HIGH STARCH RATIONS FOR RUMINANT PRODUCTION

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INTRODUCTION

Cereal grains are the principal source of starch in livestock and poultry rations. Data provided by the U.S. Department of Agriculture show a 10-year average of 287 million metric tons of cereal grains produced annually in the U. S. (corn, sorghum, wheat, oats, barley, and rye). Seventy-one percent of that production (122 million metric tons) is corn; 60% of corn grain produced is fed to livestock, and 23% is exported, mainly to Asia. I calculate from USDA data that approximately 15 million metric tons of corn grain are fed to livestock annually as part of corn silage; that amount of corn is equal to 7.5% of corn grain production. Total feed fed to livestock and poultry (on a corn equivalent basis) was 436 million metric tons; corn was 28% of that total. Finally, the USDA calculates that over the past 10 years, on average, 81 million animal units (ruminants, poultry, and swine) consumed 1.5 tons of corn annually, or an average of 8.5 lb per head daily.

Grain is fed to livestock to increase the energy density of the diet, or to allow the animal to consume sufficient energy to meet a production potential. Grain also is fed to livestock as a marketing strategy; grain is more profitable in the form of an animal product than as grain itself. High-producing dairy cows and finishing steers are examples of ruminants that are fed large amounts of grain for these reasons. With producer interest in feeding high-grain, high-starch, high-energy diets in the U.S. came research to improve the knowledge base of metabolic mechanisms of starch utilization by ruminants as well as research in technology and strategies to maximize production from high starch rations.

This paper will address starch content of common feedstuffs, digestion of starch and absorption of products of digestion, and post-absorptive metabolism of those products of digestion. This basic information then will be incorporated into aspects of feeding high starch rations to producing ruminants, with emphasis on dairy and beef cattle.

STARCH CONTENT OF FEEDSTUFFS

Generally speaking, the oldest and easiest methods of determining starch content of feedstuffs are the least accurate and precise. In vitro determination of starch content can be done by difference, equating starch to nitrogen-free extract (NFE,

anything that has not been otherwise quantified in the old proximate analysis system) or to non-structural carbohydrates (NSC, total minus NDF, protein, lipid, and ash). The relationship between starch and other components of NSC varies a great deal among feedstuffs. The tabular review of data by Nocek and Tamminga (1991) show three main groups: 1) feedstuffs in which starch contributes 25% or less of NSC (e.g., beet pulp, citrus pulp, alfalfa hay, and most high-protein meals); 2) feedstuffs in which starch contributes from 25 to 50% of NSC (e.g., whole soybeans, brewers□ dried grains, alfalfa silage, oat silage, and timothy hay); and 3) feedstuffs in which essentially all NSC is starch (e.g., canola meal, corn silage, and most cereal grains). The data also contain feedstuffs in which starch exceeds NSC, an artifact of independent analyses and(or) insufficient samples to obtain valid results. In practice, use of difference measures to estimate starch content of cereal grains may be acceptably accurate. Because NSC other than starch (including compounds such as pectins, sugars, galactans, and β-glucans) are usually readily fermented in the rumen, NSC may be functionally equivalent to starch in practical application of other feedstuffs as well. However, one should remember that differences calculations contain the sum of errors of all the direct measures that participate in the calculation.

Enzymatic methods have been used for several years to quantify starch content of feedstuffs. Samples are incubated in aqueous media, heated, stirred, and treated with amylolytic enzyme(s) to convert starch to its component glucose units. Glucose concentration then is measured enzymatically or by some chemical assay, and starch is expressed as α-linked glucose polymers (e.g., Russell et al., 1981). An adaptation of that procedure is measurement of the rate of enzymatic digestion of starch over a relatively short time, for example, 1 hour. This short-term incubation can be used to assess degree of gelatinization of processed grains, or to estimate ruminal degradability of starch (Xiong et al., 1990a).

Workers at Texas Tech University developed a scale for evaluating starch availability through an in vitro gas production procedure (Xiong et al., 1990b). Gas production from 6-h incubations correlates very well (R^2 = .97) with glucose release from enzymatic hydrolysis of starch. Gas production also correlates highly with rumen fermentability, modified by different intensities of grain processing.

