytes, 70% of the glucose is converted to lactate (Ashy and Ardawi, 1988); and in dairy cows (Okine et al., 1995) lactate and carbon dioxide are the principal end products.

Because of the energetic cost for glucose synthesis in the liver, starch digestion in the small intestine has been considered more efficient than ruminal digestion. Despite, the potential high capacity for starch digestion by the small intestine (Table 1), the glucose net flux across the portal- drained viscera (PDV) is always low or negative (Huntington and Eisemann, 1988, Huntington, 1990). The ruminants can digest the starch and absorb the glucose in the small intestine, but they can not release the absorbable glucose into the portal vein. This controversial situation of glucose absorption in ruminants could be explained by the following facts: first, ruminants have adequate SGT1 transporter for glucose absorption from the lumen, but the kinetics of this transporter differs from that of simple-stomach animals (Wolfram, 1986); second, because of limited facilitated glucose transporter, GLT2, in the intestinal epithelium (Zhao et al., 1993), the absorbable glucose is

maintained inside the enterocyte; and third, the glucose is primary used as an energy source within the enterocytes (Okine et al., 1995)

Why the glucose PDV net flux in simple-stomach animals (high) differ from ruminants (zero or negative)? This question also may be analyzed from evolutionary and genetic challenges. According to Karasov (1989), natural selection acts to maximize the acquisition of metabolizable energy. One method to save energy is to reduce the metabolic expenses of synthesizing and maintaining the molecular machinery to absorb a substrate when feeding diets containing very low levels of this substrate. During the evolutionary process of ruminants, the presence of starch or glucose in the small intestine were not a common substrate because of predominantly forage diets. On the other hand, Goodridge (1990) demonstrated in rats that glucose metabolism has a genetic regulation according to the level of energy intake. Using a high energy diet in rats, synthesis of the enzyme pyruvate kinase in the liver increased, while a low energy diet reduced the synthesis of this enzyme and increased the phosphoenolpyruvate carboxykinase (PEPCK), an enzyme involved in the gluconeogic pathway. Therefore, using the same analogy, ruminants can digest starch and absorb glucose, but perhaps ruminants can not release this glucose to the portal vein, because of the

energetic cost for furnishing the internal glucose transporter for the scanty glucose; thus, genetic information in the enterocytes probably directs the use of glucose as an energy sources.

Absorption, Metabolism, and Release of Nutrients by the Portal-Drained Viscera and the Liver.

The gut, pancreas, spleen, and omental and mesenteric fat tissues are the components of the portal-drain viscera (PDV) because blood from these tissues drain into the portal vein. The PDV and the liver are the splanchnic (SPL) tissues, which work as a unit in order to regulate absorption of nutrients from the lumen and control the release of an adequate amount of the required metabolites to the rest of the body. This system is controlled by a plethora of hormones and nerves, which work in concert. The PDV is the area of communication and absorption from the exterior; and the liver regulates the blood concentration of nutrients to the interior.

For measuring nutrient net flux (absorption, uptake, or release) by the PDV and liver, the method of multiplying the venous-arterial concentration difference of a nutrient by the blood flow is broadly accepted (Reynolds et al., 1994, Huntington and Eisemann, 1988). This technique assumes that the animal is in steady state, and the change in the

nutrient concentration across an organ implies that this nutrient has been used or synthesized by the tissue. Linsday (1993) pointed out that this technique has limitations in comparing related diets because in some nutrients (e.g. glucose and amino acids), blood concentration difference between vessels is very small.

The PDV and liver use of energy is great in maintaining metabolic or physiological activities. The oxygen consumption the SPL, is about 50% of the body (Lindsay, 1993 and Reynolds and Maltby, 1994). The SPL tissues have the ability to reduce their size and oxygen consumption, according to the level of intake of the animal, in order to save energy for maintenance when the feed is scarce (Johnson et al., 1990). Different kinds of diets affect the energy consumption for these tissues. Reynolds et al. (1991) demonstrated that a forage diet uses more oxygen than a concentrate diet at the same level of metabolic energy intake.

Glucose release or absorption by the PDV in ruminants is generally negative or close to zero (Reynolds et al., 1994, Huntington and Eisemann, 1988), for both, forage or concentrate diets; however, glucose release from the liver is always positive (Huntington, 1990). Table 3 summarizes published data from steers fed high concentrate diets. Despite, the differences in PDV metabolism and release of

glucose between ruminant and simple-stomach animals, the requirement and metabolism of glucose for the rest of the body is similar among these animals; therefore, the liver in ruminants plays an especially important role in glucose production.

A positive glucose absorption by steers fed high-concentrated diets has been demonstrated (Theurer et al., 1991 and Reynolds and Huntington, 1988) across the mesenteric drain viscera (MDV;intestines). In these experiments catheters were placed in the mesenteric vein, as well as the portal vein, and glucose absorption from starch digestion in the small intestine was detected. However, when this positive glucose net flux from MDV was combined with the flux from the stomach vein (reticulo-rumen and abomasum), the result was a negative glucose absorption from the total PDV. This result implies a high glucose consumption by the rumen, which in part explains the elevated glucose uptake by the rumen when the intake is high in energy (Huntington and Eisemann, 1988).

The liver is the principal organ for synthesizing glucose, about 85 to 90% of the whole production. The kidney plays a secondary role in this process, 10 to 15% of the whole glucose turnover is produced by this organ (Brockman, 1993). Propionate, L-lactate, amino-acids, and glycerol are the principal glucose precursors. These metabolites can be

classified by their origins: exclusive exogenous source, propionate; exclusive endogenous source, glycerol; and both sources, L-lactate and amino-acids. The proportional contribution to glucose from these precursors changes according to the level of feed intake and the physiological status of the animal. In fasting, the propionate contribution to glucose synthesis decreases dramatically while the mobilization of endogenous precursors like lactate, amino-acids, and glycerol increase their contribution to this synthesis (Danfer et al., 1995).

The propionate contribution to glucose varies from 73% (Huntington and Eisemann, 1988) to 57% (Theurer et al., 1991) assuming that the total hepatic extraction of these metabolites is used for glucose synthesis (data from Tables 3 and 4). On the other hand, when using the isotopic method (labeling an atom in the precursor and measuring this atom in the glucose), propionate accounts for 30% of glucose synthesis in sheep (Bergman et al., 1966). Huntington and Eisemann, (1988) pointed out that the first method overestimates the contribution of the precursors to gluconeogenesis because the contribution is estimated from precursor availability and does not consider other uses (i.e. energy source, synthesis of other metabolites); whereas, the isotopic method underestimates this contribution because the randomization of the label carbon

can appear in other compounds. However, Steinhour and Bauman (1988), using a new mathematical approach for analyzing the labeled propionate, glucose, acetate and beta-hydroxybutyrate in vivo, reported that the propionate conversion to glucose is 95%. In short, the proportional contribution to glucose from the different precursors is not completely understood; more studies in this area will be necessary.

The α-amino N contribution to glucose varies from 9 to 39% (Danfer et al., 1995). This variation in glucose synthesis is due to the different physiological and nutritional conditions of the experimental animals when these data were obtained. Parenteral infusion of alanine in steers (Reynolds at al., 1994) or parenteral infusion of amino-acids (Danfer et al., 1995) did not increase glucose release from the liver.

Glucose infusion by via the abomasum, mesenteric vein, artery, or jugular vein did not increase the quantity of glucose released from the liver (Reynolds et al., 1994a). Likewise, propionate or amino-acid infusions did not affect glucose production, but did decrease the uptake by the liver (Baird et al., 1980). Reynolds et al. (1994a) pointed out that glucose production and release by the liver must be tightly controlled in order to maintain a constant concentration of blood glucose.

In growing steers, glucose utilization by the extra-splanchnic tissues is principally for maintenance and accretion of fat and muscle. About 23% of the glucose is used by the adipose tissue (van der Walt, 1984), and the muscle mass consumes about 20 to 40% of the total glucose turnover (Oddy et al. 1985). The PDV uses 20 to 30% of the glucose turnover and liver utilization of glucose varies from 0 to 15% (Brockman, 1993). Glucose consumption by the brain accounts for 10% of whole body glucose utilization (Pell and Bergman, 1983).

Because of the difficulty in separating lactate absorbed from the intestinal lumen from lactate synthesized by the PDV epithelium, it is difficult to recognize the origin of the lactate release in the portal vein. The absorbed lactate by the PDV has three different sources: diet, in the case of silage; rumen bacterial fermentation; and PDV metabolism.

The lactate net flux across the PDV by steers fed a high-concentrate diet varies from 34 to 120 mmol/h (Table 3). Huntington and Eisemann (1988) pointed out that, in ruminants the PDV is the principal lactate producer; whereas, in simple-stomach animals, muscle mass is the major producer of lactate. Therefore, the glucose-lactate-glucose cycle through PDV and liver could be quantitatively more significative in ruminants than the Cori cycle in simple-

stomach animals.

In the liver, lactate is absorbed and metabolized to glucose. The lactate contribution to glucose varies from 7 to 13-% in a high-concentrate diet, assuming complete transformation from the hepatic uptake (Table 3). Brockman (1993) considered that in fed animals this contribution is less than 20% and increases in fasting animals. The lactate uptake by the liver depends on the concentration of other glucose precursors, principally propionate. Baird et al. (1980), infusing propionate in sheep, reduced the liver lactate uptake and increased the lactate concentration in the artery. The net flux of lactate in the extra-splanchnic tissues may result in uptake or release. Prior (1978) pointed out that lactate is a precursor for lipid synthesis in the bovine adipose tissue.

The VFA are the principal energetic substrates that are absorbed by ruminants. The absorbed energy from VFA produced by ruminal fermentation is about 75% of the ME intake (Bergman, 1990). Absorbed acetate is the largest single energy source, followed by absorbed propionate (Huntington, 1990).

During the absorption in the rumen, a considerable amount of VFA are metabolized, which reduces the amount of released VFA in the portal vein. In sheep fed alfalfa, Bergman (1990) concluded that 30% of acetate, 50% of

propionate, and 90% of butyrate are transformed in the rumen wall. Huntington et al. (1983) reported similar results in dry cows fed with 60:40 a forage-concentrate diet. When these authors infused acetate into the rumen, 69% was recovered in the portal vein. Infusion of sodium propionate infusion into the rumen of steers does not increase net portal flux of propionate (Harmon and Avery, 1987). With a total infusion of the VFA in the rumen of sheep, Gross et al. (1990a, and 1990b) recovered 47 to 53% for acetate, 67 to 70% for propionate, and 22 to 23% for butyrate. More cattle data on rumen wall metabolism of VFA is clearly needed.

The variation in VFA production in the rumen of cattle from different diets (forage vs concentrate) does not always match with the absorbed VFA. Huntington (1983), using corn silage vs ground corn, reported more propionate absorption in the concentrate diet. However, Reynolds et al. (1993; and 1994a), compared diets containing 75% alfalfa: 25% cracked corn soybean meal (SBM) or 25% alfalfa: 75% cracked corn SBM, at a similar levels of energy intake, reported more net absorption of acetate and butyrate for the 75% forage diets in both experiments, but unexpectedly net absorption of propionate was greater for steers fed high-forage versus high-concentrate (Reynolds et al., 1994a). In fact, a high-concentrate diet increases the propionic acid concentration

in rumen contents; however, this increase is not always reflected in the PDV net flux. A greater use of energetic metabolites by the rumen epithelium in a concentrate versus forage diets (Harmon, 1986) could explain part of these results.

In high-concentrate diets, changes in the kind of grain or in the grain processing, affect the net VFA flux in PDV and SPL (Table 4). Gross et al. (1988), using different grains, reported that wheat had more net portal flux of propionate than sorghum grain, but acetate and butyrate fluxes were not affected. Using different sorghum grain processing, dry-rolled vs steam-flaked, Theurer et al. (1991) reported that steers fed steam-flaked sorghum tended to absorb more net propionate and acetate across the PDV and 40% more acetate was released by the SPL. These increase in the net VFA absorption probably were due to greater starch digestion in the rumen of the wheat and of the steam-flaked grain.

The use of ionophores in high-concentrate diets does not result in a consistent response in VFA absorption across the PDV. Harmon et al. (1988) reported an increase in net portal flux of propionate using salynomicin and monensin. However, in propionate absorption with monensin was not demonstrated in two similar experiments (Harmon and Avery, 1987, and Harmon et al., 1989).

The amount of net acetate flux by the PDV is similar (but somewhat less) acetate release by the liver. Liver production of acetate is less than 10% of the amount of acetate released by the PDV (data from Table 4). Brockman (1993) pointed out that the acetate utilization by the liver is almost the same as the hepatic production of acetate, which is less than 5% of the whole-body acetate turnover. For the rest of the body, acetate is the principal VFA source of energy. The acetate half-life is short, ranging from 4 to 13 min, because this metabolite is extensively used by tissues (Brockman, 1993). In the whole body, 66% of the acetate is oxidized and the rest is used for lipid synthesis. The acetate utilization by the hind-limb in growing steers is 50 to 60% of the acetate released by the SPL (Huntington and Eisemann, 1988).

Propionate uptake by the liver appears to be constant; this uptake is about the 90% of the PDV released (Table 4). The infusion of propionate into mesenteric vein increases the total amount of propionic acid uptake by the liver; although, the percentage of this uptake decreases from 90 to 75% (Brockman, 1993). However, this increase in portal propionate reduces lactate uptake by the liver, and consequently, increases the lactate concentration in the blood (Brockman, 1993). In the liver, propionic acid is principally metabolized to glucose. Glucose infusion into

mesenteric vein does not affect hepatic propionate uptake (Braid et al., 1980).

About 90% of the absorbed butyrate in the rumen is transformed into ketone bodies (BHBA and acetoacetate) by the epithelium cells (Bergman, 1990). The remaining butyrate released to the portal vein is largely removed by the liver (Table 4), by metabolism to ketone bodies. The SPL released of BHBA is about twice that of BHBA absorption, due to extensive synthesis by the liver (Huntington and Eisemann, 1988; Reynolds et al., 1991).

Summary

Grains are the principal source of metabolizable energy for feedlot steers. Starch is the major component of grains. The metabolizable energy for growing steers fed high-concentrate diets is largely obtained from the starch digestion and the resultant absorption of the end products of digestion. In the rumen, microorganisms digest the starch, and the VFA are the main end products from this fermentation. L-lactate is also a secondary product from starch digestion in the rumen. The VFA and the L-lactate are absorbed by the ruminal epithelium. The metabolism of VFA by rumen epithelium is large (30% for acetate, 30 to 50% propionate, and 80 to 90% butyrate).

In the small intestine, starch is digested by the

epithelial and pancreatic enzymes; glucose is the principal end product. Then, the glucose is absorbed by the intestinal epithelium. Even though, most glucose released by starch digestion is absorbed by the small intestine, in cattle opposite to simple-stomached animals, net absorption of glucose across the PDV is usually close to zero.

Processing grain, by steam-flaking, increases the percentage of starch digested in the rumen and within the small intestine. This steam-flaking process alters the starch structure, which allows the enzymes to more easily reach the starch granules. The disruption by flaking of the protein matrix, which surrounds the starch granules, is the primary effect of the steam-flaked process on the grains. Several studies on the net absorption of nutrients, in cattle fed high-concentrate diets, have demonstrated that VFA, L-lactate, and BHBA are the principal energy-yielding substrate, which are released by the PDV. There is only one study on the effect of the flake density of steam-processing sorghum grain on digestion of nutrients in beef steers, and no data on post-absorption effects by the flake density in sorghum grain.

