THIS ARTICLE IS SPONSORED BY THE
MINNESOTA DAIRY HEALTH CONFERENCE.

UNIVERSITY OF MINNESOTA

College of Veterinary Medicine

VETERINARY CONTINUING EDUCATION

ST. PAUL, MINNESOTA
UNITED STATES OF MINNESOTA

Carbohydrate Nutrition and Manure Scoring
Part I: Carbohydrates

Mary Beth Hall, Ph.D.
U. S. Dairy Forage Research Center, USDA – Agricultural Research Service, Madison, WI

There are some elements of ration formulation for which we have no hard and fast rules. Carbohydrate supplementation is one of them. The 2001 Dairy NRC has done the best job to date in offering guidelines regarding the balance between forage & neutral detergent fiber (NDF) vs. nonfiber carbohydrates (NFC). However, there are a variety of factors that can affect what modifications to apply to those guidelines to achieve top production and animal health. To have the best sense of what changes to make, one needs a sense of how carbohydrates function in rations, knowledge of the factors that can affect how the cow performs, and examination of what the cows have to say about their interaction with the ration.

Carbohydrates: NFC & NDF

The two sources of carbohydrates in rations are neutral detergent fiber (NDF) and nonfiber (non-NDF) carbohydrates (NFC). Together, the carbohydrates account for 70% or more of the dry matter and most of the energy in the ration. These carbohydrates differ greatly in their digestion characteristics and how we consider them in ration formulation. This paper will focus largely on NFC.

NFC has typically been calculated by difference (100 - crude protein - NDF - ether extract - ash; sometimes with the value of NDFCP added back). Although the terms NFC and NSC (nonstructural carbohydrates) have often been used interchangeably, they do not describe the same carbohydrates. NSC refers only to sugars, starch and other cell contents, whereas NFC includes some cell wall carbohydrates, as well. This very diverse array of carbohydrates does not function similarly in rations. Four categories of NFC are organic acids, sugars (mono- and some oligosaccharides), starch, and neutral detergent-soluble fiber (Figure 1).

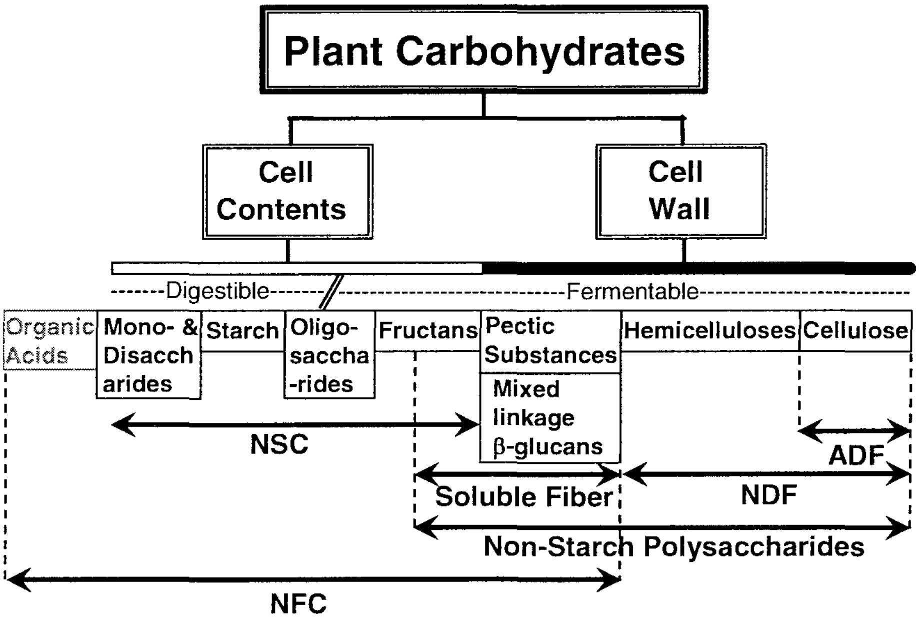
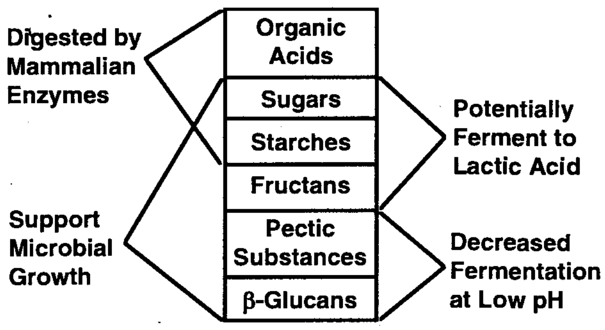