Near infrared reflectance spectroscopy can be used to evaluate starch content of grains (Orman and Schumann, 1991; Preston et al., 1993). In addition, this technique may be used to evaluate enzymatically available starch (Preston et al., 1993).

Starch content of common feedstuffs for ruminants ranges from essentially none to almost 80% of dry matter (Table 1). Some feedstuffs, such as various forms of

alfalfa, will vary in starch content in response to harvesting and storage methods. Grains are more constant in starch content than forages, but their starch also varies among varieties and growing conditions; coefficients of variation for five commercial sources of each grain were 2.4% for corn, 3.7% for sorghum, 4.1% for wheat, 5.2% for barley, and 7.1% for oats (Herrera-Saldana et al., 1990b). Preston et al. (1991) assayed 42 sorghum grain samples, and found average starch content was 68%, with a coefficient of variation of 7.1%.

DIGESTION OF STARCH AND ABSORPTION OF PRODUCTS OF DIGESTION

Site of starch digestion, extent of starch digestion, and ruminal degradability, or fermentability, of starch consumed essentially control products of starch digestion in ruminants. In turn, ruminal degradability is affected by source of the starch, processing (such as rolling or steam-flaking), and level of intake. Starch from unprocessed grain, particularly corn and sorghum, is less than 60% degraded in the rumen. Nocek and Tamminga (1991) reported a weak (R^2 = .29) negative relationship between starch content of feedstuffs and ruminal degradability of starch; feedstuffs with highest qualitative ruminal degradabilities come from feedstuffs with lowest starch content, 40% or less of dry matter. In vitro comparison of grains showed that wheat, barley, and oats have more readily degradable starch than corn or sorghum, but that all five grains had similar extents of degradability (Herrera-Saldana et al., 1990b). Generally speaking, any processing that causes disruption of cereal grains☐ seed integrity increases the proportion and decreases variability of starch that is fermented in the rumen (Nocek and Tamminga, 1991; Huntington, 1997; Theurer et al., 1999). For example, ruminal fermentation of corn may increase from 58% to over 85% of starch content in response to processing. Level of intake affects rates of particle breakdown and passage from the rumen; decreased breakdown and(or) increased passage associated with increased intake should decrease ruminal starch degradation. At very high intakes, ruminal starch degradation in lactating dairy cattle may be reduced by high passage rates from the rumen (McCarthy et al., 1989). Conversely, decreased or limited intake should decrease passage rate and increase the proportion of starch fermented in the rumen. However, published data does not show a strong relationship between level of starch intake and either ruminal or total digestion of starches (Zinn, 1990; Huntington, 1997). That may be due to relatively low intakes under experimental conditions, or due to the inherently high digestibility of starch.

It is generally presumed that there is no limit to the capacity of the rumen to digest starch. However, almost all the adversities associated with feeding high grain diets (bloat, acidosis, founder, abscessed livers) are the result of excessively rapid

fermentation of starch to organic acids. It follows that most feed additives, feed treatments, and management techniques designed to ameliorate these adversities focus on ways to slow the fermentation rate or neutralize the acids produced. Similarly, the main goal of grain processing in production situation is to increase digestibility of grain starch yet avoid "too much of a good thing" by making starch too available for ruminal fermentation.

Starch that escapes ruminal degradation is susceptible to enzymatic digestion in the small intestine, or further fermentation in the large intestine and colon. As might be expected, the more starch that escapes the rumen, the more starch is digested in the intestine; however, as the appearance of starch in the small intestine increases, digested as percentage of starch entrance decreases from approximately 90 to 50% or less (Nocek and Tamminga, 1991; Huntington, 1997). Total tract digestion of starch is more constant than ruminal or intestinal digestion because fermentation in the distal portions of the gastrointestinal tract tends to compensate for differences in more antral portions of the tract. Therefore, in practically all published reports, total tract digestibilities of starch digestion in healthy animals eating common feedstuffs range from 90 to 100%.