Table 1. Means of starch digestion of steam-flaked or dry-rolled corn and sorghum grain at different sites of the digestive tract from publish works

| | Sorghum grain[a] | | Corn[b] | |
|---|---|---|---|---|
| Item | DR | SF[c] | DR or W | SF[c] |
| Starch intake, kg | 4.3 ± .29 | 3.8 ± .57 | 3.1 ± .32 | 2.5 ± .29 |
| Digestibility, % of intake | | | | |
| Rumen | 59 ± 4.6 | 82 ± 3.1 | 75 ± 5.7 | 83 ± 1.5 |
| Post-rumen | 31 ± 4.9 | 17 ± 3.1 | 17 ± 4.1 | 15 ± 1.2 |
| Small intestine | 26 ± 6.8 | 15 ± 3.2 | 14 ± 3.9 | 15 ± 1.3 |
| Large intestine | 4.7 ± 1.2 | 1.9 ± .28 | 4 ± 1.2 | 1 ± .27 |
| Total tract | 90 ± 2.1 | 99 ± .20 | 90 ± 3.2 | 99 ± .56 |
| Digestibility, % entering intestine | | | | |
| Small intestine | 57 ± 26.0 | 80 ± 3.9 | 45 ± 10 | 89 ± 3.9 |
| Large intestine | 28 ± 6.1 | 55 ± 4.5 | 32 ± 8.9 | 47 ± 3.9 |
| Citations[b] | 1-5 | 1,6,7 | 4,8-11 | 6,8,10,11 |
| Nº trials | 6 | 6 | 5 | 6 |

[a b] Grain processing: DR = dry-rolled; SF = steam-flaked; and W = whole

[c] Average of steam-flaked grain flaked at densities of 360 g/L and below this density

[d] Citations: 1. Kartchner, 1972; 2. Stock et al., 1987; 3. Hibberd et al., 1983; 4. Streeter et al., 1990; 5. Hill et al., 1991; 6. Zinn, 1991; 7. Eck, 1991; 8. Lee et al., 1982; 9. Streeter et al., 1989; 10. Aguirre et al., 1984; 11. Zinn, 1990b

Table 2. Starch digestibility at different sited of steam-flaked corn and sorghum grain flaked at different densities

| | Sorghum grain[a] | | | | Corn[b] | | |
|---|---|---|---|---|---|---|---|
| Item | SF32 | SF28 | SF24 | SF20 | SF28 | SF24 | SF20 |
| Starch intake, kg | 3.83 | 4.00 | 3.93 | 3.98 | 3.09 | 3.05 | 3.05 |
| Digestibility, % of intake | | | | | | | |
| Rumen | 82[c] | 88 | 86 | 91 | 80 | 83 | 87 |
| Post-rumen | 15 | 10 | 13 | 8 | 18 | 16 | 12 |
| Small intestine | 12 | 8 | 9 | 7 | - | - | - |
| Large intestine | 3.3 | 1.8 | 3.2 | 1.3 | - | - | - |
| Total tract | 97[c] | 98 | 99 | 99 | 98[d] | 99 | 99 |
| Digestibility, % entering intestine | | | | | | | |
| Small intestine | 70 | 71 | 69 | 74 | - | - | - |
| Large intestine | 56 | 47 | 70 | 48 | - | - | - |

[a] Data from Eck, 1991; SF = steam-flaked; SF32, SF28, SF24, SF22 were flaked at densities of 411, 360, 308, and 257 g/L, respectively

[b] Data from Zinn, 1990a; SF = steam-flaked; SF28, SF24, SF20 were falked at densities of 360, 308, and 257 g/L, respectively

[c] Linear effect within SF sorghum grain ($P < .05$)

[d] Linear effect within SF corn ($P < .05$)

Table 3. Blood flow (L/h) and net glucose and L-lactate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissue of steers fed high-concentrate diets

| Source | Animal kg | Diet[a] | DMI kg | Blood Flow, L/h | |
|---|---|---|---|---|---|
| | | | | Portal vein | Hepatic vein |
| Huntington et al., 1981 | Steers 277 | G Corn 78% | 5.0 | 935 | |
| Huntington, 1983 | Steers 328 | C Corn 91% | 5.6 | 880 | |
| Huntington and Prior, 1983 | Heifers 295 | G Corn 78% | 5.1 | 782 | |
| Harmon and Avery, 1983 | Heifers 211 | C Corn 76% | 5.1 | 651 | |
| Gross et al., 1988 | Steers 300 | DR Wheat<br>DR Sorghum<br>Wheat/Sorg 77% | 6.2<br>6.0<br>6.1 | 741<br>774<br>817 | |
| Reynolds and Huntington, 1988a | Steers 390 | G Corn 78% | 6.0 | 750 | |
| Harmon et al., 1988 | Heifers 305 | C Corn 76% | 4.4 | 564 | |
| Huntington and Eisemann, 1988 | Steers 266 | C Corn 63% | 3.9 | | |
| Harmon et al., 1989 | Steers 252 | C Corn 76% | 5.3 | 705 | |
| Huntington, 1989 | Steers 240 | C Corn 78% | 4.3 | 575 | 713 |

Table 3. Blood flow (L/h) and net glucose and L-lactate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissues of steers fed high-concentrate diets *Continued*

| Source | Animal kg | Diet[a] | DMI kg | Blood Flow, L/h Portal vein | Blood Flow, L/h Hepatic vein |
|---|---|---|---|---|---|
| Theurer et al., 1990 | Steers 363 | DR Sorghum | 7.3 | 859 | 1071 |
| | | SF Sorghum 77% | 7.1 | 894 | 1052 |
| Reynolds and Tyrrell, 1991 | Heifers 443 | G Corn 63% | 6.5 | 634 | 777 |
| Reynolds et al., 1991 | Heifers 320 | G Corn 63% | 6.5 | 763 | 842 |
| Huntington et al., 1996 | Steers 421 | C Corn 63% | 5.9 | 638 | 776 |
| Overall means | | AVG | | 748 | 872 |
| | | SD | | 113 | 152 |

Table 3. Blood flow (L/h) and net glucose and L-lactate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissues of steers fed high-concentrate diets *Continued*

| Source | Diet[a] | Glucose[b] | | | Lactate | | |
|---|---|---|---|---|---|---|---|
| | | PDV | Liver | SPL | PDV | Liver | SPL |
| Huntington et al., 1981 | G Corn 78% | -29 | | | 34 | | |
| Huntington, 1983 | C Corn 91% | -25 | | | 113 | | |
| Huntington and Prior, 1983 | G Corn 78% | 18 | | | 118 | | |
| Harmon and Avery, 1983 | C Corn 76% | -23 | | | 85 | | |
| Gross et al., 1988 | DR Wheat | 3 | | | 85 | | |
| | DR Sorghum | 24 | | | 92 | | |
| | Wheat/Sorg 77% | 22 | | | 107 | | |
| Reynolds and Huntington, 1988a | G Corn 78% | -1 | | | 43 | | |
| Harmon et al., 1988 | C Corn 76% | -24 | | | 89 | | |
| Huntington and Eisemann, 1988 | C Corn 63% | -16 | 180 | 164 | 71 | -47 | 24 |
| Harmon et al., 1989 | C Corn 76% | -25 | | | 75 | | |
| Huntington, 1989 | C Corn 78% | -4 | 159 | 155 | | | |

Table 3. Blood flow (L/h) and net glucose and L-lactate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissues of steers fed high-concentrate diets *Continued*

| | | Glucose[b] | | | Lactate | | |
|---|---|---|---|---|---|---|---|
| Source | Diet[a] | PDV | H | SPL | PDV | H | SPL |
| Theurer et al., 1990 | DR Sorghum | -14 | 309 | 301 | 101 | -46 | 57 |
| | SF Sorghum 77% | -64 | 360 | 312 | 120 | -52 | 69 |
| Reynolds and Tyrrell, 1991 | G Corn 63% | 71 | 214 | 286 | 52 | -29 | 24 |
| Reynolds et al., 1991 | G Corn 63% | -1 | 285 | 285 | 81 | -8 | 73 |
| Huntington et al., 1996 | C Corn 63% | -12 | 174 | 161 | 73 | -38 | 35 |
| Overall means | AVG | -6 | 240 | 238 | 84 | -36 | 52 |
| | SD | 29 | 78 | 73 | 26 | 16 | 21 |

[a] G = ground, C = craked, DR = dry-rolled, SF = steam-flaked, Sorg = sorghum grain

[b] PDV = portal-drained viscera; SPL = total splanchnic tissues; H = liver

Table 4. Net VFA and ß-hydroxibutyrate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissues of steers fed high-concentrate diets

| Source | Animal kg | Diet[a] | DMI kg | Acetate[b] PDV | H | SPL |
|---|---|---|---|---|---|---|
| Huntington, 1983 | Steers 328 | C Corn 91% | 5.6 | 425 | | |
| Huntington and Prior, 1983 | Heifers 295 | G Corn 78% | 5.1 | 418 | | |
| Harmon and Avery, 1987 | Steers 211 | C Corn 76% | 5.1 | 295 | | |
| Gross et al., 1988 | Steers 300 | DR Wheat | 6.2 | 526 | | |
| | | DR Sorghum | 6.0 | 605 | | |
| | | Wheat/Sorg 77% | 6.1 | 469 | | |
| Reynolds and Huntington, 1988a | Steers 390 | G Corn 78% | 6.0 | 448 | | |
| Harmon et al., 1988 | Heifers 305 | C Corn 76% | 4.4 | 396 | | |
| Huntington and Eisemann, 1988 | Steers 266 | C Corn 63% | 3.9 | 419 | 53 | 475 |
| Harmon et al., 1989 | Steers 252 | C Corn 76% | 5.3 | 423 | | |
| Theurer et al., 1991 | Steers 363 | DR Sorghum | 7.3 | 616 | -55 | 587 |
| | | SF Sorghum 77% | 7.1 | 785 | 51 | 839 |
| Reynolds et al., 1991 | Heifers 320 | C Corn 63% | 6.5 | | | |
| Reynolds et al., 1993 | Heifers 321 | C Corn 63% | | 561 | 39 | 600 |
| Reynolds et al., 1994 | Heifers 443 | C Corn 63% | 6.5 | 605 | 56 | 662 |
| Huntington et al., 1996 | Steers 421 | C Corn 63% | 5.9 | 648 | 59 | 706 |
| Overall means | | AVG | | 509 | 34 | 645 |
| | | SD | | 126 | 44 | 123 |

Table 4. Net VFA and ß-hydroxibutyrate flux (mmol/h) across portal-drained viscera, liver, and splanchnic tissues of steers fed high-concentrate diets *continued*

| | Propionate[b] | | | Butyrate | | | BHBA[c] | | |
|---|---|---|---|---|---|---|---|---|---|
| Source | PDV | H | SP | PDV | H | SP | PDV | H | SP |
| Huntington, 1983 | 339 | | | 25 | | | | | |
| Huntington and Prior, 1983 | 284 | | | 52 | | | | | |
| Harmon and Avery, 1987 | 348 | | | 34 | | | | | |
| Gross et al., 1988 | 481 | | | 31 | | | | | |
| | 465 | | | 25 | | | | | |
| | 335 | | | 33 | | | | | |
| Reynolds and Huntington,1988 | 178 | | | 93 | | | 106 | | |
| Harmon et al., 1988 | 175 | | | 46 | | | 94 | | |
| Huntington and Eisemann, 1988 | 299 | -263 | 29 | 46 | -38 | 8 | 55 | 50 | 105 |
| Harmon et al., 1989 | 448 | | | 47 | | | 45 | | |
| Theurer et al., | 400 | -352 | 46 | 69 | -54 | 13 | | | |
| 1991 | 480 | -426 | 56 | 74 | -56 | 16 | | | |
| Reynolds et al., 1991 | | | | | | | 79 | 94 | 171 |
| Reynolds et al., 1993 | 387 | -360 | 27 | 54 | -45 | 9 | | | |
| Reynolds et al., 1994 | 280 | -252 | 28 | 96 | -72 | 24 | | | |
| Huntington et al., 1996 | 254 | -240 | 14 | 40 | -35 | 5 | | | |
| Overall means | | | | | | | | | |
| AVG | 344 | -316 | 33 | 51 | -50 | 12 | 76 | 72 | 138 |
| SD | 101 | 75 | 15 | 23 | 14 | 7 | 26 | 31 | 47 |

[a] G = ground, C = craked, DR = dry-rolled, SF = steam-flaked, Sorg = sorghum grain

[b] PDV = portal-drained viscera; H = liver; SP = Total splanchnic tissues [c] BHBA = ß-hydroxibutyrate

# CHAPTER 3

## STEAM-PROCESSED CORN AND SORGHUM GRAIN FLAKED AT DIFFERENT DENSITIES ALTERS RUMINAL, SMALL INTESTINAL, AND TOTAL TRACT DIGESTIBILITY OF STARCH BY STEERS

## SYNOPSIS

The objectives were to determine DM and starch digestion in the rumen and intestines by steers (Cr ratio and 3-d collection) fed diets containing 77% grain: Trial 1. sorghum grain, dry-rolled (DR) or steam-processing (SF) at densities of 437, 360, and 283 g/L; and Trial 2. corn, SF at densities of 437 and 283 g/L (SF34 and SF22). Seven steers (400 kg BW) with duodenal and ileal cannulas were used in a randomized block design for both trial. In the sorghum trial, daily intakes of DM (6.6 kg) and starch (3.8 kg) were similar among treatments. Steers fed SF versus DR sorghum increased starch digestibility in the rumen (23%; $P < .01$), total tract (2.3%; $P < .01$), and in the small intestine (6%; $P < .01$, as percentage of starch entering duodenum). Decreasing flake density of SF sorghum grain increased linearly ($P < .05$) starch digestion (percentage of intake) in the rumen and total tract, and diminished linearly ($P < .05$) starch digestibilities post-ruminally and in the small intestine. Digestibility of DM was higher (23%; $P = .04$) for steers fed SF versus DR sorghum grain, and ruminal DM

digestion increased linearly (P = .05) as flake density decreased within SF diets. In the corn trial, steers fed SF22 had higher starch digestibility (percent of intake) in the rumen (12%; P = .02) and total tract (2 %; P = .09), and lower starch digestion (P < .10) in the small and large intestines compared with SF34. Percent dietary corn or sorghum starch digested in the large intestine was less than 2% of intake. Reduction of the flake density of steam-processed corn and sorghum grain consistently and linearly increased starch digestibility in the rumen and total tract of growing steers.

## INTRODUCTION

Grains are the principal source of metabolizable energy (ME) for rapidly growing cattle. Processing of grain by steam-flaking is widely used by feedlot operations. An increase in ruminal and total starch digestion is the principal effect of the steam-flaking process (Theurer, 1986; Theurer et al, 1996a, b). Concentrations of ME for steam-flaked (SF) corn and sorghum grain were increased by 5.8% and 9.5% respectively, compared to minimal processing, dry rolled (DR) or ground (NRC, 1984). Steam-flaking of these two grains improves efficiency of feed utilization in growing steers (Hale et al., 1980; Zinn, 1990; Xiong et al., 1991; Swingle et al. 1991). Studies with beef cattle to

determine the effect of altering flake density (degree of processing) of steam-processed corn or sorghum grain on starch digestibility in the rumen, small intestine, and large intestine are very limited. Zinn (1990) reported a linear increase in post-ruminal (as a percentage of starch flow to duodenum) and total starch digestion in steers fed SF corn when flake density was decreased, but reduction in flake density did not affect ruminal starch digestion or steer performance. With SF sorghum grain, Eck (1991) found a linear increase in ruminal and total starch digestion as flake density decreased. The objective of the present study is to determine the DM and starch digestibility by steers at different gastro-intestinal sites using steam-processed corn and sorghum grain flaked at different densities. The sorghum trial is a companion study to the post-absorptive study reported in Chapter 4; steers from the same pool of 32 animals were fed the same diets in both studies.

## MATERIALS AND METHODS

Trial 1. Seven crossbred steers (400 kg initial BW) were fitted with "T" type cannulas in the proximal duodenum (8 cm from the pyloric sphincter) and in the distal ileum (20 cm from the ileal-cecal valve). Steers were housed in individual pens 2.5 to 5 m, where they had free access to water. Steers were allowed free movement at all times except

during sampling. Experimental diets (Table 5) contained 77% sorghum grain, and were formulated to meet crude protein and ME for steers gaining 1.0 kg/d (NRC, 1984). The four dietary treatments were DR sorghum grain and SF sorghum grain flaked at densities of 437, 360, and 283 g/L (SF34, SF28, and SF22, respectively, referring to pounds per bushel as used in the field). Chromium oxide was added as a flow digesta marker at .3% of the diet. Grain was steamed for about 45 min in a vertical steam chamber, then the grain was passed through a roller mill (45 cm diameter by 75 cm long); rollers were adjusted to produce a specific flake density.

The experimental design was a randomized complete block using steer and period as block criteria. The experimental period consisted of 14 d, with 11 d adjustment, and 3 d for sample collections. Diets were offered at 0700 and 1900 daily; amounts fed were about 10 % in excess of steer consumption. Feed and ort samples were taken daily during the last 5 d of each period. Duodenal, ileal, and fresh fecal samples were collected four times daily, every 6 h during 3 d. This collection system provides a total of 12 samples, representing each 2 h of a 24 h period. Individual samples consisted of approximately 300 g feed, 300 ml duodenal chyme, 200 ml ileal chyme and 300 g (wet basis) of feces. Two duodenal samples were collected each sampling, one for nutrient analysis and the other for microbial

protein analyses. Preparations and analysis of the latter sample to determine bacterial cell N is outlined by Alio (1997). All other samples were kept frozen at -4 °C and later composited for each steer and collection period.

Samples of feed, orts, feces and digesta were dried at 50 °C for 48 h and grounded in a cyclone mill through a 1 mm screen. These samples were used for the following analyses: DM (oven drying at 105 °C 24 h; AOAC, 1984); starch (Poore et al., 1989), and chromium (Fenton and Fenton 1979). In addition, the rate of in vitro starch hydrolyzed by amyloglucosidase (Diazyme L-200, Miles Inc. Elkart, IN), expressed as a percentage of total starch, was determined for DR and for each of the densities of SF sorghum grain (Poore et al., 1989).

Digestibilities of nutrients at different sites of the digestive tract were determined from ratios of Cr concentration in consumed feed and Cr concentration in duodenal digesta, ileal digesta, or feces. Ruminal DM digestion was corrected for microbial DM flow to the duodenum (data from Alio, 1997). Actual nutrients and Cr intakes were adjusted for amounts determined in orts.

Data were analyzed by GLM (MINITAB, 1996) for DR versus the average of all SF treatments, and for linear and quadratics effect within the SF treatments.

Statistical model was:

$$Y_{ijk} = \mu + T_i + P_j + S_k + E_{ijk}$$

Where

$\mu$ = overall means
T = treatment effect
P = period block effect
S = steer block effect
E = random error

Probability values of $P \leq .05$ were considered significant and $.05 > P \leq .15$ were considered a tendency.

Trial 2. The same animals (420 kg initial BW) and experimental and analytical procedures for trial 1 were used. Diet composition was the same, except that steam-processed corn, which was flaked at 437 and 283 g/L (SF34 and SF22 referring to pounds per bushel commonly used in the field) was substituted for SF sorghum grain (Table 5).

## RESULTS AND DISCUSSION

Trial 1. The in vitro rate of starch hydrolysis during 30 min was much greater ($P < .01$) for SF sorghum grain than for DR grain (66 vs 35% of the total grain starch; Table 6). Rate of starch hydrolysis also increased linearly from 52 to 79% ($P < .01$) as flake density decreased from SF34 to SF22. The hydrolysis rate for SF22 was more than twice that for DR sorghum grain (79 vs 35%) and 50% higher than for SF34.