Figure 1. Plant carbohydrates. ADF = acid detergent fiber, NDF = neutral detergent fiber, NFC = non-NDF carbohydrates, soluble fiber = non-starch polysaccharides soluble in neutral detergent, Sugars = mono- and disaccharides. "Digestible": potentially digestible by mammalian enzymes.



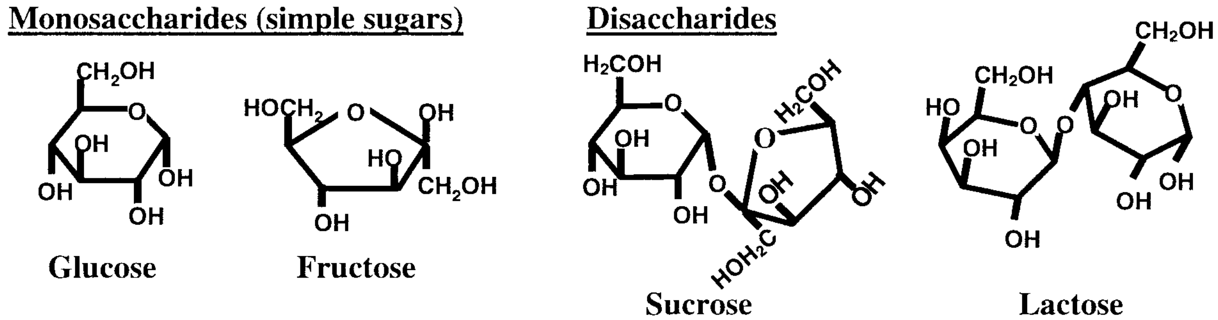
<u>Typical Fermentation Rates</u>
Organic acids: 0-?%/h
Sugars: +/-35%/h
Starch: variable, 4 - 30%/h
Soluble fiber: 20-40%/h
(exception: soyhulls at 4%/h)

Figure 2. Nutritional characteristics of non-NDF carbohydrates.

♦ **<u>Organic acids.</u>**
These include the fermentation acids found in silage (acetate, propionate, butyrate, lactate) and plant organic acids found in fresh forage and hay (malate, citrate, quinate, etc.). Those from fermented feeds, may be utilized by the animal, but do not support appreciable microbial growth in the rumen (Figure 2). They are not carbohydrates, but are included in the NFC by default because NFC is calculated by difference.

♦ **<u>Sugars (monosaccharides and disaccharides).</u>**
Includes both simple sugars (glucose, fructose, etc.) and disaccharides (sucrose, lactose). The main sugars in plants are glucose, fructose and sucrose. Lactose is found in milk products. Sugars tend to ferment rapidly, and may ferment to lactic acid. Fermentation of sugars tends to yield more butyrate than the other NFC, and levels of propionate similar to starch (Strobel and Russell, 1986). Some sugar is converted to microbial glycogen (an alpha-linked glucan like starch) in the rumen (Thomas, 1960). Cattle cannot digest sucrose themselves, but it is likely that little reaches the small intestine. Common sources of sugars include molasses, citrus pulp, almond hulls, bakery waste, soybean meal, and fresh forages or hays. The carbohydrates in silages that analyze as sugars may be unfermented sugars, or short chains of other carbohydrates that were hydrolyzed by the acid conditions (Jones et al., 1992). The latter may have different fermentation characteristics than the naturally occurring sugars (W. Hoover, personal communication).

The organic acid fermentation products of sucrose and lactose can include lactic acid (Thivend and Ehouinsou, 1977; Strobel and Russell, 1986); these sugars have been reported to yield more butyrate than other NFC (Strobel and Russell, 1986; DeFrain et al., 2004).