Ruminal starch fermentation produces organic acids (short-chain fatty acids and lactate) as well as microbial protein (Poore et al., 1993; Philippeau et al., 1999). The organic acids are absorbed from the rumen, and microbial protein is digested and absorbed as amino acids in the small intestine. Enzymes from the pancreas and intestinal mucosa release glucose from starch digestion in the small intestine. The preponderance of data and opinion indicate that complete digestion of all starch entering the small intestine and absorption glucose from that digestion is limited primarily by lack of sufficient activity of pancreatic amylase (Kreikemeier et al., 1991; Huntington, 1997). It is interesting to note that pancreatic secretion of amylase appears to be more a function of energy intake, rather than diet composition or productive function (Harmon, 1992), especially in view of the following discussion of glucose metabolism.

Many computerized ration formulators or feeding systems recognize the importance of synchronizing availability of fermentable of carbohydrate and nitrogen sources in the rumen. The relatively high rate of absorption of ammonia by ruminants suggests energy availability limits the use of available nitrogen by ruminal protozoa and bacteria. At the high intakes of dairy cows, ruminal fluid and particulate turnover or washout likely increase the energy shortage. The advantages of increasing the fermentability of sorghum in the rumen of lactating cows (Herrera-Saldana and Huber, 1989; Herrera-Saldana et al., 1990b; Poore et al., 1993) or of adding starch to forage diets fed to steers (Elizalde et al., 1999; Olson et al., 1999) confirm that synchronizing

the ruminal fermentability of starch and nitrogen (protein) sources increases outflow of bacterial protein from the rumen. The increased energy supply from ruminal fermentation of starch plus the increased supply of amino acids from intestinal digestion of the extra bacterial protein are used to increase nitrogen digestibility or milk protein output, usually without marked adverse effects on milk fat yield or fat-corrected milk production. Synchronization of ruminal fermentability of starch and protein increased nitrogen retention of growing lambs as a percentage of nitrogen intake (Matras et al., 1991). However, addition of starch to high fiber diets likely will reduce fiber digestibility and voluntary intake of fibrous feedstuffs (DeVisser et al., 1998; Olson et al., 1999).

POST-ABSORPTIVE METABOLISM OF STARCH DIGESTION PRODUCTS

Glucose is the major intermediary metabolite of interest from starch digestion and absorption. Glucose may come directly from starch digestion in the small intestine, or indirectly through contributions of propionate, lactate, or amino acids to gluconeogenesis. Ruminants derive 25% or less of their glucose supply directly from starch digestion (Huntington, 1997), so gluconeogenesis is the principal route of glucose supply for ruminants. Metabolic requirements for glucose are linked to production demands and priorities; they can be estimated or calculated as a function of digestible energy (DE) or metabolizable energy intake across a wide range of body weights, breeds, or productive purposes, at least in cattle (Herbein et al., 1978; Russell et al., 1986, Wieghart et al., 1986). Figure 1 shows two linear regression lines of glucose metabolism as a function of DE intake of beef and dairy cattle; one line represents glucose irreversible loss from 24 data points (Herbein et al., 1978; Schmidt and Keith, 1983; Lyle et al., 1984; Armentano et al., 1984; Bauman et al., 1988; Veenhuizen et al., 1988; Amaral et al., 1990; Knowlton et al., 1998), and the other represents liver gluconeogenesis from 26 data points (Baird et al., 1980; Wieghart et al., 1986; Reynolds et al., 1988; 1991, 1992; Huntington 1989, 1996; Guerino et al., 1991; Casse et al., 1994; Taniguchi et al., 1995; Eisemann et al., 1996; Bruckental et al., 1997; De Visser et al., 1997). Coefficients of correlation (R^2) are .92 for regression of irreversible loss on DE intake and .80 for regression of liver gluconeogenesis on DE intake. Therefore, these relationships of glucose metabolism with DE intake can explain most of the variation in the data sets across a variety of body weights, diet composition, and production priorities. Of course, those items are reflected in DE intake; for example, the data points for high DE intake came from large, lactating, Holstein cows. Further, the most likely way to increase DE intake is to increase energy density of the diet by including grain or other starch-containing feedstuffs.