Daily intake of DM (6.6 kg) and starch (3.8 kg) were similar among treatments (Table 7). Corrected DM flow to the duodenum tended ($P = .06$) to increase (3.23 vs 2.59 kg/d)

for steers fed DR vs SF sorghum diets; thus, corrected ruminal DM digestion was 17% higher (61 vs 52%; P = .04) for steers fed SF vs DR diets (Table 7). Ruminal DM digestion increased linearly (P = .05) from 56 to 65% when flake density decreased within SF diets. Total DM digestion was similar (79%) between DR and SF diets. However, within SF diets total DM digestion tended to increase linearly (P = .07) from 77 to 82% with decreasing flake density. These changes in ruminal DM digestibility are primarily attributed to similar but greater changes in starch digestibility, because ruminal crude protein digestibility was not altered by treatment (Alio, 1997).

Starch flow to the duodenum for steers fed DR sorghum was almost twice (P < .01) that for steers fed SF sorghum (1.32 vs .67 kg/d). Starch flow to the ileum (191 vs 60 g/d) and fecal starch (145 vs 42 g/d) also were three times greater (P < .01) for DR compared to SF diets. Within SF diets, reduction of flake density decreased linearly the quantity of starch flow to the duodenum (P = .06) and ileum (P = .04), and fecal starch excretion (P = .03).

Percentage of sorghum starch digested by steers throughout the digestive tract was altered by SF versus DR processes and by the degree of flaking for SF grain. These changes follow similar patterns at the different sites within the gut. Steers fed SF diets had a 23% higher ruminal

(83 vs 67%) and greater (P < .01) total starch digestion (99.6 vs 97.7%) compared to steers fed the DR diet. Consequently, starch digestion, as a percentage of starch intake, was lower for steers fed SF in relation to DR: post-ruminally (16 vs 30%; P = .01), in the small intestine (16 vs 28%; P = .01), and in the large intestine (.5 vs 1.2%; P = .05). As expected, starch digested within the small intestine, as a percentage of starch presented to the duodenum, was 6% higher (91 vs 85%; P = .01) by steers fed SF vs DR diets. In the large intestine, starch digestion (as a percentage of starch presented to the ileum) was low (31%) and similar between DR and SF diets, ranging from 28 to 40% by treatment.

Within SF diets, reducing flake density increased linearly the percentage of starch digested by steers in the rumen from 77 to 89% (P = .03), and in the total tract from 97.7 to 99.6% (P = .03). This resulted in a linear decrease in starch digestion, as a percentage of intake, post-ruminally from 21 to 10% (P = .04) and in the small intestine from 20 to 10% (P = .04), but not in the large intestine. Flake density did not alter starch digestion (as a percentage of starch presented) in the small or large intestine.

Ruminal starch digestibility of DR sorghum in the present study was 13% higher (67 vs 59%) than the average of

five early trials (Table 1). Data from the present study is similar to that reported by Streeter et al. (1990), Hill et al. (1991), Spicer et al. (1986), and Hibberd et al. (1983), but it was higher compared to other authors (Kartchner, 1972; Garcia et al., 1981; and Stock et al., 1987). The low ruminal starch digestibility reported in these latter studies may due in part to variability among sorghum grains, or that recent varieties of sorghum grain may have more digestible starch in the kernel.

In the small intestine, the digestibility of the starch from DR sorghum grain in the present study, as percentage of intake, was similar (29 vs 26%) to the average from five trials (Table 1); however, digestibility in the small intestine, as a percentage of starch entry, was 45% higher in the present study (85 vs 57%) compared to the reports in Table 1, where the variation is high (CV = 46%). The starch digestion in the small intestine in the present study was similar (85 vs 88%) to data reported by Kartchner (1972), but it was twice that reported by Hibberd et al. (1983), Stock et al. (1987), Streeter et al. (1990), and Hill et al. (1991).

Starch digestion of SF sorghum grain at different sites in the present study were similar to the average from three previous trials (Table 1). Starch digestibility at different digestive sites, reported by Eck (1991; Table 2) for steers

fed steam-processed sorghum grain flaked at different densities, followed similar responses to flaked density to the present study, except in the percentages of starch digested in the small intestine, as percentage of starch flowing to the duodenum, were 20 percentage units lower than in the present study.

Trial 2. As with SF sorghum, the in vitro rate of starch hydrolysis during 30 min for corn greatly increased ($P < .01$) when the flake density decreased from SF34 to SF22 (Table 6). Rate of hydrolysis for SF34 and SF22 corn appeared to be lower than for SF34 and SF22 sorghum grain (40% and 69% versus 52% and 79%, respectively). However, the values between SF34 and SF22 changed more for corn than sorghum grain (75% vs 50% improvement). The in vitro starch hydrolysis provides an excellent laboratory measure of the degree of processing or flake density, and it is superior to the birefringence method ("gelatinization"), which changes minimally with decreased flake density (Swingle et al., 1991).

Daily intake of DM tended to increase ($P = .06$) for steers fed SF22 corn, consequently, starch intake was 7% higher ($P = .01$) for steer fed SF22 compared to SF34 (4.85 vs 4.55 kg/d). These differences were not expected since previous performance studies with different densities of SF corn indicated similar intakes in DM (Zinn, 1990a)

Corrected DM flow to duodenum (3.89 kg/d) and apparent DM in the feces (1.96 kg/d) were similar between steers fed SF34 and SF22 corn. Likewise, the percentage of corrected DM digested in the rumen (52.4%) and the percentage of apparent DM digested in the total tract (75.9%) did not differ between flaked treatments (Table 8).

Even though, starch intake by steers fed SF22 corn was 7% higher, the amount of starch flow to the duodenum (P = .03) and ileum (P = .06), and fecal starch excretion (P = .09) were lower in the steers fed SF22 (Table 8). These differences in starch flow between steers fed SF22 and SF34 corn resulted from increased starch digestibility in the rumen (85 vs 76%; P = .02), and the tendency to increase total tract digestion (99 vs 97%; P = .09) in steers fed SF22 versus SF34 corn. Because of the large amount of starch flow to duodenum by steers fed SF34, these steers tended to digest more starch post-ruminally (21 vs 14%; P = .06), in the small intestine (19 vs 14%; P = .09), and in the large intestine (1.7 vs .4; P = .09) compared with SF22 corn (Table 8). Similar to steers fed SF sorghum, decreasing flake density of steam-processed corn did not alter starch digestibility in the small (88%) or in the large intestine (34%) as a percentage of starch presented to the duodenum or ileum.

Coefficients of starch digestibilities at the different

sites by steers fed SF22 in the present study are consistent with the average coefficients for four previous studies with SF corn (Table 1). Zinn (1990a) also reported that decreasing flake density of steam-processed corn increased linearly post-ruminal and total tract starch digestibilities. Ruminal digestibilities followed the same pattern, but were not significantly different among flake densities (Table 2).

From infused corn starch into the abomasum of steers fed alfalfa hay, Kreikemeier et al. (1991) and Kreikemeier and Harmon (1995) concluded that there is a limit to the amount of starch digested in the small intestine due to insufficient pancreatic α-amylase and the brush border enzyme α-1,4 glucosidase. These authors reported that 55% and 66% corn starch disappeared within the small intestine when 1440 and 1584 g/d, respectively, of starch was infused into the abomasum. However, in the present study (Tables 7 and 8) and in studies by Kartchner (1972), 84% or more of the 1.1 to 2.9 kg of dietary starch which flowed to the duodenum disappeared within the small intestine. Perhaps starch digestion within the small intestine is lower when starch is infused into the abomasum in contrast to dietary starch flowing into the duodenum. According to Owens et al. (1986), infusion studies may cause changes to the normal digesta flow, which is regulated by the digestive tract;

therefore, the artificial increase of starch flow could affect the normal physiology of digestion. Also, according to Harmon (1992), who concluded that the energy intake is the main factor to increase pancreatic secretion of enzymes, the ME of the alfalfa hay diets, in the infusion trials, may not have been enough to trigger an increment in the pancreatic secretion, including α-amylase. Starch digestibility within the small intestine by steers requires more studies with high-concentrate diets.

Steam-processing of corn and sorghum grain to the same extent (same flake density) results in more uniform starch digestibility at the same sites within the digestive tract. In the present study, steam-processed corn and sorghum grain flaked at the same densities had similar coefficients of starch digestibility, respectively, for the rumen (SF34: 76 vs 77%; SF22: 85 vs 89%), post-rumen (SF34: 21 vs 21%; SF22: 14 vs 10%), small-intestine (SF34: 19 vs 20%; SF22: 14 vs 10%), and total tract (SF34: 97.3 vs 97.7%; SF22: 99.1 vs 99.6%). In the same way, starch digestibilities at different digestive sites reported by Zinn (1991) for steers fed SF corn (300 g/L or SF23 density) or SF sorghum grain (360 g/L or SF28 density) did not differ by grain source, and the digestibility coefficients are similar to those for the present study for steers fed SF22 corn and sorghum grain. These similar starch digestibility values for steers fed

steam-processed corn or sorghum grain at the same flake density appears to be due to the disruption of starch granules, and the gelatinization process which may provide more uniform starch degradation throughout the tract because starch degradation of the grain is approaching complete digestion.

In the present study, the maximum means for corn or sorghum starch flow to the ileum represent less than 5% of the dietary intake and less than 20% of the starch flow to the duodenum (Tables 7 and 8). Corresponding values for SF22 corn or sorghum were less than 1.5 and 9%, respectively. These results are contrary to corn starch infusion studies (Kreikemeier et al., 1991; Kreikemeier and Harmon, 1995), where 42 and 34% of the 1440 and 1584 g/d, respectively, of starch infused in abomasum reaching the large intestine.

Starch digestion in the large intestine, as a percentage of intake, for steers fed corn or sorghum grain was very low (mean = .78% ranging from 1.7 to .3%; Tables 7 and 8) and much lower than average values from previous studies (4.7 to 1%; Table 1). The coefficient of variation for both DR grains exceeds 60%. Several authors (Hibberd et al., 1983; Streeter et al., 1989 and 1990; Zinn, 1990b; Hill et al., 1991) have reported 6 to 8% of the dietary starch was digested in the large intestine. However, results from the present study and data from Kartchner (1972), Lee et al.

(1982), Aguirre et al. (1984), Zinn (1991), and Eck (1991) suggest that starch digestion in the large intestine is quantitatively not important (2% or less of starch intake).

The variation in starch digestion throughout the digestive tract are consistent with the increase in the rate of starch hydrolysis when the flake density decreases. The greatest changes with the steam-flaking process comparing to the dry-rolled grain is in increased starch digestion in the rumen, and ruminal starch digestion consistently increases when flake density decreases.

## IMPLICATIONS

Increasing the degree of grain processing by decreasing the flake density of steam-processed corn or sorghum grain linearly increased the proportion of starch digestion in the rumen and total tract digestion, resulting in less starch digestibility post-ruminally and in the small intestine (as percent of starch flow to duodenum) by beef steers fed high-concentrate diets. Similar responses were found in comparing steam-flaked sorghum to dry-rolled sorghum. This shift to greater ruminal starch fermentation should increase VFA absorption and may partially explain the improved efficiency of gain by feedlot steers fed steam-flaked corn or sorghum grain.

Table 5. Composition of experimental diets trial 1 (% of dry basis)

| Item | Diets[a] | | | |
|---|---|---|---|---|
| | DR | SF-34 | SF-28 | SF-22 |
| Ingredients: | | | | |
| Dry rolled sorghum grain | 76.7 | -- | -- | -- |
| Steam flaked sorghum grain | -- | 76.7 | 76.7 | 76.7 |
| Ground alfalfa hay | 15.0 | 15.0 | 15.0 | 15.0 |
| Sugar cane molasses | 4.0 | 4.0 | 4.0 | 4.0 |
| Cotton seed meal | 2.3 | 2.3 | 2.3 | 2.3 |
| Urea | 0.3 | 0.3 | 0.3 | 0.3 |
| Limestone | 0.9 | 0.9 | 0.9 | 0.9 |
| Salt | 0.5 | 0.5 | 0.5 | 0.5 |
| Vitamin A[b] | + | + | + | + |
| Chromium oxide | 0.3 | 0.3 | 0.3 | 0.3 |
| Nutrient analysis | | | | |
| DM, % | 89.6 | 87.3 | 86.9 | 86.7 |
| Crude protein, % | 12.3 | 13.1 | 12.8 | 12.8 |
| Starch, % | 59.5 | 55.8 | 57.4 | 57.6 |
| ME, Mcal/kg (calculated)[c] | 2.82 | 3.04 | 3.04 | 3.04 |

[a] DR = dry-rolled, SF = steam-flaked; SF34, SF28, SF22 were flaked at densities of 437, 360, and 283 g/L, respectively.

[b] 3,300 UI/kg

[c] Based on ME values for dry-rolled (3.04 Mcal/kg) and steam-flaked (3.33 Mcal/kg) sorghum grain (NRC, 1984).

Table 6. In vitro rate of starch hydrolysis (%) as influenced by processing of corn and sorghum grain[a]

| | Grain process[b] | | | | | Probability[c] | | |
|---|---|---|---|---|---|---|---|---|
| Grain | DR | SF34 | SF28 | SF22 | SEM | C | L | Q |
| Sorghum | 35.3 | 52.4 | 67.5 | 78.6 | 2.67 | .01 | .01 | .49 |
| Corn | | 39.7 | | 69.0 | 3.65 | .01 | | |

[a] Percentage of grain starch degraded to glucose (as a percent of total starch) in 30 min by in vitro incubation with amyloglucosidase (4 samples/treatment)

[b] DR = dry-rolled, SF = steam-flaked; SF34, SF28, SF22 were flaked at densities of 437, 360, and 283 g/L, respectively

[c] C = contrast for sorghum, DR vs (SF34, SF28, and SF22); C = constrast for corn, SF34 vs SF22; L = linear and Q = quadratic effect within SF sorghum treatments

Table 7. Influence of processing sorghum grain on DM and starch digestion at different sites by growig beef steers[a]

| | Diets[b] | | | | | Probability[c] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Daily intake, g/d | | | | | | | | |
| DM | 6,761 | 6,456 | 6,895 | 6,700 | 255 | .78 | .40 | .39 |
| Starch | 4,002 | 3,612 | 3,760 | 3,867 | 164 | .20 | .28 | .96 |
| Flow to duodenum, g/d | | | | | | | | |
| DM[d] | 3,228 | 2,879 | 2,542 | 2,339 | 302 | .06 | .18 | .64 |
| Starch | 1,322 | 864 | 717 | 416 | 149 | .01 | .06 | .64 |
| Flow to ileum, g/d | | | | | | | | |
| Starch | 191 | 108 | 42 | 30 | 21 | .01 | .04 | .35 |
| Fecal excretion, kg/d | | | | | | | | |
| DM | 1,528 | 1,479 | 1,291 | 1,181 | 145 | .23 | .18 | .66 |
| Starch | 145 | 82 | 28 | 17 | 21 | .01 | .03 | .25 |
| DM digestion, % of intake | | | | | | | | |
| Ruminal[d] | 52.0 | 55.8 | 61.8 | 65.3 | 3.7 | .04 | .05 | .64 |
| Total | 77.6 | 77.2 | 80.1 | 82.5 | 1.8 | .28 | .07 | .76 |

Table 7. Influence of processing sorghum grain on DM and starch digestion at different sites by growig beef steers[a] *continued*

| | Diets[b] | | | | | Probability[c] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Starch digestion, % of intake | | | | | | | | |
| Rumen | 66.8 | 76.6 | 81.5 | 89.4 | 3.8 | .01 | .03 | .67 |
| Post-rumen | 29.8 | 21.1 | 17.8 | 10.1 | 3.6 | .01 | .04 | .54 |
| Small intestine | 28.5 | 20.5 | 17.5 | 9.8 | 3.6 | .01 | .04 | .52 |
| Large intestine | 1.24 | .69 | .36 | .34 | .31 | .05 | .17 | .75 |
| Total | 96.5 | 97.7 | 99.3 | 99.6 | .50 | .01 | .03 | .25 |
| Starch digestion, % entering intestine | | | | | | | | |
| Small-intestine | 85.0 | 88.7 | 93.4 | 91.5 | 1.9 | .01 | .38 | .25 |
| Large-intestine | 27.7 | 27.5 | 40.0 | 30.7 | 8.4 | .61 | .91 | .20 |

[a] Means for seven steers per treatment
[b] DR = dry-rolled, SF = steam-flaked; SF34, SF28, SF22 were flaked at densities of 437, 360, and 283 g/L, respectively
[c] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments
[d] Ruminal DM flow to the duodenum and ruminal digestion were corrected for microbial DM flow to the duodenum (Alio, 1997)

Table 8. Influence of processing corn on DM and starch digestion at different sites by growing beef steers[a]

| | Diet[b] | | | |
|---|---|---|---|---|
| Item | SF34 | SF22 | SEM | P value |
| Daily intake, kg/d | | | | |
| DM | 7,984 | 8,255 | 79 | .06 |
| Starch | 4,551 | 4,865 | 28 | .01 |
| Flow to duodenum, g/d | | | | |
| DM[c] | 3,982 | 3,786 | 295 | .64 |
| Starch | 1,108 | 752 | 84 | .03 |
| Flow to ileum, g/d | | | | |
| Starch | 214 | 66 | 42 | .06 |
| Fecal excretion, kg/d | | | | |
| DM | 2,004 | 1,933 | 109 | .64 |
| Starch | 132 | 47 | 29 | .09 |
| DM digestion, % of intake | | | | |
| Ruminal[c] | 50.4 | 54.4 | 3.7 | .45 |
| Total | 75.3 | 76.5 | 1.3 | .48 |
| Starch digestion, % of intake | | | | |
| Rumen | 76.2 | 84.6 | 1.7 | .02 |
| Post-rumen | 21.1 | 14.4 | 1.9 | .06 |
| Small intestine | 19.4 | 14.0 | 1.9 | .09 |
| Large intestine | 1.7 | 0.4 | 0.3 | .09 |
| Total | 97.3 | 99.1 | 0.6 | .09 |
| Starch digestion, % entering intestine | | | | |
| Small-intestine | 84.1 | 91.2 | 3.4 | .19 |
| Large- intestine | 39.6 | 27.9 | 8.0 | .33 |