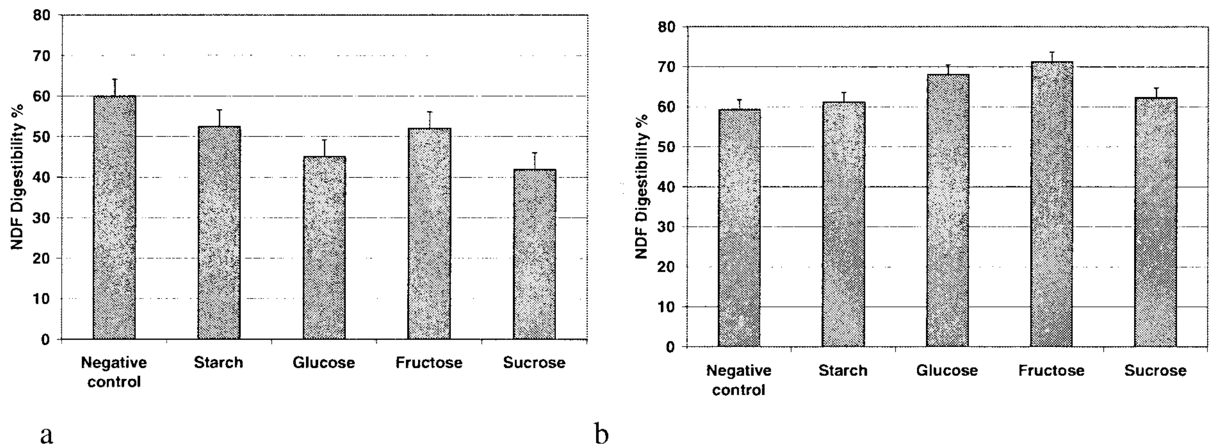


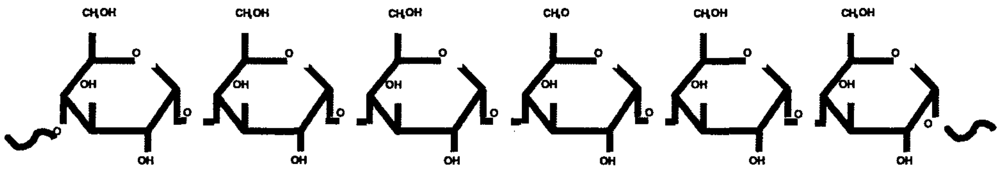
Figure 3. Total tract digestibility of NDF with different NFC and ruminally degradable protein supplementation (in beef cattle). Graph a: RDP supplemented at 0.031% of bodyweight; Graph b: RDP supplemented at 0.122% of bodyweight (Heldt et al., 1999).

Ruminally, cows consuming diets containing glucose, sucrose and lactose have lower concentrations of branched chain volatile fatty acids than do diets containing more starch (DeFrain et al., 2004; Hristov et al., 2005). Supplementation of feeds high in sugar has been reported to depress fiber digestion, even when pH is not greatly reduced (Pate, 1983). Sugar supplements can depress fiber digestion by ruminal microbes through effects of pH, inhibitors produced by the microbes (Piwonka and Firkins, 1996), and if rumen degradable protein is limiting (Heldt et al., 1999). However, there is some evidence that it may increase fiber digestion if protein is not limiting (Heldt et al., 1999) (Figure 3).

♦ **Starch.**

Starch is by far the most common form of NFC fed in dairy cattle diets in the United States. It is composed of alpha-linked chains of glucose that are stored in crystalline granules by plants. Starch can be digested by microbes and by the cow, but there is great variation in the rate of fermentation or digestion depending upon the processing, storage method, or plant source of the starch. The finer the particle size, the more rapid the fermentation (Galyean et al., 1981). Small grains like wheat, barley and oats will tend to ferment at a more rapid rate than corn or sorghum (Herrera-Saldana et al., 1990). The rate of starch fermentation can increase with the amount of starch fed, with the rate of high moisture corn increasing more than more slowly fermenting dry ground corn (Oba and Allen, 2003). In vitro fermentation of starch gave a higher maximum yield of microbial protein than citrus pectin or sucrose (Hall and Herejk, 2001). Starch fermentations may yield lactic acid. Common sources of starch include small grains, corn and sorghum grains, silages and by-products, potatoes, and bakery waste.