In addition to exemplifying the relationship between energy intake and glucose metabolism in cattle, Figure 1 also sheds some light on the recycling of glucose in response to production needs. If liver gluconeogenesis represents 75% or more of glucose entry rate and irreversible loss represents permanent removal of glucose (for example, excretion as a milk lactose, or exhalation as CO_2), then the space between the lines represents a minimal estimate glucose recycling within the animal's body. Possible avenues of recycling include glycogen production and glycogenolysis in the liver, similar interactions in muscle glycogen, movement of carbon through glucogenic amino acids, or movement of carbon through lipid metabolism in the form of glycerol. Therefore, the energy delivered by high starch diets moves through many metabolites to meet needs in carbohydrate, protein, and lipid metabolism. Those metabolites may be the result of ruminal fermentation (propionate, lactate, amino acids) or may emanate from pathways of intermediary metabolism involved in recycling of glucose carbon. Glucose oxidation to CO_2 in growing Holstein steers consuming a 30% concentrate diet (44.4% of irreversible loss, Veenhuizen et al., 1988) and glucose oxidation to CO_2 in lactating dairy cows that need glucose for milk lactose synthesis (17.2% of irreversible loss, Bauman et al., 1988) show that ruminants have more than adequate gluconeogenic capacity to meet glucose needs as well as to meet other requirements for metabolic balance, or homeostasis. The growing gap between liver gluconeogenesis and irreversible loss at higher DE intakes (Figure 1) indicates that recycling of glucose carbon is metabolically more significant in lactating dairy cows than in growing animals.

Veenhuizen et al. (1988) fed steers 600 g/d of sodium propionate and increased gluconeogenesis from propionate, increased irreversible loss of glucose by 59 %, increased oxidation of glucose to CO_2, and increased the percentage of CO_2 supplied by oxidation of glucose from 7.8 to 13.1%. Increased oxidation of glucose to CO_2 accounted for essentially all of the increased irreversible loss by the steers. Amaral et al. (1990) increased glucose supply for lactating cows by intravenous infusion of glucose (up to 737 g/d) and increased milk production by 6% (not statistically significant), increased irreversible loss of glucose by 53%, decreased gluconeogenesis from propionate, and increased the percentage of CO_2 supplied by oxidation of glucose from 4.1 to 6.8%. Knowlton et al. (1998) increased potential glucose supply in lactating cows by abomasal infusion of 1500 g/d of partially hydrolyzed starch and increased milk production by 5%, increased irreversible loss of glucose by 21%, and increased the percentage of CO_2 supplied by oxidation of glucose from 5.4 to 7%. Taken together, these results indicate that glucose supply was not a major limitation to milk production in these studies, and that it is difficult to push the metabolic system by enhancing glucose supply. Therefore, the intensive, metabolic studies tell us that ruminants are

capable of synthesizing sufficient glucose for their needs, and will oxidize, or ⬚burn off⬚ excess glucose that does not fit into their metabolic balance.

PRACTICAL APPLICATION OF BASIC INFORMATION

Practical application of basic information on feed composition, starch digestion, absorption of digestion products, and post-absorptive use of these products for production can be summarized in two basic questions - how much glucose does the animal need, and how can the producer maximize starch digestion, yet avoid fermentation upsets in the rumen? Ruminants usually derive 25% or less of their glucose supply directly from intestinal starch digestion, but glucose precursors are available in adequate supply. Table 2 contains two general examples, one for a lactating dairy cow and one for a growing beef steer. I provided the animals DE intakes to support their production, then calculated parameters of glucose metabolism and starch intake required to support that glucose metabolism. The calculations in Table 2 indicate that a diet containing 19% of DM as starch for the dairy cow, and 30% of DM as starch for the beef steer should be more than capable of providing all the glucose required to meet their needs. I believe that the assumptions are conservative, both for glucose metabolism and starch intakes. However, even doubling the starch required to support glucose metabolism would still fall in the range of normal diets. Growing or finishing beef cattle are less likely than lactating cows to face a glucose deficiency because their diets routinely contain more than 50% of DM as corn or sorghum grain. We can conclude that ruminants can synthesize all the glucose they need, if the appropriate precursors are available. Therefore, there is little need to worry about a requirement for starch escaping rumen fermentation to be digested and absorbed as glucose. High grain, high starch diets will support higher production through a general increase in energy supply. Although I used DE for calculations, the principles can be applied on the basis of total digestible nutrients (TDN), metabolizable energy (ME), or net energy (NE).