[a] Means for seven steers on SF34 and six steers on SF22
[b] SF34 and SF22 steam-processed corn flaked at densities of 437 and 283 g/L, respectively
[c] Ruminal DM flow to the duodenum and ruminal digestion were corrected for microbial DM flow to the duodenum (Alio, 1997)

# CHAPTER 4

## NET ABSORPTION AND HEPATIC METABOLISM OF GLUCOSE, L-LACTATE, AND VOLATILE FATTY ACIDS BY STEERS FED DIETS CONTAINING SORGHUM GRAIN PROCESSED AS DRY-ROLLED OR STEAM-FLAKED AT DIFFERENT DENSITIES

## SYNOPSIS

The objective was to determine effects of feeding beef steers dry-rolled (DR) or steam-flaked (SF) sorghum grain with flake densities (FD) of 437, 360, and 283 g/L (SF34, SF28, SF22) on net flux of glucose, L-lactate, VFA, and beta-hydroxybutyrate (BHBA) across portal-drained viscera (PDV), liver, and total splanchnic (SPL; gut + liver) tissues. Eight multicatheterized steers (340 kg) were used in a randomized block design. Steers were fed every 12 h, and six blood samples per day were taken at 2 h intervals for each diet and steer. Intakes of DM (6.9 kg/d) and starch (4.4 kg/d) were similar among diets. Portal blood flow tended to be 11% higher (P = .12) for DR versus SF diets. Hepatic blood flow was similar (978 L/h) between DR versus SF diets. Steers fed SF28 had lower hepatic blood flow than SF34 and SF22 (quadratic effect, P = .03). Feeding Sf compared to DR did not alter net absorption and uptake or release of energy-yielding nutrients across SPL tissues, except net PDV absorption of acetate tended to be greater (P = .13) for steers for DR. As expected, net PDV absorption of

glucose was negative (-.60 mol/d). Incrementally decreasing FD of SF sorghum grain linearly increased net PDV absorption of lactate ($P = .04$), glucose synthesis by the liver ($P = .06$), and SPL output of glucose ($P < .01$) and L-lactate ($P = .03$). Reducing FD also linearly decreased SPL output of BHBA ($P = .06$). Net propionate PDV absorption ($P = .18$), hepatic uptake ($P = .21$), and SPL output tended to increased with lower FD. Increasing degree of grain processing, by incrementally decreasing FD, linearly increased net absorption of glucose precursors (propionate and lactate) resulting in increased hepatic synthesis and greater output of glucose from the gut and liver to the rest of the body for protein and fat accretion.

## INTRODUCTION

From recent reviews (Theurer et al. 1996a, b; Huntington 1997), increasing the proportion of starch digested in the rumen, at expense of the amount of starch digested in the small intestine, results in greater total starch digestion and efficiency of production by beef and dairy cattle. Steam-flaked (SF) compared to dry-rolled (DR) sorghum grain, consistently increases ruminal and total starch digestion in ruminants, as a consequence of the disruption of the protein matrix surrounding the starch

granules in the grain endosperm (Rooney and Plugfelder, 1986). Efficiency of gain by feedlot steers is improved by feeding SF versus DR sorghum grain and by decreasing the density of SF grain (Hale, 1980; Zinn, 1987, 1988, 1990a; Xiong et al. 1991; Swingle et al., 1991). These production response must be due in part to greater absorption and different partitioning of nutrients by gut and liver (splanchnic) tissues.

Net absorption across the portal-drained viscera (PDV) and hepatic metabolism of glucose, L-lactate, and VFA have been reported for beef animals fed high-concentrate diets (Gross et al., 1988; Reynolds and Tyrrell, 1991; Huntington, 1996; Reynolds and Huntington, 1991). Gross et al. (1988) found greater net absorption of propionate by steers fed more ruminally-fermentable (wheat) compared to less fermentable (DR sorghum) high-concentrate diets. However, studies to determine the effect of steam-flaked grain on post-absorptive metabolism of nutrients are limited. Theurer et al. (1990, 1991), comparing DR versus SF sorghum grain, reported more net absorption of acetate, propionate, and L-lactate, but lower absorption of glucose for SF. These authors also reported much greater splanchnic output of acetate to the rest to the body for SF versus DR, but no effect on gluconeogenesis. The objectives for this study are to determine: (1) net absorption, hepatic metabolism, and

splanchnic output by growing steers of major energy-yielding nutrients [glucose, L-lactate, VFA, and ß-hydroxibutyrate (BHBA)] in response to decreasing the flake density of steam-processed sorghum grain from 437 g/L to 360 g/L to 283 g/L (SF34, SF28, and SF22, respectively), and (2) to determine the effect of feeding diets containing SF compared to DR sorghum grain on pot-absorptive metabolism of these same metabolites.

## MATERIAL AND METHODS

### Animals and Diets

This experiment was conducted with the approval and under the supervision of the University of Arizona Care and Use committee. The University of Arizona is accredited by the American Association of Laboratory Animal Care for Farm Animals. Eight crossbred steers, weighing on average 340 kg at the start of the trial, were surgically prepared with chronic indwelling catheters, which were implanted into the mesenteric artery and the portal, hepatic, and two mesenteric veins. Surgery, catheter preparation, and implantation were according to Huntington et al. (1989). Steers were withdrawn from feed 24 h and from water 12 h prior to surgery. The hepatic vein was catheterized using a linear ultrasound scanner equipped with a 5 MHz probe (Aloka-500V Corometrics Medical Systems Inc., CT, USA),

first to locate the vein and then, to confirm the normal placement of the catheter. Before and after surgery, steers were housed in individual pens 2.5 by 5 m. Steers had free access to water and were allowed free movement at all times except during sampling. After surgery, the steers were fed alfalfa hay to stimulate gastric and intestinal motility and function, and then switched progressively to experimental diets.

The experimental diets contained 77% sorghum grain (Table 9), and were formulated to meet crude protein and ME concentration requirements for steers gaining 1.0 kg/d (NRC 1984). The four processing treatments were: DR; and SF at densities of 437, 360, and 283 g/L (or SF34, SF28, and SF22, respectively, relating to pounds/bushel which is the common way of referring to density in feedlot studies). The steers were fed ad libitum and feed was offered twice daily at 0700 and 1900. Diets were iso-nitrogenous and formulated to contain 12 % crude protein (Table 9). All steers were given ad libitum access to feed by 1 wk after surgery. During the experiment, diets were switched over a 5-d period, and steers were maintained on the diet for 7-d prior to blood sampling.

Catheter patency was checked 7 to 10 d post-surgery and at least every 7 d throughout the experiment. Portal and hepatic blood flows were checked 10 to 14 d post-surgery. As

outlined by Huntington et al. (1989), a 10% (wt/vol) p-aminohippuric acid solution (PAH) was infused into the appropriate mesenteric vein catheters. Infusion started with a priming dose, 15 times the normal rate for 2 min, followed by the normal infusion rate of 6000 mg/h for 20 min on each mesenteric vein catheter (proximal, distal, and both). At the end of each sequence, 5 to 10 ml of blood were withdrawn simultaneously from mesenteric artery and portal and hepatic veins. Choice of PAH infusion site was made based on the blood flow check results.

Blood Sampling and Analysis

Blood sampling started 3 wk after surgery, when steers were fully recovered. Six blood samples (for each steer on each sampling day) were drawn simultaneously from the mesenteric artery and portal and hepatic veins. Sampling started at 0700, before morning feeding, and continued every 2 h until 1700. Blood samples of 10 ml were slowly drawn (≈ 2 min) from the vessels into heparinized tubes. A priming dose of PAH (15 times normal rate) was given initially via one of the mesenteric veins for 2 min, followed by continuous infusion of a 10% PAH solution at a rate of 6000 mg/h. The infusion rate was increased to 7200 mg/h as the steers became heavier to maintain adequate blood PAH concentration. Blood samples were collected 40 min after PAH

infusion. The samples were immediately placed on ice until analyses of PAH, glucose, and L-lactate on fresh blood were completed, usually within 2 h after sampling. Aliquots of blood samples were frozen at -80 °C and kept for later use.

Fresh individual blood samples were analyzed for PAH, glucose and L-lactate. The PAH concentrations in fresh whole blood were determined by the method described by Huntington and Reynolds (1986) using automated procedures (Bran + Luebbe Analyzing Techn., Elmford, NY). Concentration of glucose and L-lactate in fresh whole blood were determined by the enzyme sensor technology of Yellow Spring Instrument Inc. (YSI Model 2700, Yellow Spring, Ohio). This technic employs an enzyme- catalyzed reaction to produce hydrogen peroxide, which is oxidized and originates a signal current.

Analyses of acetate, propionate, n-butyrate, iso-butyrate, 2-methyl-butyrate, and BHBA were conducted using composite samples stored frozen, for each steer and each diet. Blood samples were deproteinized and prepared for chromatographic analysis using cation and anion exchange columns according to the procedure described by Reynolds et al. (1986), with the following modifications: the internal standard (ISTD) was added to the supernatant after the deproteinization step; 0.5 ml of 1 M tris buffer was added to the ISTD and supernatant mixture to stabilize pH at 6.7

to 6.9, and 10 ml of 10 mM NaOH in 10% ethanol was used as eluent to improve recovery of ISTD and VFA from the anion exchange column. Determination of individual VFA and BHBA concentrations was by gas-liquid chromatography (VA 3300; Varian Associates INC., Walnut Creek, CA) using a packed glass column (Carbopak B-DA 4% Carbowax, 20 M; Supelco, INC., Bellefonte, PA) with injector, column and detector temperatures set at 200, 175, and 230 °C, respectively. Valerate and 3-methyl-butyrate were not reported. Valerate concentrations was not detected by the gas-liquid chromatograph, and the 3-methyl-butyrate concentration was eluted with lactate.

Samples of feed, collected 4-d before and on sampling day, were composited and analyzed for dry matter (DM), nitrogen (AOAC, 1984), and for starch (Poore et al., 1989). Starch was determined indirectly as glucose following hydrolysis of samples using amyloglucosidase (Diazyme L-200, Miles Inc. Elkart, IN). In vitro rate of starch hydrolysis (30 min) was determined for four samples of DR, SF34, SF28, and SF22 sorghum grain collected throughout the experiment. Details of this analytical procedure have been described by Poore et al. (1991).

Hepatic and portal blood flows were determined by down-stream dilution of PAH as described by Katz and Bergman (1969). Net nutrient fluxes were calculated as the

mathematical product of the venous-arterial concentration differences times blood flow. Negatives values indicate uptake or utilization of the nutrient, and positive values denote net absorption or release of the nutrient. Hepatic extraction ratio for L-lactate, propionate, n-butyrate, and the other VFA with four carbons were determined according to Brockman and Bergman (1975). Maximal contributions of L-lactate, propionate, and amino-acids (α-amino N) to glucose synthesis were calculated assuming a contribution of three carbons per mol of precursor utilized (Reynolds et al. 1994a).

## Statistical Analysis

The experiment was a randomized complete block design with four treatments (DR, SF34, SF28, and SF22), where steer was the block criteria. Means blood flows and nutrient concentrations were determined for each sampling day; thus, each steer on a treatment was the experimental unit. The experimental model was: $Y_{ijk} = \mu + T_i + \beta_j + \epsilon_{ijk}$ ,where $\mu$ = grand mean, $T_i$ = treatment effect, $\beta_j$ = block effect, and $\epsilon_{ijk}$ = experimental error. Data analysis initially included period effect, which was not significant; therefore variance due to period was included in experimental error.

There were missing values because of difficulty in sampling some catheters; therefore, means presented in

tables are least square means. Data were analyzed (GLM, Minitab, 1996) for DR versus SF (means of SF34, SF28, and SF22) treatments. Regression effects (linear and quadratic) were determined within SF treatments. DR and SF22 treatments were also analyzed together with data from steers fed similar diets (Theurer et al., 1990; 1991), as a DR versus SF20 or SF22 comparison. Treatment significance level was set at $P \leq .10$ and tendency for $.11 \leq P \leq .20$.

## RESULTS AND DISCUSSION

### Starch Degradation, Energy Intake and Blood Flow

Nutrient composition of diets was similar across treatments with an average of 64.1% of starch and 2.99 Mcal ME/kg DM. As expected, the percentage of grain starch hydrolyzed in vitro by amyloglucosidase in 30 min was much less (21 vs 67%, $P < .01$) for DR than SF (SF34, SF28, and SF22; Table 10). Rate of in vitro starch hydrolysis of SF grains also linearly increased ($P < .01$) from 54 to 80% as flake density was reduced. These changes in rate of starch hydrolysis are similar to those obtained in the companion digestion trial (Chapter 3). Daily intake of dry matter (6.9 ± .3 kg/d), starch (4.4 ± .2 kg/d), and ME (21.0 ± .8 Mcal/d) were similar among treatments (Table 10).

Despite similar ME intakes, steers fed DR tended to

increase (P = .12) portal blood flow by 11% (879 s 782 L/h) in relation to steers fed SF diets, but portal flow was not altered by flake density (Table 11). Hepatic blood flow (978 L/h) of steers did not differ between DR and SF treatments, but there was a quadratic effect (P = .03) due to flake density; steers fed SF28 had 15% smaller hepatic blood flow than steers fed SF34 and SF22 diets. An explanation for these blood flow differences is not known.

Portal and hepatic blood flows were comparable to those reported by Theurer et al. (1990) for steers with similar DM intakes of DR and SF20 (258 g/L; 20 pounds/bushel) sorghum grain. Means of portal and hepatic blood flows (807 and 978 L/h, respectively) in the present study were greater than other blood flows previously reported (Table 3; Huntington, 1989; Reynolds et al. 1991; Reynolds and Tyrrell, 1991; Huntington et al., 1996; Whitt et al. 1996) with high-concentrated diets primarily due to lower DM intakes.

Glucose and L-lactate

Net glucose absorption across the PDV (-24 mmol/h or -104 g/d) was similar between DR and SF diets, and was not altered by flaking density (Table 12). It was expected that glucose absorption would be greater for DR than SF diets, because there was about .5 kg more starch from DR digested in the small intestine by steers fed the same diets in a

companion study to the present one (Chapter 3). In contrast to the present study, Theurer et al. (1990) reported that net glucose absorption across PDV was less negative for DR than SF20 sorghum grain diets. This latter effect would be expected for SF versus DR, because summaries from recent reviews (Theurer et al., 1996a and 1996b; Huntington, 1997) clearly established that steam-flaking compared to dry-rolling of sorghum grain consistently increases the proportion of starch digested in the rumen and decreases the proportion digested in the small intestine.

Net absorption of glucose across the PDV in most studies is usually negative, reflecting that uptake of arterial glucose by PDV exceeds net absorption of luminal glucose (Huntington and Eisemann, 1988; Huntington, 1990). In 14 previously reported studies (Table 3) steers fed high-concentrate diets, net glucose absorption across the PDV ranged from -64 to 71 mmol/h (-276 to 306 g/d) and average -6 mmol/h (-26 g/d).

The fate of absorbed glucose within the intestinal cells of ruminants is uncertain. Although, the presence of sufficient Na-glucose transporters, SGT1, allows glucose absorption into the enterocytes (Shirazi-Beechey et al., 1991; Bird et al. 1996), the lack of sufficient glucose transporters, GLT2, inside the enterocytes to transport this metabolite to the blood in ruminants (Zhao et al., 1993) may

reduce the amount of glucose released to the mesenteric vein. Reynolds and Huntington (1988a) and Theurer et al. (1990) demonstrated a net release of glucose by the mesenteric-drained viscera (primary intestines) and uptake of glucose by the stomach or rumen tissues.

Okine et al. (1994 and 1995), using layers of intestinal epithelium from dairy cows, demonstrated that glucose is extensively used (~50%) as an energy source by enterocytes. In contrast to simple-stomached animals, the bovine enterocyte produces more ATP from glucose than from glutamine (Okine et al., 1995). Furthermore, Harmon (1986) determined greater glucose metabolism or uptake by isolated rumen epithelial cells when energy intake by steers was increased. High protein turnover in gastrointestinal cells requires extensive oxygen (or energy) use (Reynolds and Maltby, 1994). Because of the extensive use of glucose for energy by enterocytes and high glucose metabolism by ruminal epithelium, net glucose absorption by the PDV apparently is quantitatively not significant in rapidly growing ruminants fed high-concentrate diets.

Hepatic gluconeogenesis (327 mmol/h; 1413 g/d) and splanchnic output (308 mmol/h; 1331 g/d) of glucose to the rest of the body did not differ for steers fed DR compared to SF diets, even though, hepatic-arterial concentration differences were greater for DR. These values were similar

to those of Theurer et al. (1990) with steers fed similar diets, but much higher than other experiments with steer fed lower amount of high-concentrate diets (Huntington, 1989; Reynolds et al. 1991; Reynolds and Tyrrel, 1991; Huntington et al. 1996). However, across SF diets, net glucose synthesis by the liver ($P = .06$) and splanchnic glucose released ($P < .01$) increased linearly by about 50% when flake density of SF diets diminished. These linear effects were largely due to the linear increases ($P < .01$) in hepatic-arterial concentration differences of glucose as flake density decreased (Table 14). Probably, the greater availability of glucose precursors increased liver glucose synthesis. Net PDV absorption of propionate and L-lactate (Table 12), and $\alpha$-amino N (from Alio, 1997; using same steers) showed similar linear responses with decreasing flake density.