Starch



- **<u>Soluble fiber.</u>**

Includes pectic substances, (1->3)(1->4)-beta-glucans, fructans, and other non-starch polysaccharides not included in NDF. These carbohydrates cannot be digested by mammalian enzymes, and must be fermented by microbes to be digested. Soluble fiber tends to ferment very rapidly, except for that in soyhulls, which ferments at a fairly slow rate (~4%/hour). Pectins, which are the main type of soluble fiber in legume forages, citrus pulp, and sugarbeet pulp, tend to yield more acetate than the other NFC (Strobel and Russell, 1986). With the exception of fructans, soluble fiber fermentation yields little or no lactate, and its fermentation is depressed when the rumen pH is more acidic in a fashion similar to the fermentation of NDF. Common sources of soluble fiber include legume forages, citrus pulp, beet pulp, soyhulls, and soybean meal. Fructans are the principal storage carbohydrates of temperate cool season grasses (Smith, 1983).

Although the types of organic acids produced from their fermentations differ, NFC have been considered to give similar yields of microbial protein when pH is relatively neutral and fermentation rates are similar. Animal and in vitro data do not support this.

- **<u>NDF</u>**

NDF serves the dual role in acting as a fermentable carbohydrate source to rumen microbes and providing the cow with physical form in the ration to maintain good rumination and rumen function. The cow cannot digest NDF and relies on microbes in her gut to do so. The NDF in forage, in particular tends to be relatively more slowly digested and of the correct form to stimulate rumination. Maintaining rumination is crucial to reducing the incidence of ruminal acidosis in herds. At the same time, if the forage is coarse, very slowly digested, and makes up a large portion of the ration, intake may be reduced due to rumen capacity issues. The NDF in some byproduct feeds such as citrus or beet pulps may be very rapidly fermented (Hall et al., 1998). The fermentation of NDF tends to be reduced when rumen pH is low (Strobel and Russell, 1986), or when degradable protein is limiting.

Animal Performance

With the exception of starch, comparatively few research trials have evaluated the impact of different NFC on the performance of lactating cows. Most research evaluated feedstuffs rather than carbohydrate types, owing to a lack of methods with which to measure NFC fractions.

Some things that recent research and observations over time suggest regarding differences among NFC:

- Sugars can depress fiber digestion if rumen degradable protein is limiting (Heldt et al., 1999), or increase fiber digestion if protein is not limiting (Heldt et al., 1999; Holtshausen and Hall, 2002).
- In in vitro fermentations, starch had a higher maximum yield of microbial protein than citrus pectin or sucrose (Hall and Herejk, 2001).
- Microbes store a portion of the sugars as glycogen ("microbial starch") (Thomas, 1960), so not all fermented sugars are converted to microbes or organic acids.
- Starch seems to be the NFC source that can most readily increase production and/or drive animals into ruminal acidosis.
- Sugars cannot be simply considered "fast starch".

Several studies do suggest that the profile of NFC in the diet can affect animal performance. Table 1 shows the results of studies in which lactating cows were fed diets that contained a greater proportion of soluble fiber and sugars (from citrus pulp or beet pulp), or more starch (from corn products). Cows fed citrus or beet pulp diets had lower intakes (on two studies), decreased milk protein % and yield (on

Table 1. Lactation studies comparing starch and soluble fiber sources.

	Mansfield et al., 1994		Solomon et al., 2000		Leiva et al., 2000	
	Corn	Beet Pulp	Corn	Citrus	Hominy	Citrus
DM Intake, lb	47.4*	44.8*	46.1*	44.8*	47.2	46.1
Milk, lb	71.0	70.3	78.3	76.3	72.3	69.0
Fat %	3.64*	3.82*	3.33	3.38	3.43	3.54
Fat lb	2.60	2.67	2.60	2.56	2.47	2.45
Protein %	3.01*	2.90*	3.00*	2.93*	2.83*	2.71*
Protein, lb	2.14*	2.03*	2.31†	2.23†	2.05†	1.87†
Milk N/Intake N	0.24x	0.25x	0.31x	0.29x	0.24†	0.22†
3.5FPCM/DMI	1.51x	1.59x	1.63x	1.64x	1.48x	1.45x