Feed grains are routinely processed (ground, rolled, steamed, or flaked) to improve acquisition of nutrients by animals fed the grains, and thereby improve production per unit of feed input, or feed efficiency. Comparison of feed grains usually shows corn to be superior to other grains in terms of performance response. Varieties of sorghum or corn vary in their digestibility, hence their feeding value, generally in relation to the thickness or density of the seed coat (Huntington, 1994; Phillippeau et al., 1999). Sorghum will respond more to processing than other grains, mostly because it has a relatively dense seed coat that resists fermentation and digestion. Therefore, grain processing uses mechanical and chemical means to disrupt the seed coat and(or)

the starch itself to make it more susceptible to ruminal fermentation.

Work with dairy cattle (Theurer et al., 1996) shows improved milk production from processing corn and sorghum, with improved use of dietary nutrients linked to processing that increases fermentation of starch in the rumen rather increased ruminal escape of starch. They reported steam-flaked vs. steam-rolled corn increased total tract starch digestibility by 10%, milk yield by 6%, and milk protein yield by 8%. Greater ruminal fermentation of starch decreases milk fat percentage, but not milk fat yield. The cows in these studies were eating 25 to 26 kg/d of DM, and producing 36 to 38 kg/d of milk. Performance of growing cattle also is improved by processing feed grains, with the possible exception of oats. As with dairy cattle, feed consumption rarely increases in response to steam-flaking vs. dry-rolling of grains, but increased ruminal digestibility and energy availability translates into greater weight gains, or 8 to 15% more efficient gain (Huntington, 1994).

Consumption of diets that contain high levels of starch or other readily fermentable carbohydrates is associated with several metabolic or physiological disorders, including acute or subacute acidosis, liver abscesses, and low milk fat. These disorders are based on changes in ruminal fermentation patterns and products that are absorbed and subsequently affect intermediary metabolism of the host ruminant. Almost all of these disorders can be treated or avoided by management techniques that avoid sudden changes in diet composition or sudden changes in feed consumption by individual animals. In addition, feed additives such as buffers or ionophores can be used effectively to control these disorders (Huntington, 1994).

SUMMARY AND CONCLUSIONS

Starch supply by ruminants should be related to the animals' glucose needs. The choice of an optimal level of dietary starch from a metabolic (and likely, economic) standpoint will match starch digestion to the glucose needs under a given production scenario. For example, excess availability and subsequent oxidation of glucose from starch digested in the small intestine will be less efficient than fermentation of more starch in the rumen and subsequent benefit of those fermentation products in the form of enhanced microbial protein yield and absorption of organic acids.

The availability of grain starch is a function of the seed structure, mostly a function of the type and extent of protein matrix that encapsulates the starch in the kernel. All grains except oats respond positively to processing, particularly processing that involves application of steam and mechanical rolling or flaking; the response is most dramatic for sorghum, least dramatic for wheat. Processing increases starch digested in the rumen, and in the total digestive tract. For corn, sorghum, and barley the response to adding heat or

moisture to the processing ranges from 8 to 15% improvement in a production parameter, e.g., increased gain per unit feed or output of milk protein. Corn is still the U.S. "king" among grains in terms of versatility and reputation, but with processing and differentials in market price, other grains can and do play a major role as sources of starch for growing ruminants and lactating cows. The challenge for the production manager is to adjust processing techniques and ration formulation to accommodate the characteristics of the available sources of starch. Intensive studies that have quantified the limits on glucose supply from postruminal digestion, and production studies with processed grains indicate decisively that grain starch is used best when it is extensively fermented in the rumen. There is sufficient information available to estimate how much starch might escape ruminal fermentation for a given starch source and processing method; I suggest targets or general goals of 200 g or less of ruminal starch escape for a feedlot lamb (.70 to 1 kg/d starch intake) 1 kg/d or less for a feedlot steer (5 to 7 kg/d starch intake) and 2 kg/d or less for a high producing dairy cow (35 kg milk/day or more, about 25 kg/d dry matter intake).