Net L-lactate flux across PDV (120 mmol/h), liver (-72 mmol/h), and splanchnic tissues (54 mmol/h) did not differ between DR versus all SF diets (Table 12). However, within the SF diets, net L-lactate released by the PDV ($P = .04$) and splanchnic tissues ($P = .03$) increased linearly as flake density decreased; these L-lactate fluxes also had a quadratic effect for splanchnic release ($P = .06$) and a quadratic tendency for PDV absorption ($P = .12$). The portal-arterial ($P = .03$) and hepatic-arterial ($P < .01$)

concentration differences for L-lactate also increased linearly by 20 and 200%, respectively, with decreasing flake density (Table 14); which largely accounts for the linear response for net fluxes of L-lactate across PDV and splanchnic tissues. The large linear increase in hepatic gluconeogenesis and splanchnic output of glucose to muscle and other peripheral tissues, with increased degree of grain processing (decreased flake density), suggests that optimum feedlot performance should occur with the lowest flake density, which will not substantially decrease DMI of growing-finishing steers.

VFA and ß-hydroxibutyrate (BHBA)

Net acetate absorption across the PDV tended (P = .13) to be 20% smaller (431 vs 547 mmol/h), with no changes in net propionate absorption (351 mmol/h) for steers fed all SF diets compared to DR diet (Table 12). The lower acetate absorption with SF diets is due in part to lower portal blood flow by steers fed SF versus DR. The greater ruminal digestion of starch for SF compared to DR by steers fed the same diets in a companion trial (Chapter 3) to the present study suggests greater, not smaller absorption of acetate and propionate for steers fed SF diets. Net fluxes of acetate and propionate across liver and splanchnic tissues were not altered by DR versus SF treatments.

These data are in contrast with the tendency for more net absorption of acetate and propionate, and greater splanchnic output of acetate, by steers fed similar diets containing SF20 versus DR sorghum grain (Theurer et al., 1991). Gross et al. (1988) also demonstrated greater PDV absorption for propionate, but not acetate, with DR wheat in relation to DR sorghum grain. The PDV fluxes for acetate (415 to 547 mmol/h) were similar to most previous studies conducted with steers fed high-concentrate diets (Table 3); even though, blood acetate concentrations in arterial, portal, and hepatic blood were lower (Table 13) than published values (Reynolds et al. 1994, Gross et al. 1988, and Harmon et al. 1988 and 1989). Thus, portal-arterial concentration differences for acetate must have been similar to the latter studies. Feeding steers SF versus DR sorghum grain did not alter net absorption, liver uptake or splanchnic output of n-butyrate, iso-butyrate, 2-methyl-butyrate or BHBA (Table 12).

Decreasing the flake density of SF sorghum did not alter flux of acetate across PDV, hepatic and splanchnic tissues, but tended to increase net absorption and splanchnic output ($P = .15$) of propionate (Table 12). Reducing flake density tended to linearly increase net absorption across PDV of iso-butyrate ($P = .17$) and linearly decreased 2-methyl-butyrate ($P = .09$). Liver uptake of 2-

methyl-butyrate (P = .19) and BHBA (P = .16) tended to decrease linearly as flake density was lowered, but liver uptake was not altered for N-butyrate or iso-butyrate. Release from splanchnic tissues of BHBA linearly decreased (P = .06) when flake density decreased. Most of these flux changes were reflected in corresponding changes in venous-arterial concentration differences (Table 14).

Using data from the companion digestion trial with the same SF treatments (Chapter 3), amounts of starch digested in the rumen were linearly increased (3.4, 3.6, and 4.0 kg for SF34, SF28, and SF22, respectively) with decreasing flake density. Based on number of carbons, this incremental increase in ruminal starch digestion could explain in part the tendency for the incremental increase in net absorption of propionate. The 434% increase in net amount of propionate taken up by the liver with decreasing flake densities largely responsible for the 48% increase in hepatic glucose synthesis.

## Liver Extraction Ratio and Maximal Nutrient Contribution to Gluconeogenesis

Hepatic extraction ratio of propionate and its maximal contribution (49%) to the amount of glucose synthesized were relatively constant among the treatments (Table 15). The maximal contribution (20%) of α-amino N (from Alio, 1997) to

gluconeogenesis also did not differ among treatments. However, L-lactate tended to decline linearly in the hepatic extraction ratio (P = .18), and its maximal contribution to glucose synthesis also decreased (P = .06) from 20 to 6% with diminishing flake density diminish (Table 15). This linear decline in glucose contribution from L-lactate matched the linear increment on net propionate PDV absorption (Table 12). According to Brockman (1993) greater PDV propionate availability affects the hepatic uptake of other metabolites; principally, it reduces the lactate uptake by the liver. In the present study, the linear increase in the net PDV absorption of L-lactate and propionate matched the linear increase in glucose synthesis by the liver when the flake density decreased.

The maximal percentage of glucose synthesized from propionate by the liver did not change with flake density; however, linear increases in the net amounts of glucose synthesized, due to decreasing flake density, resulted largely from linear increases in net amount of propionate absorbed from PDV.

## Energy Metabolism

The estimated net absorption of energy (Mcal/d; based on heat of combustion) by the PDV and net release of energy from splanchnic to peripheral tissues (Table 16) from the

different metabolites followed the same pattern among the treatments as did the net PDV and SPL fluxes of nutrients. Comparing SF versus DR diets, only the net PDV energy from acetate absorption (P = .13) and the total energy from all metabolites (9.9 vs 11.9 Mcal/d; P = .18) tended to decrease in steers fed SF diets. The total energy released by the SPL was similar between DR and SF diets. The regression effects (linear or quadratic) on the energy metabolism due to decreasing flake density for the steers fed SF diets were similar to the net PDV and SPL fluxes of nutrients (Table 12).

Propionate provided the most net absorption of energy (3.2 Mcal/d or 30% of total), and the VFA provided 60% of the estimated total energy absorbed by these steers. Theurer et al. (1991) reported similar results for steers fed DR and SF20 sorghum grain. Glucose provided almost 50% of the estimated total amount of energy released by the gut and liver (splanchnic tissues) to muscle and other peripheral tissues; acetate release provided about one-half of the energy released from glucose.

## Two Trial Summary

Because of high experimental cost and intensive labor requirement, post-absorptive studies seldom include adequate numbers to measure 10% changes in nutrient uptake or

release. Thus, summarizing repetitive trials can enhance biological interpretations.

From a summary of two trials with growing steers fed the same diets (Theurer et al. 1990 and 1991, and the present study), steam-flaking compared to dry-rolling of sorghum grain tended to decrease (P = .12) net glucose PDV absorption of glucose and tended to increase (P = .12) glucose synthesis by 14% (374 vs 327 mmol/h or 1616 vs 1413 g/d), and numerically increased splanchnic output of glucose by 9% (Table 17). Even though, net PDV absorption propionate was numerically higher by 9% for the steers fed SF versus DR sorghum, the values did not differ significantly. The splanchnic release of propionate was greater for SF (P = .03). Net liver release of acetate tended to be greater (P = .20) and the splanchnic release of acetate was 21% higher (P = .09) for steers fed SF compared to DR diets. The release of L-lactate tended to increase (P = .20) for steers fed the SF diets.

Based on these two trials, the greatest post-absorptive responses to steam-flaking sorghum grain to flake densities of 257 and 283 g/L (SF20 and SF22, respectively) compared to dry-rolling the grain were increases glucose synthesis by the liver and increased splanchnic output of acetate. Estimated splanchnic output of energy for all metabolites was 16% greater for steers fed SF sorghum (data not shown).

Efficiency of N metabolism (reported by Alio, 1997) also was improved by steam-flaking, due to greater net absorption of α-amino N (percent of N intake) and increased urea recycling to the rumen via transfer from blood across the rumen wall.

In conclusion, steers fed in the present study, which were fed SF sorghum grain at densities of 437, 360, and 283 g/L (SF34, SF28, and SF22, respectively) compared to feeding DR grain, did not alter net absorption across the PDV, liver uptake or release, or splanchnic (gut and liver) release of glucose, L-lactate, VFA, or BHBA. However the SF treatments did alter N metabolism by these same steers across these tissues (reported by Alio, 1997) by increasing net absorption of α-amino N across the PDV and by greater transfer of urea N to the gut. The lack of changes in net absorption and splanchnic output of VFA were unexpected, because in a similar study, Theurer et al. (1990, 1991) found substantial increases in net absorption of acetate and propionate, and that 40% more acetate was released by splanchnic tissue of steers fed similar SF versus DR sorghum diets. This lack of response in net VFA absorption in the present study also does not agree with the results of the companion digestibility study (Chapter 3) or summaries from recent reviews: Theurer et al. (1996a and b); Huntington (1977), in which ruminal starch digestion was increased by steers fed these same SF diets compared to the same DR

diets.

Increasing the degree of grain processing, by incrementally decreasing the flake density of SF sorghum grain, alters the partitioning of energy-yielding nutrients by the gut and liver of growing steers. The large linear increases, resulting from decreasing flake density, in hepatic synthesis and splanchnic release of glucose in the present study were due to large linear increases in availability of glucose precursors (net PDV absorption of propionate and L-lactate). In addition, decreasing flake density also increased net absorption of α-amino N and urea recycling to the gut (reported by Alio, 1997). These results are in agreement with those from the companion digestion study (Chapter 3; Alio, 1977), in which decreasing flake density of SF sorghum linearly increased the proportion of starch degraded in the rumen, and increased total digestibility of starch and N by steers fed these same SF diets.

The optimum flake density of SF sorghum grain is 283 g/L (SF22), or lower, based on results from the present study. This density is lower than the optimal flake density of 309 to 360 g/L (SF24 to SF28) for maximal efficiency of gain by feedlot steers (Theurer et al., 1996a). In feedlot trials, steers fed SF22 or SF20 sorghum grain consumed less DM and were no more efficient than steers fed higher flake

densities.

## IMPLICATIONS

Increasing the degree of grain processing by decreasing the flake density of steam-processed sorghum grain altered the partitioning of energy-yielding nutrients by the gut and liver of growing steers fed high-grain diets. Decreasing flake density from 437 to 283 g/L (34 to 22 pounds/bushel) linearly increased availability of glucose precursors (propionate and L-lactate absorption) resulting in linear increases in glucose synthesis by the liver and greater output of glucose from the gut and liver to muscle and other body tissues. These improvements in glucose availability help explain the improved efficiency of gain by feedlot steers fed moderately steam-flaked sorghum grain (309 to 360 g/L or 24 to 28 pounds/bushel).

Table 9. Composition and nutrient analyses of the experimental diets (% dry basis)

| Item | Diets[a] | | | |
|---|---|---|---|---|
| | DR | SF34 | SF28 | SF22 |
| Ingredients: | | | | |
| Dry-rolled sorghum grain | 77.0 | -- | -- | -- |
| Steam-flaked sorghum grain | -- | 77.0 | 77.0 | 77.0 |
| Ground alfalfa hay | 15.0 | 15.0 | 15.0 | 15.0 |
| Sugar cane molasses | 4.0 | 4.0 | 4.0 | 4.0 |
| Cotton seed meal | 2.3 | 2.3 | 2.3 | 2.3 |
| Urea | 0.3 | 0.3 | 0.3 | 0.3 |
| Limestone | 0.9 | 0.9 | 0.9 | 0.9 |
| Salt | 0.5 | 0.5 | 0.5 | 0.5 |
| Vitamin A[b] | + | + | + | + |
| Nutrient analysis | | | | |
| DM, % | 88.9 | 85.7 | 85.3 | 85.2 |
| Crude protein, % | 12.8 | 12.8 | 12.9 | 12.8 |
| Starch, % | 63.1 | 65.1 | 64.3 | 63.4 |
| ME, Mcal/kg (calculated)[c] | 2.82 | 3.04 | 3.04 | 3.04 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, and 283 g/L, respectively.

[b] 3,300 UI/kg

[c] based on ME values for dry-rolled (3.04 Mcal/kg) and steam-flaked (3.33 Mcal/kg) sorghum grain (NRC 1984)

Table 10. Means of stach hydrolysis rate and daily intakes by steers of DM, starch, and ME

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Starch degradation in vitro, %[c] | 20.7 | 54.4 | 67.0 | 79.8 | 3.8 | .01 | .01 | .76 |
| DMI, kg/d[d] | 7.12 | 6.72 | 6.92 | 6.97 | .28 | .44 | .54 | .82 |
| Starch, kg/d[d] | 4.50 | 4.37 | 4.45 | 4.46 | .18 | .74 | .76 | .87 |
| ME, Mcal/d[de] | 21.1 | 20.5 | 21.1 | 21.2 | .84 | .41 | .53 | .82 |

[a] DR = dry-rolled; SF = steam-flaked sorghum grain; SF34, SF28, and SF22 were flaked at densities of 437, 360, and 283 g/L, respectively

[b] DRvsSF = contrast DR versus (SF34, SF28, and SF22); L = linear and Q = quadratic effects within SF treatments

[c] Percentage of grain starch degraded to glucose (as a percent of total starch) by 30 min in vitro incubation with amyloglucosidase (4 samples per treatment)

[d] Means based on eight steers/treatment

[e] Based on ME Mcal/kg values for dry-rolled (3.04) and steam-flaked (3.33) sorghum grain and other ingredients (NRC 1984)

Table 11. Means of portal and hepatic blood flow in steers fed dry-rolled or steam-flaked sorghum grain flaked at different densities

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Site | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Blood flow, L/h | | | | | | | | |
| Portal[c] | 879 | 800 | 769 | 778 | 53.2 | .12 | .86 | .80 |
| Hepatic[d] | 962 | 1050 | 886 | 1015 | 45.2 | .63 | .39 | .03 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively.

[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments.

[c] Number of steers; 6, 7, 7, and 6 for DR, SF34, SF 28, and SF22, respectively

[d] Number of steers; 7, 5, 6, and 6 for DR, SF34, SF 28, and SF22, respectively

Table 12. Means of net portal-drained viscera absorption, liver uptake or release, and splanchnic output of energy-yielding nutrients by steers fed 77% sorghum grain with different processing (mmol/h)

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item[c] | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Glucose | | | | | | | | |
| PDV[d] | -24 | -35 | -11 | -28 | 19.4 | .99 | .79 | .51 |
| Liver[e] | 348 | 259 | 315 | 387 | 33.6 | .46 | .06 | .83 |
| SPL[f] | 329 | 239 | 294 | 372 | 20.0 | .21 | .01 | .46 |
| L-lactate | | | | | | | | |
| PDV[g] | 135 | 111 | 98 | 137 | 15.5 | .23 | .04 | .12 |
| Liver[h] | -79 | -96 | -52 | -61 | 24.6 | .67 | .36 | .61 |
| SPL[i] | 59 | 36 | 35 | 86 | 14.5 | .60 | .03 | .06 |
| Acetate | | | | | | | | |
| PDV[d] | 547 | 415 | 450 | 428 | 64.9 | .13 | .78 | .61 |
| Liver[j] | -33 | 2.7 | -14 | 14 | 51.7 | .54 | .99 | .85 |
| SPL[i] | 521 | 494 | 417 | 487 | 66.9 | .42 | .61 | .31 |
| Propionate | | | | | | | | |
| PDV[d] | 403 | 275 | 371 | 408 | 66.5 | .50 | .18 | .68 |
| Liver[k] | -374 | -251 | -333 | -359 | 68.7 | .43 | .21 | .67 |
| SPL[i] | 33 | 37 | 39 | 58 | 10.5 | .31 | .15 | .44 |
| n-Butyrate | | | | | | | | |
| PDV[d] | 42 | 37 | 37 | 26 | 6.37 | .21 | .30 | .59 |
| Liver[j] | -35 | -32 | -28 | -20 | 6.13 | .21 | .33 | .72 |
| SPL[i] | 8.6 | 11.2 | 7.9 | 6.3 | 3.21 | .98 | .22 | .91 |
| iso-Butyrate | | | | | | | | |
| PDV[d] | 5.6 | 4.7 | 5.2 | 5.8 | 0.86 | .69 | .17 | .91 |
| Liver[j] | -5.8 | -5.9 | -5.2 | -6.7 | 1.32 | .93 | .60 | .93 |
| SPL[i] | -.50 | -.42 | -.26 | -.38 | 1.38 | .92 | .81 | .84 |

Table 12. Means of net portal-drained viscera absorption, liver uptake or release, and splanchnic output of energy-yielding nutrients by steers fed 77% sorghum grain with different processing (mmol/h) *continued*

| | Dietsa | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item[c] | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| 2-methyl-Butyrate | | | | | | | | |
| PDV[d] | 11.3 | 10.3 | 8.6 | 5.2 | 2.47 | .26 | .09 | .64 |
| Liver[j] | -8.3 | -9.3 | -8.8 | -2.9 | 3.11 | .68 | .19 | .29 |
| SPL[i] | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| ß-hidroxybutyric acid | | | | | | | | |
| PDV[d] | 100 | 69 | 96 | 54 | 21.0 | .27 | .65 | .18 |
| Liver[j] | 47 | 101 | 9 | 40 | 22.9 | .92 | .16 | .12 |
| SPL[i] | 153 | 164 | 92 | 91 | 29.0 | .22 | .06 | .27 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively.
[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments.
[c] PDV = portal-drained viseras; SPL = total splanchnic tissues
[d] Number of steers; 6, 7, 7, and 6 for DR, SF34, SF 28, and SF22, respectively
[e] Number of steers; 4, 4, 5, and 4 for DR, SF34, SF 28, and SF22, respectively
[f] Number of steers; 6, 5, 6, and 6 for DR, SF34, SF 28, and SF22, respectively
[g] Number of steers; 6, 6, 7, and 5 for DR, SF34, SF 28, and SF22, respectively
[h] Number of steers; 5, 3, 5, and 3 for DR, SF34, SF 28, and SF22, respectively
[i] Number of steers; 7, 4, 6, and 6 for DR, SF34, SF 28, and SF22,respectively
[j] Number of steers; 5, 4, 5, and 4 for DR, SF34, SF 28, and SF22, respectively
[k] Number of steers; 5, 5, 5, and 5 for DR, SF34, SF 28, and SF22, respectively