* $P < 0.05$, † $P < 0.15$.
x = calculated from data in paper.
Milk N/Intake N = milk nitrogen divided by intake nitrogen, a measure of feed efficiency.
3.5FPCM/DMI = 3.5% fat- and protein-corrected milk divided by dry matter intake; a measure of feed efficiency.

three studies), and increased butterfat % (on two studies). In another study, comparing citrus and corn, cows fed alfalfa silage-based diets containing 19% citrus pulp + 19% high moisture shell corn showed greater milk and protein yield responses to supplemental rumen escape protein from expeller soybean meal than did cows on 39% high moisture corn diets (Mertens et al., 1994). This suggested a poorer utilization of nonprotein nitrogen/better response to bypass protein with citrus. The decreases in milk protein and response to rumen bypass protein may be related to the relatively lower microbial protein yield from sucrose and pectin as compared to starch (Hall and Herejk, 2001). If the lower microbial yields also occur in the animal, they could translate to reduced amounts of amino acids available to the cow, which could explain the reductions in milk protein.

There have been many questions from the field about feeding sugars. Substituting sucrose for starch appears to increase butterfat yield, but other results are mixed. When sucrose was substituted for corn starch (0 to 7.5% of diet dry matter, diet NFC ~ 43% of DM; alfalfa silage, corn silage, high moisture shell corn-based diet; Broderick et al., 2000), there were linear increases in dry matter intake, milk fat content and fat yield. Fat-corrected milk production tended to increase (Table 2). In terms of feed efficiency, milk / dry matter intake and milk nitrogen / intake nitrogen decreased linearly with increasing substitution of sucrose for starch. The fat- and protein-corrected milk feed efficiency did not appear to change with increasing sucrose (no statistics applied).

It's been suggested that the increased intake with sucrose could be related to improved palatability, or to increased passage rate (Piwonka et al., 1994). The decreased efficiency in use of dietary protein (nitrogen) could still relate to the relative decrease in microbial protein yield noted for sucrose as compared to starch (Hall and Herejk, 2001; Sannes et al., 2002).

Table 2. Changes in milk yield and composition with changes in sucrose and starch supplementation. (Broderick et al., 2000).

Sucrose% of diet DM	0	2.5	5.0	7.5
Starch% of diet DM	7.5	5.0	2.5	0
DM Intake, lb*	54.0	56.4	57.3	57.3
Milk, lb†	85.8	89.1	88.2	86.9
Fat, lb*	3.24	3.37	3.64	3.57
Protein, lb	2.73	2.82	2.84	2.82
Rumen pH	6.19	6.16	6.19	6.21
Milk/DMI*	1.60	1.58	1.54	1.52
FPCM/DMI	1.64x	1.63x	1.66x	1.64x
MN/IN*	0.312	0.291	0.291	0.295

$P < 0.05$, † $P < 0.10$
DM = dry matter, DMI = dry matter intake, FPCM = 3.5% fat- and protein-corrected milk; MN = milk nitrogen, IN = intake nitrogen.
x = calculated from data tables.

An entire month or more could be devoted to the issue of starch feeding, in part because so much more research has been done in this area. Some basic concepts should be kept in mind:

- The finer the grind of the starchy grain, the more rapidly digestible it will be.
- Steam flaking tends to increase rate of fermentation, but that depends upon its degree of steam flaking.
- Small grains like wheat, barley and oats will tend to ferment faster than corn or sorghum.
- High moisture grains will ferment more rapidly than dry, all other things equal.

Some practical observations:

- Particles from ground corn retained on #4 (1/4 to whole kernels) or #8 (coarse cracked corn) standard sieves seem to be more likely to pass undigested into manure.
- Visible whole or ground grain in the manure will still contain appreciable starch that was not digested.
- The amount of forage and effective fiber in the diet seem to set the upper limit for the amount of starch that can be included in the ration to enhance production and not cause acidosis. This value is also affected by feeding management, available bunk space, etc.
- If starch is overfed, or the rumen is not functioning properly (acidosis?), symptoms of increased hindgut fermentation will be seen (foamy manure, diarrhea, mucin casts, etc.).