Starch interacts with other components in the diet and with the dynamics of ruminal fermentation. Synchronization of fermentation of protein and energy sources in the rumen, control of fermentation processes by type and amount of forage, and feed additives in the diet have shown great promise in research results during the past few years, in terms of ability to affect either the rate of production or composition of product.

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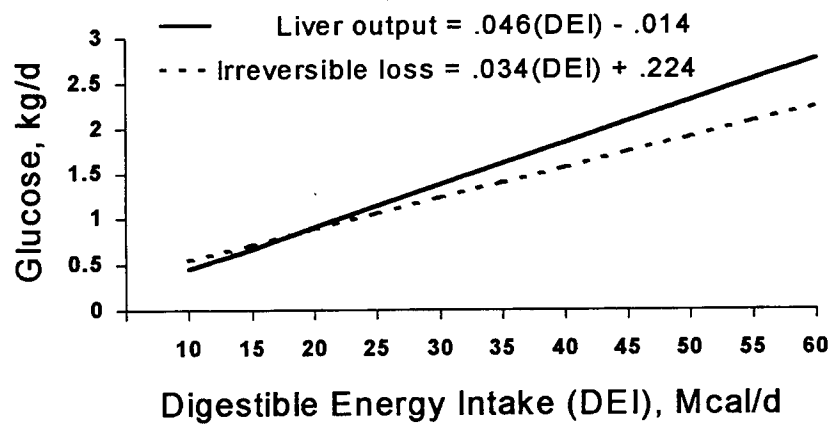
Figure 1. Glucose Metabolism in Cattle

Liver output = .046(DEI) - .014
Irreversible loss = .034(DEI) + .224

Glucose, kg/d

Digestible Energy Intake (DEI), Mcal/d

Table 1. Starch Content of Common Feedstuffs[a]

Feedstuff	Starch, % DM
Wheat grain	77
Corn grain	72
Sorghum grain	68-72
Barley, oat grain	57-58
Corn silage	22-35
Alfalfa hay, alfalfa silage	3-20
Wheat middlings	20-24
Rice Bran	18-32
Beet pulp	1.5
Corn gluten feed	40
Corn gluten meal	20
Soybean meal	7
Fish meal	8

[a] From reviews of Nocek and Tamminga (1991) and Huntington (1997).

Table 2. Glucose and starch needs of a lactating dairy cow and a growing beef steer

	Dairy cow	Beef steer
Body Weight, kg	600	500
Digestible Energy Intake, Mcal/d	60	44
Liver gluconeogenesis, kg/d[a]	2.75	2.01
Glucose irreversible loss, kg/d[a]	2.26	1.72
Glucose oxidized to CO_2, kg/d[b]	.38	.76
Milk yield, kg/d[c]	36	
Gluconeogenesis from blood supply of precursors, %[d]		
Propionate	67	67
Lactate	10	12
Amino acids, other precursors	23	21
Dry Matter Intake, kg/d	22	11
Starch Intake, kg/d[e]		
No ruminal fermentation of dietary starch	4.10	3.13
50% of dietary starch fermented in rumen	4.22	3.21
75% of dietary starch fermented in rumen	4.25	3.25

[a] Calculated from regressions in Figure 1.
[b] Calculated as .172 times irreversible loss for dairy cows (Bauman et al., 1988) and .444 times irreversible loss for beef steers (Veenhuizen et al., 1988).
[c] Assumes 80% of irreversible loss is milk lactose, and milk is 5% lactose by weight.
[d] Estimated from data summarized by Huntington (1997).
[e] Calculated from the irreversible loss in the table and the following assumptions: all ruminal propionate comes from starch; 35% of ruminal propionate production appears as blood glucose (Veenhuizen et al., 1988; Amaral et al., 1990); 67% of glucose irreversible loss is replaced by propionate; and 55% of starch entering the small intestine appears as blood glucose (Kreikemeier et al., 1991).