Table 13. Means blood concentrations (mmol/L) in mesenteric artery and portal and hepatic veins of energy-yielding nutrients by steers fed 77% sorghum grain with different processing

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Glucose | | | | | | | | |
| Artery[c] | 3.76 | 3.70 | 3.79 | 3.77 | .092 | .94 | .63 | .63 |
| Portal[d] | 3.82 | 3.66 | 3.80 | 3.78 | .121 | .61 | .57 | .75 |
| Hepatic[e] | 4.13 | 3.92 | 4.04 | 4.12 | .132 | .42 | .36 | .96 |
| L-lactate | | | | | | | | |
| Artery[f] | .382 | .406 | .492 | .403 | .034 | .18 | .59 | .02 |
| Portal[g] | .599 | .560 | .638 | .590 | .042 | .95 | .76 | .36 |
| Hepatic[h] | .440 | .428 | .532 | .507 | .064 | .39 | .66 | .42 |
| Acetate | | | | | | | | |
| Artery[c] | .599 | .485 | .631 | .522 | .045 | .28 | .52 | .05 |
| Portal[d] | 1.25 | 0.97 | 1.25 | 1.06 | .098 | .17 | .47 | .05 |
| Hepatic[e] | 1.12 | 0.97 | 1.09 | 1.06 | .093 | .41 | .65 | .51 |
| Propionate | | | | | | | | |
| Artery[c] | .050 | .035 | .058 | .055 | .008 | .98 | .17 | .28 |
| Portal[d] | .500 | .345 | .517 | .557 | .065 | .71 | .12 | .56 |
| Hepatic[e] | .080 | .070 | .089 | .123 | .020 | .52 | .07 | .68 |
| n-butyrate | | | | | | | | |
| Artery[c] | .009 | .013 | .011 | .010 | .002 | .36 | .42 | .81 |
| Portal[d] | .059 | .060 | .061 | .041 | .011 | .70 | .31 | .53 |
| Hepatic[e] | .018 | .025 | .020 | .017 | .006 | .68 | .33 | .95 |
| Iso-Butyrate | | | | | | | | |
| Artery[c] | .003 | .002 | .002 | .003 | .000 | .71 | .47 | .83 |
| Portal[d] | .010 | .008 | .009 | .010 | .001 | .32 | .07 | .63 |
| Hepatic[e] | .002 | .002 | .002 | .002 | .001 | .92 | .14 | .65 |

Table 13. Means blood concentrations (mmol/L) in mesenteric artery and portal and hepatic veins of energy-yielding nutrients by steers fed 77% sorghum grain with different processing *continued*

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| 2-methyl-Butyrate | | | | | | | | |
| Artery[c] | 0 | 0 | 0 | 0 | 0 | | | |
| Portal[d] | .014 | .014 | .012 | .008 | .003 | .54 | .20 | .70 |
| Hepatic[e] | 0 | 0 | 0 | 0 | 0 | | | |
| ß-Hydroxibutyrate | | | | | | | | |
| Artery[c] | .342 | .395 | .352 | .329 | .032 | .65 | .20 | .76 |
| Portal[d] | .502 | .489 | .499 | .411 | .044 | .47 | .29 | .43 |
| Hepatic[e] | .482 | .541 | .448 | .404 | .066 | .79 | .15 | .75 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively.

[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments.

[c] Number of steers; 8, 8, 8, and 8 for DR, SF34, SF 28, and SF22, respectively

[d] Number of steers; 6, 7, 7, and 6 for DR, SF34, SF 28, and SF22, respectively

[e] Number of steers; 7, 5, 6, and 6 for DR, SF34, SF 28, and SF22, respectively

[f] Number of steers; 8, 7, 7, and 8 for DR, SF34, SF 28, and SF22, respectively

[g] Number of steers; 6, 6, 7, and 5 for DR, SF34, SF 28, and SF22, respectively

[h] Number of steers; 7, 4, 6, and 5 for DR, SF34, SF 28, and SF22, respectively

Table 14. Means of portal- and hepatic-arterial concentration differences (mmol/L) of energy-yielding nutrients by steers fed 77% sorghum grain with different processing

| | Diets [a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Glucose[c] | | | | | | | | |
| P-A[d] | -.037 | -.044 | -.012 | -.045 | .023 | .91 | .98 | .33 |
| H-A[e] | .353 | .208 | .325 | .375 | .018 | .02 | .01 | .15 |
| L-lactate | | | | | | | | |
| P-A[f] | .158 | .141 | .129 | .170 | .013 | .37 | .03 | .01 |
| H-A[g] | .063 | .028 | .038 | .084 | .016 | .36 | .01 | .14 |
| Acetate | | | | | | | | |
| P-A[d] | .639 | .513 | .607 | .560 | .067 | .31 | .52 | .28 |
| H-A[h] | .548 | .461 | .485 | .485 | .059 | .24 | .96 | .87 |
| Propionate | | | | | | | | |
| P-A[d] | .444 | .314 | .463 | .504 | .057 | .79 | .11 | .59 |
| H-A[e] | .057 | .031 | .041 | .057 | .010 | .46 | .07 | .69 |
| n-Butyrate | | | | | | | | |
| P-A[d] | .049 | .047 | .050 | .033 | .009 | .60 | .37 | .45 |
| H-A[h] | .009 | .010 | .009 | .006 | .003 | .94 | .31 | .74 |
| iso-Butyrate | | | | | | | | |
| P-A[d] | .007 | .006 | .007 | .008 | .001 | .86 | .09 | .83 |
| H-A[h] | -.001 | -.001 | -.001 | -.001 | .001 | .81 | .76 | .87 |
| 2-methyl-Butyrate | | | | | | | | |
| P-A[d] | .014 | .014 | .012 | .008 | .003 | .54 | .20 | .70 |
| H-A[h] | 0 | 0 | 0 | 0 | 0 | | | |

Table 14. Means of portal- and hepatic-arterial concentration differences (mmol/L) of energy-yielding nutrients by steers fed 77% sorghum grain with different processing *continued*

| | Diets[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| ß-hydroxibutyrate | | | | | | | | |
| P-A[d] | .121 | .090 | .137 | .078 | .028 | .54 | .80 | .15 |
| H-A[h] | .159 | .162 | .111 | .097 | .027 | .20 | .08 | .55 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively.

[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments.

[c] P-A = portal-arterial concentration differences; H-A = hepatic-arterial concentration differences

[d] Number of steers; 6, 7, 7, and 6 for DR, SF34, SF 28, and SF22, respectively

[e] Number of steers; 6, 5, 6, and 6 for DR, SF34, SF 28, and SF22, respectively

[f] Number of steers; 6, 6, 7, and 5 for DR, SF34, SF 28, and SF22, respectively

[g] Number of steers; 7, 4, 6, and 5 for DR, SF34, SF 28, and SF22, respectively

[h] Number of steers; 7, 5, 6, and 5 for DR, SF34, SF 28, and SF22, respectively

Table 15. Means of hepatic extraction ratios for L-lactate and VFA, and maximal gluconeogenesis contribution from propionate, L-lactate, and α-amino N by steers fed 77% sorghum grain with different processing

| | Diet[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Hepatic extraction ratio, %[c] | | | | | | | | |
| L-lactate | 13.2 | 19.0 | 9.1 | 8.2 | 4.8 | .81 | .18 | .60 |
| Propionate | 82.3 | 77.7 | 79.3 | 79.5 | 2.7 | .29 | .61 | .48 |
| n-Butyrate | 64.1 | 62.0 | 64.4 | 68.1 | 4.9 | .89 | .19 | .38 |
| iso-Butyrate | 70.1 | 73.1 | 73.6 | 86.0 | 11.7 | .55 | .33 | .83 |
| 2-methyl-Butyrate | 100 | 100 | 100 | 100 | | | | |
| Maximal gluconeogenesis contribution, %[d] | | | | | | | | |
| Propionate | 45.2 | 53.7 | 43.0 | 53.5 | 10.3 | .67 | .99 | .42 |
| L-lactate | 9.1 | 19.5 | 9.9 | 6.1 | 3.9 | .46 | .06 | .44 |
| α-amino N | 17.0 | 21.5 | 21.2 | 19.2 | 4.2 | .44 | .73 | .87 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively.

[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments.

[c] Determined according to Brockman and Bergman (1975).

[d] Calculated assuming a contribution of three carbons per mol of precursor removed (Reynolds et al., 1994a)

Table 16. Means of estimated net portal-drained viscera absorption and splanchnic release of energy from energy-yielding nutrients by steers fed 77% sorghum grain with different processing

| | Diet[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Estimated net PDV absorption of energy, Mcal/d[c] | | | | | | | | |
| Glucose | -.39 | -.56 | -.18 | -.45 | .31 | .99 | .79 | .51 |
| L-lactate | 1.06 | .87 | .77 | 1.07 | .12 | .23 | .04 | .12 |
| α-amino N[d] | 2.50 | 1.74 | 2.50 | 2.66 | .27 | .52 | .05 | .34 |
| Acetate | 2.75 | 2.09 | 2.26 | 2.15 | .33 | .13 | .78 | .61 |
| Propionate | 3.53 | 2.41 | 3.24 | 3.58 | .58 | .50 | .18 | .68 |
| n-Butyrate | .56 | .49 | .48 | .34 | .08 | .21 | .30 | .59 |
| BHBA | 1.32 | .91 | 1.28 | .72 | .28 | .27 | .85 | .17 |
| 4-carbon VFA | .22 | .20 | .18 | .15 | .04 | .27 | .23 | .70 |
| Total | 11.9 | 8.5 | 10.7 | 10.4 | 1.3 | .18 | .30 | .41 |

Table 16. Means of estimated net portal-drained viscera absorption and splanchnic release of energy from energy-yielding nutrients by steers fed 77% sorghum grain with different processing *continued*

| | Diet[a] | | | | | Probability[b] | | |
|---|---|---|---|---|---|---|---|---|
| Item | DR | SF34 | SF28 | SF22 | SEM | DRvsSF | L | Q |
| Estimate splanchnic output of energy, Mcal/d[c] | | | | | | | | |
| Glucose | 5.29 | 3.84 | 4.72 | 5.99 | .32 | .21 | .01 | .46 |
| L-lactate | .46 | .29 | .27 | .68 | .11 | .59 | .03 | .06 |
| α-Amino N[d] | .80 | .96 | .79 | 1.09 | .20 | .46 | .44 | .16 |
| Acetate | 2.62 | 2.48 | 2.10 | 2.45 | .34 | .42 | .63 | .30 |
| Propionate | .29 | .32 | .34 | .51 | .09 | .31 | .15 | .44 |
| n-Butyrate | .11 | .15 | .11 | .08 | .04 | .98 | .22 | .91 |
| BHBA | 2.03 | 2.18 | 1.21 | 1.20 | .38 | .22 | .06 | .27 |
| 4-carbon VFA | -.01 | -.01 | -.00 | -.01 | .01 | .91 | .81 | .84 |
| Total | 11.5 | 10.3 | 9.6 | 11.9 | 1.0 | .45 | .37 | .16 |

[a] DR = dry-rolled; SF = steam-flaked; SF34, SF28, and SF22 were flaked at densities of 437, 360, or 283 g/L, respectively

[b] DRvsSF = contrast DR vs (SF34, SF28, and SF22); L = linear and Q = quadratic effect within SF treatments

[c] Calculated from heats of combustion (Gross et al. 1988), BHBA assumed equal to 4-carbon VFA

[d] Net flux from Alio (1997)

Table 17. Means of net portal-drained viscera (PDV) absorption, liver uptake or release, and splanchnic output of glucose, L-lactate, and VFA in steers fed steam-flaked or dry-rolled sorghum grain from two different trials[a]

| | Diet[b] | | | |
|---|---|---|---|---|
| Item[c] | DR | SF22 or SF20 | SEM | P Value |
| Glucose | | | | |
| PDV | -15 | -41 | 10.7 | .12 |
| Liver | 327 | 374 | 19.1 | .12 |
| Splanchnic | 300 | 327 | 19.7 | .33 |
| L-lactate | | | | |
| PDV | 116 | 124 | 9.1 | .51 |
| Liver | -52 | -53 | 8.9 | .94 |
| Splanchnic | 58 | 75 | 8.6 | .20 |
| Acetate | | | | |
| PDV | 597 | 607 | 50.1 | .88 |
| Liver | -31 | 56 | 42.5 | .20 |
| Splanchnic | 573 | 696 | 44.8 | .09 |
| Propionate | | | | |
| PDV | 425 | 464 | 37.1 | .48 |
| Liver | -368 | -411 | 43.0 | .48 |
| Splanchnic | 36 | 55 | 5.4 | .03 |
| n-Butyrate | | | | |
| PDV | 58 | 52 | 5.1 | .40 |
| Liver | -48 | -42 | 5.6 | .49 |
| Splanchnic | 11 | 11 | 2.2 | .99 |

[a] Data from Theurer et al. (1990 and 1991), personal communication of individual steer values; and data from the present study

[b] DR = dry-rolled sorghum grain; SF22 or SF20 = steam-flaked sorghum grain at densities of 283 or 257 g/L (20 or 22 pounds/bushel)

[c] Number of steers were 12 in PDV and splanchnic and 10 in liver in all the metabolites

# CHAPTER 5

## SUMMARY AND CONCLUSIONS

Even though steam-flaking of grain is widely used currently in the feedlot industry, because of the consistent improvement in feed efficiency comparing to dry-rolling of grain in growing steers, there is limited published data on the effects of steam-flaking on ruminal, small intestinal, and large intestinal starch digestion, and, on post-absorptive nutrient metabolism. The present digestion and splanchnic metabolism studies address the reasons for improved performance by growing-finishing steers fed steam-processed grains flaked at various densities. The conclusions of the present study are:

1. Steam-flaking comparing to dry-rolling of sorghum grain alters starch digestibility throughout the segments of the digestive tract. Ruminal starch digestion by steers fed SF sorghum grain is much greater than for steers fed DR sorghum. The SF sorghum grain treatments also increases the starch digestibility in the small intestine, as a percentage of the starch flow to the duodenum, and in the total tract.

2. Decreasing flake density of the SF sorghum grain increases linearly starch digestibility throughout the digestive tract. Rumina and total starch digestion increases

linearly when flake density decreases from 437 to 360 to 283 g/L (SF34 to SF28 to SF22). Within the small intestine, starch digestibility, as a percentage of the starch flow to duodenum, also increases as flake density is reduced. Similar responses in starch digestibility occur when flake density of SF corn decreases from 437 to 283 g/L (SF34 to SF22).

3. When both SF corn and SF sorghum grain are flaked to the same densities, rumina, intestinal, and total starch digestibility are similar for both grains.

4. Splanchnic (gut and liver) output of glucose, L-lactate, VFA, or BHBA to the rest of the body by steers fed SF sorghum grain is not different from that of steers fed DR sorghum grain. Within SF sorghum diets, glucose synthesis by the liver and splanchnic release of glucose increases linearly when the flake density decreases. The net absorption of L-lactate and propionate increases linearly as flake density of SF sorghum grain decreases. The increased absorption of these two glucose precursors probably causes the greater glucose synthesis by the liver.

5. In contrast to a previous report (Theurer et al. 1991), net PDV absorption of acetate across the PDV tends to decrease in steers fed SF diets versus DR sorghum diets. However, using data summarized from two similar trials (Theurer et al. 1991 and the present study) net acetate

output from splanchnic tissues increases in steers fed SF versus DR diets.

6. The SF sorghum grain consistently increases the rumina starch digestion where the VFA are the principal end products; however, net absorption of these VFA does not correspond with the amount of digested starch in DR and SF diets. Therefore, it is necessary to conduct studies to analyze changes in the daily rumina production of VFA by steers fed SF in comparison with DR sorghum grain. In addition, investigations to determine the extent of VFA metabolism inside the rumen epithelial cells by steers fed high-concentrate diets are indispensable for improving understanding the of fate of these VFA after luminal absorption. Most published studies are with sheep fed forage diets (Bergman 1990) or receiving complete intra-ruminal VFA infusions (Gross et al. 1990a and 1990b).

7. In summary, increasing the degree of sorghum grain processing, by decreasing flake density of the steam-flaked grain has a positive effect in growing steers because of the tendency for increased net splanchnic output of acetate (21%, P = .09), glucose (9%, P = .33), and L-lactate (29%, P = .20). These nutrients have an important impact in muscle and lipid accretion.

# APPENDIX A. INDIVIDUAL STEER DATA

## DIGESTION TRIAL

Appendix A. Table 1. Individual data of DM and starch digestion at different sites by steers fed 77% sorghum grain on different process

| | Steer number | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 420 | 427 |
| Diet, DRY-ROLLED | | | | | | | |
| Period | 4 | 2 | 2 | 3 | 4 | 1 | 3 |
| Daily intake, g | | | | | | | |
| DM | 7614 | 6087 | 5894 | 6468 | 7587 | 6246 | 7616 |
| Starch | 4354 | 3609 | 3526 | 3831 | 4387 | 4007 | 4537 |
| Ruminal digestion, % | | | | | | | |
| DM corrected | 49.1 | 32.6 | 61.0 | 48.4 | 58.1 | 57.6 | 54.1 |
| Starch | 62.0 | 44.5 | 68.4 | 65.8 | 79.6 | 78.1 | 69.6 |
| Small intestine, % | | | | | | | |
| Starch, % intake | 28.8 | 52.2 | 25.6 | 30.4 | 17.3 | 18.1 | 26.8 |
| Starch, % entry | 75.7 | 93.9 | 81.0 | 89.0 | 84.9 | 82.6 | 88.2 |
| Large intestine, % | | | | | | | |
| Starch, % intake | 0.08 | 2.30 | 4.29 | 0.24 | 0.55 | 1.14 | 0.02 |
| Starch, % entry | 0.9 | 68.3 | 71.5 | 6.4 | 17.7 | 29.9 | 0.6 |
| Total tract digestion, % | | | | | | | |
| DM apparent | 71.1 | 81.9 | 84.9 | 73.8 | 79.6 | 79.6 | 75.1 |
| Starch | 90.9 | 98.9 | 98.3 | 96.5 | 97.5 | 97.3 | 96.4 |

Appendix A. Table 1. Individual data of DM and starch digestion at different sites by steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 420 | 427 |
| Diet, STEAM-FLAKED | 34 | | | | | | |
| Period | 1 | 3 | 3 | 2 | 1 | 4 | 2 |
| Daily intake, g | | | | | | | |
| DM | 6407 | 5873 | 6415 | 5510 | 6467 | 6788 | 7509 |
| Starch | 3482 | 3267 | 3618 | 3180 | 3833 | 3572 | 4382 |
| Ruminal digestion, % | | | | | | | |
| DM corrected | 45.5 | 67.6 | 46.4 | 61.7 | 59.8 | 57.8 | 51.8 |
| Starch | 70.7 | 84.1 | 60.7 | 85.3 | 85.7 | 78.9 | 69.6 |
| Small intestine, % | | | | | | | |
| Starch, % intake | 20.9 | 15.3 | 35.1 | 13.5 | 13.4 | 19.0 | 27.7 |
| Starch, % entry | 71.2 | 96.3 | 89.2 | 91.7 | 94.0 | 90.0 | 91.2 |
| Large intestine, % | | | | | | | |
| Starch, % intake | 1.94 | 0.18 | 0.63 | 0.53 | 0.29 | -.01 | 1.55 |
| Starch, % entry | 23.0 | 30.7 | 14.8 | 43.5 | 33.9 | -0.5 | 58.2 |
| Total tract digestion, % | | | | | | | |
| DM apparent | 59.1 | 86.3 | 75.9 | 80.7 | 80.9 | 74.4 | 83.9 |
| Starch | 93.5 | 99.6 | 96.4 | 99.3 | 99.4 | 97.9 | 98.9 |

Appendix A. Table 1. Individual data of DM and starch digestion at different sites by steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 420 | 427 |
| Diet, STEAM-FLAKED | 28 | | | | | | |
| Period | 2 | 4 | 4 | 1 | 2 | 3 | 1 |
| Daily intake, g | | | | | | | |
| DM | 6972 | 6679 | 7326 | 3860 | 6970 | 6975 | 6901 |
| Starch | 3916 | 3833 | 4093 | 2639 | 3994 | 4055 | 4063 |
| Ruminal digestion, % | | | | | | | |
| DM corrected | 54.6 | 55.8 | 62.7 | 74.7 | 57.3 | 56.9 | - |
| Starch | 83.8 | 77.8 | 84.0 | 87.1 | 89.3 | 87.0 | 60.4 |
| Small intestine, % | | | | | | | |
| Starch, % intake | 14.8 | 20.5 | 13.9 | 12.5 | 9.8 | 12.3 | 38.7 |
| Starch, % entry | 91.1 | 92.5 | 87.1 | 97.0 | 92.0 | 94.4 | 97.9 |
| Large intestine, % | | | | | | | |
| Starch, % intake | 0.14 | 0.91 | 0.59 | 0.21 | 0.37 | 0.41 | 0.30 |
| Starch, % entry | 9.9 | 55.0 | 28.9 | 54.0 | 43.2 | 56.2 | 36.0 |
| Total tract digestion, % | | | | | | | |
| DM apparent | 77.8 | 78.5 | 82.7 | 78.0 | 83.7 | 80.9 | 78.5 |
| Starch | 98.7 | 99.3 | 98.5 | 99.8 | 99.5 | 99.7 | 99.5 |

Appendix A. Table 1. Individual data of DM and starch digestion at different sites by steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 420 | 427 |
| Diet, STEAM-FLAKED | 22 | | | | | | |
| Period | 3 | 1 | 1 | 4 | 3 | 2 | 4 |
| Daily intake, g | | | | | | | |
| DM | 6741 | 6361 | 6864 | 6977 | 7422 | 6929 | 5758 |
| Starch | 4090 | 3789 | 4177 | 3885 | 4179 | 3934 | 3372 |
| Ruminal digestion, % | | | | | | | |
| DM corrected | 71.1 | 68.3 | 64.1 | 62.6 | 66.6 | 57.9 | 70.1 |
| Starch | 91.6 | 93.0 | 82.2 | 82.2 | 94.1 | 88.7 | 95.6 |
| Small intestine, % | | | | | | | |
| Starch, % intake | 7.8 | 6.8 | 15.9 | 16.9 | 5.1 | 10.8 | 3.7 |
| Starch, % entry | 92.6 | 96.8 | 89.7 | 94.8 | 86.2 | 94.9 | 84.0 |
| Large intestine, % | | | | | | | |
| Starch, % intake | 0.07 | 0.01 | 0.54 | 0.06 | 0.54 | 0.23 | 0.27 |
| Starch, % entry | 11.3 | 6.5 | 29.3 | 6.8 | 66.5 | 40.2 | 38.2 |
| Total tract digestion, % | | | | | | | |
| DM apparent | 83.6 | 83.3 | 77.3 | 80.1 | 84.2 | 80.7 | 85.1 |
| Starch | 99.5 | 99.8 | 98.7 | 99.1 | 99.7 | 99.7 | 99.6 |

Appendix A. Table 2. Individual data of DM and starch digestion at different sites by steers fed 77% corn on different process

| | Steer number | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 420 | 427 |
| Diet, STEAM-FLAKED | 34 | | | | | | |
| Period | 1 | 1 | 2 | 2 | 1 | 1 | 2 |
| Daily intake, g | | | | | | | |
| DM | 7042 | 6926 | 8587 | 8798 | 8035 | 7655 | 8784 |
| Starch | 4219 | 3903 | 7936 | 4895 | 4343 | 4454 | 5031 |
| Ruminal digestion, % | | | | | | | |
| DM corrected | 62.3 | 44.7 | 38.3 | 51.0 | 54.9 | 49.1 | 51.8 |
| Starch | 82.0 | 80.5 | 63.4 | 70.9 | 88.8 | 77.2 | 72.3 |
| Small intestine, % | | | | | | | |
| Starch, % intake | 16.4 | 18.3 | 27.9 | 17.7 | 10.7 | 20.1 | 24.0 |
| Starch, % entry | 91.2 | 94.1 | 76.3 | 60.9 | 95.4 | 88.0 | 86.6 |
| Large intestine, % | | | | | | | |
| Starch, % intake | 0.3 | 0.7 | 3.8 | 3.6 | 0.1 | 1.4 | 1.3 |
| Starch, % entry | 20.4 | 67.9 | 43.8 | 31.8 | 27.8 | 51.3 | 33.7 |
| Total tract digestion, % | | | | | | | |
| DM apparent | 81.5 | 78.5 | 68.0 | 68.9 | 77.7 | 78.4 | 76.2 |
| Starch | 98.7 | 99.6 | 95.1 | 92.2 | 99.6 | 98.7 | 97.5 |

Appendix A. Table 2. Individual data of DM and starch digestion at different sites by steers fed 77% corn on different process *Continued*

| | Steer number | | | | | |
|---|---|---|---|---|---|---|
| Item | 410 | 411 | 412 | 418 | 419 | 427 |
| Diet, STEAM-FLAKED 22 | | | | | | |
| Period | 2 | 2 | 1 | 1 | 2 | 1 |
| Daily intake, g | | | | | | |
| DM | 7661 | 6943 | 8889 | 8822 | 8586 | 8895 |
| Starch | 4734 | 4233 | 5056 | 5134 | 4880 | 5179 |
| Ruminal digestion, % | | | | | | |
| DM corrected | 54.3 | 61.2 | 54.6 | 54.1 | 56.8 | 46.3 |
| Starch | 89.2 | 87.5 | 83.5 | 79.4 | 88.6 | 80.5 |
| Small intestine, % | | | | | | |
| Starch, % intake | 10.3 | 11.7 | 13.6 | 19.0 | 10.5 | 17.7 |
| Starch, % entry | 95.5 | 93.3 | 82.6 | 91.9 | 92.4 | 90.9 |
| Large intestine, % | | | | | | |
| Starch, % intake | 0.04 | 0.18 | 0.69 | 0.36 | 0.46 | 0.49 |
| Starch, % entry | 7.6 | 21.4 | 24.2 | 21.4 | 53.3 | 27.7 |
| Total tract digestion, % | | | | | | |
| DM apparent | 75.4 | 76.7 | 78.9 | 76.1 | 74.7 | 76.7 |
| Starch | 99.6 | 99.3 | 97.8 | 98.7 | 99.6 | 98.7 |

# APPENDIX B. INDIVIDUAL STEER DATA

## POST-ABSORPTION TRIAL

Appendix B. Table 1. Individual data of daily intake of DM and starch, and blood flow in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Daily intake, g | | | | | | | | |
| DM | 6125 | 7334 | 8472 | 4712 | 7628 | 6694 | 8890 | 7130 |
| Starch | 3967 | 4631 | 5349 | 2975 | 4816 | 4227 | 5613 | 4502 |
| Blood flow, L/h | | | | | | | | |
| Portal | | 978 | 982 | | 1028 | 1060 | 863 | 704 |
| Hepatic | 963 | 1170 | 1184 | 574 | 1049 | | 1005 | 796 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Daily intake, kg | | | | | | | | |
| DM | 6065 | 7273 | 8035 | 4214 | 6827 | 6210 | 8926 | 6193 |
| Starch | 3949 | 4735 | 5232 | 2744 | 4445 | 4044 | 5812 | 4032 |
| Blood flow, L/h | | | | | | | | |
| Portal | 552 | 848 | | 612 | 1069 | 898 | 767 | 851 |
| Hepatic | | | 1197 | 681 | 1128 | | 1028 | 895 |

Appendix B. Table 1. Individual data of daily intake of DM and starch, and blood flow in steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Daily intake, kg | | | | | | | | |
| DM | 6886 | 7492 | 7654 | 5888 | 6417 | 8183 | 6929 | 5913 |
| Starch | 4429 | 4819 | 4923 | 3787 | 4127 | 5263 | 4457 | 3803 |
| Blood flow, L/h | | | | | | | | |
| Portal | 695 | 923 | 774 | 598 | | 948 | 697 | 539 |
| Hepatic | | 1243 | 911 | 620 | 966 | | 905 | 620 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Daily intake, kg | | | | | | | | |
| DM | 6988 | 7644 | 6059 | 5752 | 7218 | 6306 | 8181 | 7585 |
| Starch | 4468 | 4888 | 3874 | 3678 | 4615 | 4032 | 5231 | 4850 |
| Blood flow, L/h | | | | | | | | |
| Portal | | 960 | 684 | | 773 | 835 | 1054 | 701 |
| Hepatic | 1117 | 1263 | | 788 | 825 | | 1125 | 843 |

Appendix B. Table 2. Individual data of concentration and net flux of glucose in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 3.78 | 4.47 | 3.90 | 3.12 | 4.01 | 3.68 | 3.70 | 3.42 |
| Portal | | 4.42 | 3.91 | | 4.02 | 3.67 | 3.68 | 3.40 |
| Hepatic | 4.07 | 4.76 | 4.44 | 3.47 | 4.40 | | 4.04 | 3.74 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | -49 | 10 | | 8 | -11 | -17 | -14 |
| Hepatic | | 388 | | | 403 | | 359 | 269 |
| SPL | 279 | 339 | | 201 | 411 | | 342 | 255 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | 3.78 | 4.10 | 3.93 | 3.70 | 3.88 | 3.86 | 3.20 | 3.15 |
| Portal | 3.74 | 3.99 | | 3.52 | 3.78 | 3.80 | 3.27 | 3.22 |
| Hepatic | | | 4.26 | 3.82 | 4.12 | | 3.41 | 3.41 |
| Net flux, mmol/h | | | | | | | | |
| PDV | -22 | -93 | | -110 | -107 | -54 | 54 | 60 |
| Hepatic | | | | 192 | 178 | | 162 | 173 |
| SPL | | | 395 | 82 | 271 | | 216 | 233 |

Appendix B. Table 2. Individual data of concentration and net flux of glucose in steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 4.03 | 4.39 | 4.26 | 3.41 | 3.50 | 4.09 | 3.50 | 3.14 |
| Portal | 3.99 | 4.31 | 4.35 | 3.28 | | 4.10 | 3.51 | 3.20 |
| Hepatic | | 4.71 | 4.73 | 3.67 | 3.89 | | 3.84 | 3.41 |
| Net flux, mmol/h | | | | | | | | |
| PDV | -28 | -74 | 70 | -78 | | 9 | 7 | 32 |
| Hepatic | | 472 | 359 | 238 | | | 301 | 135 |
| SPL | | 398 | 428 | 161 | 377 | | 308 | 167 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | 3.87 | 4.35 | 4.18 | 3.26 | 3.11 | 3.79 | 3.79 | 3.78 |
| Portal | | 4.38 | 4.10 | | 3.06 | 3.76 | 3.78 | 3.79 |
| Hepatic | 4.11 | 4.73 | | 3.59 | 3.57 | | 4.16 | 4.12 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 29 | -55 | | -39 | -25 | -11 | 7 |
| Hepatic | | 451 | | | 416 | | 427 | 280 |
| SPL | 268 | 480 | | 260 | 377 | | 416 | 287 |

Appendix B. Table 3. Individual data of concentration and net flux of L-lactose in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .333 | .392 | .401 | .332 | .383 | .418 | .366 | .434 |
| Portal | | .506 | .597 | | .525 | .531 | .502 | .567 |
| Hepatic | .360 | .437 | .475 | .381 | .473 | | .374 | .581 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 111 | 192 | | 146 | 119 | 118 | 94 |
| Hepatic | | -58 | -105 | | -52 | | -109 | 24 |
| SPL | 26 | 53 | 87 | 28 | 94 | | 9 | 117 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .320 | .535 | .425 | | .432 | .389 | .292 | .296 |
| Portal | .422 | .706 | | | .599 | .487 | .368 | .384 |
| Hepatic | | | .522 | | .515 | | .283 | .317 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 56 | 145 | | | 179 | 88 | 59 | 75 |
| Hepatic | | | | | -85 | | -67 | -56 |
| SPL | | | 115 | | 93 | | -9 | 19 |

Appendix B. Table 3. Individual data of concentration and net flux of L-lactose in steers fed 77% sorghum grain on different process *Continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .512 | .650 | .472 | .804 | .351 | .420 | .361 | .368 |
| Portal | .637 | .793 | .578 | 1.07 | | .516 | .422 | .467 |
| Hepatic | | .708 | .559 | .822 | .424 | | .364 | .408 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 87 | 132 | 82 | 160 | | 90 | 43 | 53 |
| Hepatic | | -60 | -3 | -149 | | | -40 | -29 |
| SPL | | 72 | 79 | 11 | 70 | | 3 | 25 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .389 | .405 | .363 | .591 | | .351 | .337 | .419 |
| Portal | | .579 | .529 | | | .460 | .478 | .560 |
| Hepatic | .404 | .488 | | .626 | | | .398 | .562 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 167 | 113 | | | 90 | 148 | 98 |
| Hepatic | | -61 | | | | | -80 | 22 |
| SPL | 17 | 105 | | 27 | | | 68 | 120 |

Appendix B. Table 4. Individual data of concentration and net flux of acetate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .525 | .489 | .601 | .571 | .565 | .763 | .750 | .528 |
| Portal | | .981 | 1.24 | | 1.16 | 1.16 | 1.64 | 1.07 |
| Hepatic | 1.01 | .888 | 1.17 | 1.16 | 1.10 | | 1.43 | 1.11 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 481 | 626 | | 613 | 422 | 769 | 384 |
| Hepatic | | -14 | 46 | | -53 | | -83 | 77 |
| SPL | 465 | 467 | 672 | 338 | 560 | | 687 | 461 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .521 | .281 | .644 | .302 | .449 | .443 | .558 | .680 |
| Portal | 1.21 | .637 | | .753 | 1.12 | .906 | .974 | 1.34 |
| Hepatic | | | 1.14 | .598 | .947 | | .989 | 1.33 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 380 | 302 | | 276 | 717 | 416 | 319 | 564 |
| Hepatic | | | | -75 | -155 | | 124 | 19 |
| SPL | | | 598 | 202 | 562 | | 443 | 584 |

Appendix B. Table 4. Individual data of concentration and net flux of acetate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .709 | .655 | .774 | .658 | .519 | .611 | .607 | .512 |
| Portal | 1.31 | 1.24 | 1.14 | 1.70 | | 1.14 | 1.10 | 1.12 |
| Hepatic | | 1.21 | .972 | 1.33 | .993 | | 1.14 | 1.06 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 420 | 539 | 281 | 622 | | 505 | 341 | 330 |
| Hepatic | | 150 | -100 | -208 | | | 143 | 8 |
| SPL | | 689 | 180 | 414 | 458 | | 483 | 338 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | | .548 | .350 | .616 | .517 | .457 | .571 | .583 |
| Portal | | 1.12 | .803 | | 1.03 | .903 | 1.09 | 1.17 |
| Hepatic | | 1.09 | | 1.11 | 1.01 | | 1.05 | 1.15 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 547 | 310 | | 400 | 372 | 543 | 411 |
| Hepatic | | 137 | | | 5 | | -10 | 64 |
| SPL | | 685 | | 389 | 405 | | 533 | 475 |

Appendix B. Table 5. Individual data of concentration and net flux of propionate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .033 | .069 | .058 | .018 | .062 | .072 | .034 | .052 |
| Portal | | .550 | .648 | | .634 | .475 | .364 | .514 |
| Hepatic | .055 | .135 | .070 | .032 | | | .053 | .118 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 471 | 579 | | 588 | 427 | 285 | 325 |
| Hepatic | | -393 | -565 | | | | -264 | -273 |
| SPL | 21 | 77 | 14 | 8 | | | 19 | 53 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .013 | .026 | .071 | .010 | .045 | 035 | .060 | .023 |
| Portal | .227 | .250 | | .102 | .692 | .526 | .333 | .253 |
| Hepatic | | | .125 | .016 | .084 | | .088 | .046 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 118 | 190 | | 56 | 692 | 441 | 209 | 296 |
| Hepatic | | | | -52 | -648 | | -181 | -175 |
| SPL | | | 65 | 4 | 44 | | 29 | 21 |

Appendix B. Table 5. Individual data of concentration and net flux of propionate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .087 | .064 | .077 | .032 | .091 | .061 | .032 | .022 |
| Portal | .670 | .621 | .581 | .351 | | .662 | .295 | .260 |
| Hepatic | | .126 | .120 | .055 | .176 | | .059 | .046 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 405 | 514 | 390 | 191 | | 570 | 183 | 128 |
| Hepatic | | -437 | -350 | -177 | | | -159 | -113 |
| SPL | | 77 | 39 | 14 | 82 | | 24 | 15 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .028 | .066 | .030 | .085 | .048 | .037 | .087 | .058 |
| Portal | | .685 | .434 | | .621 | .476 | .691 | .619 |
| Hepatic | .058 | .145 | | .154 | .079 | | .156 | .122 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 594 | 276 | | 443 | 366 | 637 | 393 |
| Hepatic | | -494 | | | -418 | | -559 | -339 |
| SPL | 34 | 100 | | 54 | 26 | | 78 | 54 |

Appendix B. Table 6. Individual data of concentration and net flux of butyrate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .003 | .008 | .007 | .006 | .010 | .010 | .019 | .012 |
| Portal | | .054 | .045 | | .058 | .039 | .101 | .057 |
| Hepatic | .008 | .016 | .011 | .013 | .028 | | .030 | .021 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 45 | 37 | | 49 | 31 | 71 | 32 |
| Hepatic | | -36 | -33 | | -30 | | -60 | -25 |
| SPL | 5 | 9 | 5 | 4 | 19 | | 11 | 7 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .004 | .009 | .011 | .007 | .007 | .013 | .042 | .011 |
| Portal | .066 | .024 | | .022 | .043 | .061 | .172 | .048 |
| Hepatic | | | .019 | .010 | .011 | | .075 | .016 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 34 | 13 | | 9 | 38 | 43 | 100 | 31 |
| Hepatic | | | | -7 | -34 | | -66 | -27 |
| SPL | | | 10 | 2 | 5 | | 34 | 4 |

Appendix B. Table 6. Individual data of concentration and net flux of butyrate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .009 | .007 | .008 | .014 | .010 | .011 | .018 | .011 |
| Portal | .059 | .049 | .037 | .093 | | .051 | .086 | .060 |
| Hepatic | | .014 | .014 | .027 | .016 | | .033 | .018 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 35 | 39 | 22 | 47 | | 38 | 47 | 26 |
| Hepatic | | -30 | -17 | -39 | | | -34 | -22 |
| SPL | | 8.7 | 5.5 | 8.1 | 5.8 | | 13.6 | 4.3 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .041 | .004 | .008 | .017 | .007 | .010 | .014 | .009 |
| Portal | | .032 | .035 | | .033 | .053 | .057 | .037 |
| Hepatic | .026 | .008 | | .03 | .009 | | .021 | .012 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 27 | 18 | | 20 | 36 | 45 | 20 |
| Hepatic | | -22 | | | -18 | | -37 | -17 |
| SPL | 13.4 | 5.1 | | 10.2 | 1.7 | | 7.9 | 2.5 |

Appendix B. Table 7. Individual data of concentration and net flux of iso-butyrate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 0 | .006 | .004 | 0 | .001 | .005 | .002 | .002 |
| Portal | | .008 | .010 | | .008 | .013 | .008 | .010 |
| Hepatic | 0 | 0 | .002 | .003 | .005 | | .002 | .002 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 2.0 | 5.9 | | 7.2 | 8.5 | 5.2 | 5.6 |
| Hepatic | | -9.0 | -8.3 | | -3.0 | | -5.2 | -5.6 |
| SPL | 0 | -7.0 | -2.5 | 1.7 | 4.2 | | 0 | 0 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | 0 | .004 | .003 | .001 | .005 | .003 |
| Portal | .008 | .008 | | .008 | .009 | .010 | .007 | .008 |
| Hepatic | | 0 | .004 | .004 | 0 | | .003 | .002 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 4.4 | 6.8 | | 2.4 | 6.4 | 8.1 | 1.5 | 4.3 |
| Hepatic | | | | -2.4 | -9.8 | | -3.6 | -5.2 |
| SPL | | | 4.8 | 0 | -3.4 | | -2.1 | -0.9 |

Appendix B. Table 7. Individual data of concentration and net flux of iso-butyrate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | .002 | .002 | .002 | .004 | .003 | .004 |
| Portal | .009 | .010 | .006 | .011 | | .009 | .007 | .011 |
| Hepatic | | 0 | .002 | .003 | 0 | | .003 | .002 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 6.3 | 9.2 | 3.1 | 5.4 | | 4.7 | 2.8 | 3.8 |
| Hepatic | | -9.2 | -3.1 | -4.8 | | | -2.8 | -5.0 |
| SPL | | 0 | 0 | 0.6 | -1.9 | | 0 | -1.2 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .003 | 0 | .003 | .003 | .004 | .003 | .003 | .001 |
| Portal | | .009 | .010 | | .011 | .011 | .007 | .009 |
| Hepatic | .004 | .001 | | .003 | 0 | | 0 | .002 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 8.6 | 4.8 | | 5.4 | 6.7 | 4.2 | 5.6 |
| Hepatic | | -7.4 | | | -8.7 | | -7.6 | -4.8 |
| SPL | 1.1 | 1.3 | | 0 | -3.3 | | -3.4 | 0.8 |

Appendix B. Table 8. Individual data of concentration and net flux of 2-methyl-butyrate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Portal | | .007 | .007 | | 0 | .021 | .022 | .006 |
| Hepatic | 0 | 0 | 0 | 0 | 0 | | 0 | 0 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 6.8 | 6.9 | | 0 | 22 | 19 | 4.2 |
| Hepatic | | -6.8 | -6.9 | | 0 | | -19 | -4.2 |
| SPL | | | | | | | | |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Portal | .029 | .007 | | .016 | .004 | .014 | .014 | .018 |
| Hepatic | | | 0 | 0 | 0 | | 0 | 0 |
| Net flux mmol/h | | | | | | | | |
| PDV | 16 | 5.9 | | 9.8 | 4.3 | 12.6 | 11 | 15 |
| Hepatic | | | | -9.8 | -4.3 | | -11 | -15 |
| SPL | | | 0 | 0 | 0 | | 0 | 0 |

Appendix B. Table 8. Individual data of concentration and net flux of 2-methyl-butyrate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Portal | .001 | .014 | .006 | .035 | | .008 | .008 | .013 |
| Hepatic | | 0 | 0 | 0 | 0 | | 0 | 0 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 7.6 | 13 | 4.6 | 21 | | 7.6 | 5.6 | 7.0 |
| Hepatic | | -13 | -4.6 | -21 | | | -5.6 | -7.0 |
| SPL | | 0 | 0 | 0 | | | 0 | 0 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Portal | | 0 | .009 | | .005 | .009 | 0 | .008 |
| Hepatic | 0 | 0 | | 0 | 0 | | 0 | 0 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 0 | 6.2 | | 3.9 | 7.5 | 0 | 5.6 |
| Hepatic | | 0 | | | -3.9 | | 0 | -5.6 |
| SPL | 0 | 0 | | 0 | 0 | | 0 | 0 |

Appendix B. Table 9. Individual data of concentration and net flux of ß-hydroxibutyrate in steers fed 77% sorghum grain on different process

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, DRY-ROLLED | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .306 | .198 | .304 | .332 | .304 | .478 | .468 | .348 |
| Portal | | .261 | .413 | | .466 | .485 | .635 | .467 |
| Hepatic | .435 | .284 | .482 | .475 | .489 | | .686 | .523 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 61 | 107 | | 167 | 7 | 144 | 84 |
| Hepatic | | 39 | 104 | | 27 | | 75 | 55 |
| SPL | 124 | 101 | 211 | 82 | 194 | | 219 | 139 |
| Diet, STEAM-FLAKED 34 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | .384 | .356 | .310 | .498 | .219 | .393 | .591 | .405 |
| Portal | .529 | .382 | | .639 | .39 | .414 | .705 | .513 |
| Hepatic | | | .432 | .655 | .365 | | .848 | .596 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 80 | 22 | | 86 | 118 | 19 | 87 | 92 |
| Hepatic | | | | 21 | 47 | | 177 | 79 |
| SPL | | | 146 | 107 | 165 | | 264 | 171 |

Appendix B. Table 9. Individual data of concentration and net flux of ß-hydroxibutyrate in steers fed 77% sorghum grain on different process *continued*

| | Steer number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Item | 401 | 402 | 403 | 404 | 406 | 408 | 423 | 428 |
| Diet, STEAM-FLAKED 28 | | | | | | | | |
| Blood Concentration, mmol | | | | | | | | |
| Arterial | .461 | .258 | .309 | .557 | .208 | .316 | .371 | .334 |
| Portal | .531 | .330 | .329 | .848 | | .442 | .510 | .581 |
| Hepatic | | .390 | .391 | .776 | .236 | | .477 | .464 |
| Net flux, mmol/h | | | | | | | | |
| PDV | 49 | 66 | 15 | 174 | | 119 | 97 | 133 |
| Hepatic | | 98 | 59 | -38 | | | -0.8 | -53 |
| SPL | | 164 | 74 | 136 | 27 | | 96 | 80 |
| Diet, STEAM-FLAKED 22 | | | | | | | | |
| Blood concentration, mmol | | | | | | | | |
| Arterial | | .178 | .297 | .469 | .375 | .389 | .229 | .343 |
| Portal | | .204 | .396 | | .378 | .522 | .271 | .409 |
| Hepatic | | .226 | | .705 | .439 | | .303 | .451 |
| Net flux, mmol/h | | | | | | | | |
| PDV | | 25 | 68 | | 2.3 | 111 | 44 | 46 |
| Hepatic | | 36 | | | 50 | | 39 | 45 |
| SPL | | 61 | | 186 | 52 | | 83 | 91 |

# APPENDIX C. CORN AND SORGHUM STARCH DIGESTIBILITY DATA FROM PUBLISHED TRIAL

Appendix C. Table 1. Starch digestibility of dry-rolled sorghum grain at different sites of the gastro-intestinal tract

| | | Starch digestiblity, % | | | | | |
|---|---|---|---|---|---|---|---|
| | | | Intestine | | | | |
| | | | Small[a] | | Large[a] | | |
| Source | Starch intake kg/d | Rumen | Int | Ent | Int | Ent | Tot[b] |
| Kartchner, 1972 | 5.20 | 45 | 48 | 88 | 3 | 39 | 96 |
| Kartchner, 1972 | 4.18 | 58 | 37 | 89 | 0 | 0 | 95 |
| Stock et al., 1987 | 4.44 | 46 | 37 | 54 | 4 | 24 | 87 |
| Hibberd et al., 1983 | 4.82 | 69 | 10 | 33 | 8 | 37 | 87 |
| Streeter et al., 1990 | 3.21 | 67 | 9 | 29 | 7 | 29 | 83 |
| Hill et al., 1991 | 3.81 | 70 | 15 | 51 | 6 | 39 | 91 |
| Means | 4.28 | 59 | 26 | 57 | 4.7 | 28 | 90 |
| SD | .71 | 11 | 17 | 26 | 2.9 | 15 | 5.1 |
| SEM | .29 | 4.6 | 6.8 | 11 | 1.2 | 6.1 | 2.1 |
| CV | 16.5 | 19.3 | 64 | 46 | 62 | 54 | 5.7 |

[a] Int = as a percentage of starch intake; Ent = as a percentage of starch entry

[b] Tot = total tract

Appendix C. Table 2. Starch digestibility of steam-flaked sorghum grain at different sites of the gastro-intestinal tract

| | | | Starch digestiblity, % | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Intestine | | | | |
| | | | | Small[b] | | Large[b] | | |
| Source | Flake density[a] | Starch intake kg/d | Rumen | Int | Ent | Int | Ent | Tot[c] |
| Kartchner, 1972 | 24 | 5.59 | 76 | 20 | 85 | 2 | 44 | 98 |
| Kartchner, 1972 | 24 | 4.24 | 71 | 27 | 93 | 1 | 51 | 99 |
| Zinn, 1991 | 28 | 1.28 | 80 | 17 | 85 | 2 | 67 | 99 |
| Eck, 1991 | 28 | 4.00 | 88 | 8.4 | 71 | 1.8 | 47 | 98 |
| Eck, 1991 | 24 | 3.93 | 86 | 9.4 | 69 | 3.2 | 70 | 99 |
| Eck, 1991 | 20 | 3.98 | 91 | 7 | 74 | 1.3 | 48 | 99 |
| Means | | 3.84 | 82 | 15 | 79 | 1.9 | 54 | 98.6 |
| SD | | 1.4 | 7.7 | 7.9 | 9.5 | .7 | 11 | .5 |
| SEM | | .57 | 3.1 | 3.2 | 3.9 | .28 | 4.5 | .20 |
| CV | | 36.8 | 9.4 | 53 | 12 | 37 | 20 | .51 |

[a] Flake density in pounds per bushell

[b] Int = as a percentage of starch intake; Ent = as a percentage of starch entry

[c] Tot = total tract

Appendix C. Table 3. Starch digestibility of dry-rolled or whole corn at different sites of the gastro-intestinal tract

| | | Starch digestiblity, % | | | | | |
|---|---|---|---|---|---|---|---|
| | | | Intestine | | | | |
| | | | Small[a] | | Large[a] | | |
| Source | Starch intake kg/d | Rumen | Int | Ent | Int | Ent | Tot[b] |
| Lee et al., 1982 | 3.26 | 56 | 21 | 48 | 1 | 4 | 78 |
| Aguirre et al., 1984 | 2.20 | 78 | 16 | 71 | 2 | 37 | 96 |
| Streeter et al., 1989 | 4.14 | 86 | 1 | 10 | 7 | 57 | 94 |
| Streeter et al., 1990 | 3.13 | 86 | 5 | 40 | 2 | 22 | 93 |
| Zinn, 1990b | 2.71 | 68 | 17 | 54 | 6 | 39 | 91 |
| Means | 3.09 | 75 | 12 | 45 | 3.6 | 32 | 90 |
| SD | .72 | 13 | 8.5 | 22 | 2.6 | 20 | 7.2 |
| SEM | .32 | 5.7 | 3.8 | 10 | 1.2 | 8.9 | 3.2 |
| CV | 23.3 | 17 | 71 | 50 | 74 | 63 | 7.9 |

[a] Int = as a percentage of starch intake; Ent = as a percentage of starch entry

[b] Tot = total tract

Appendix C. Table 4. Starch digestibility of steam-flaked corn at different sites of the gastro-intestinal tract

| Source | Flake density[a] | Starch intake kg/d | Starch digestiblity, % | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Intestine | | | | |
| | | | | Small[b] | | Large[b] | | |
| | | | Rumen | Int | Ent | Int | Ent | Tot[c] |
| Lee et al., 1982 | | 3.26 | 86 | 12 | 86 | 1 | 50 | 99 |
| Aguirre et al., 1984 | | 2.20 | 78 | 16 | 71 | 2 | 54 | 99 |
| Zinn, 1991 | 23 | 1.22 | 86 | 12 | 89 | 1 | 50 | 99 |
| Zinn, 1990b | 26 | 2.71 | 85 | 14 | 94 | .5 | 44 | 99.4 |
| Zinn, 1990b | 26 | 2.71 | 79 | 20 | 96 | .2 | 29 | 99.4 |
| Zinn, 1990b | 26 | 2.71 | 86 | 13 | 96 | .3 | 55 | 99.7 |
| Means | | 2.47 | 83.3 | 15 | 89 | .8 | 47 | 99.3 |
| SD | | .70 | 3.8 | 3.1 | 9.5 | .7 | 9.6 | .3 |
| SEM | | .29 | 1.5 | 1.3 | 3.9 | .27 | 3.9 | .12 |
| CV | | 28.3 | 4.5 | 21 | 11 | 80 | 20 | .3 |

[a] Flake density in pounds per bushell

[b] Int = as a percentage of starch intake; Ent = as a percentage of starch entry

[c] Tot = total tract

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