It appears that altering the proportions of sugars, starch and soluble fiber can alter animal performance. However, most of these studies did not report the total amounts of the various NFC in the ration. That missing information is crucial for us to evaluate what proportions of dietary sugars, starch or soluble fiber fed under what conditions will optimize performance.

Protein x Carbohydrate Interactions?

A possible relationship between ruminally degradable protein and low ruminal pH has been reported when rapidly fermenting carbohydrates are provided (Aldrich et al., 1993; Hatfield et al., 1998). Lactating dairy cows consuming diets providing higher concentrations of ruminally degradable protein (RDP) had lower ruminal pH (6.28) than animals fed more ruminally undegradable protein (6.39; $P < 0.01$), irrespective of whether the nonstructural carbohydrates (starch from high moisture shell corn or ground ear corn) was more or less ruminally degradable (Aldrich et al., 1993). The same type of response was noted for molasses-fed sheep, where an 18% crude protein diet gave a lower ruminal pH than a 10% crude protein diet achieved by supplementing soybean meal ($P = 0.02$; Hatfield et al., 1998). Based on current thought, this should not happen – more ruminally degradable protein should yield more microbes, not more acid. However, the cows and sheep are not wrong. There is some evidence that the presence of ammonia decreased glycogen storage and increased conversion of glucose to acetate and succinate in a ruminal fibrolytic bacterium (Matheron et al., 1999), but this falls short of giving the complete information needed to explain the impact of RDP on the entire ruminal contents.

Animal Health

The main health disorder associated with the feeding of carbohydrates is ruminal acidosis. It often finds its start in an imbalance between the physically effective form of the diet needed to keep the rumen functioning through rumination and passage, and the amount of rapidly fermented carbohydrate provided. In the field, the roots of ruminal acidosis problems typically involve the cow, the ration, and management of both. Very rapidly and extensively digestible carbohydrates are likely to be implicated.

Among the NFC, there appear to be differences in their likelihood of causing ruminal acidosis. Both starch and sugars have both been used to induce acute ruminal acidosis. However, in practical application, starch seems to be the NFC source that has been associated both with the potential for high production as well as with problems related to ruminal acidosis (Sutton et al., 1987; Nocek, 1997) which leads to impaired health and production. Starch from corn, sorghum and small grains has been most commonly associated with ruminal acidosis, possibly due to their predominance as an NFC source. However, sugars in molasses, and fructooligosaccharides (short chain fructans) have also been used to induce acute ruminal acidosis in unadapted animals. Pectic substances found in citrus and beet pulps as well as in legume forages, and soluble fiber in general, have not been associated with this disorder (part of the reason for this may be the difficulty in overfeeding them or feeding them in excess of meeting NDF needs). Of interest is that fructooligosaccharides have been used to reliably induce bovine laminitis (Thoefner et al., 2004), whereas similar results have not been reported for sucrose.

Ration Formulation

The obvious question is: "How should we formulate for NFC?" In an attempt to examine this issue, rations were obtained in a survey of U.S. lactating cow diets that supported high milk production and good health (Hall and Van Horn, 2001). The NFC values for individual feeds were estimated using calculated NFC values (100-CP-NDF-EE-Ash). The proportions of NFC as sugars, starch and soluble fiber were estimated based on feed analyses previously performed in our laboratory (Hall, 2000). The nutritionists who provided the rations indicated that cows consumed rations resembling what was on paper. Some of the results of the survey are shown in Figure 4. Animal health can be affected by the types and amounts of NFC fed relative to amounts of forage/effective fiber in the ration, so NFC vs. forage values were compared.

Soluble fiber was relatively constant across forage levels. Starch and sugar contents varied inversely -- as forage content increased, starch increased and sugars decreased. **<u>HOWEVER, those changes may be a function of feeds that were available in that geographic area, rather than deliberately formulating optimal rations.</u>** On the low forage diets, citrus pulp which contains high levels of sugars (26%) and soluble fiber (33%) was typically included in the rations. Aside from citrus pulp, almond hulls, candy waste, some bakery waste, and molasses, there are not many sugar-rich feedstuffs available, but starch sources are abundant.

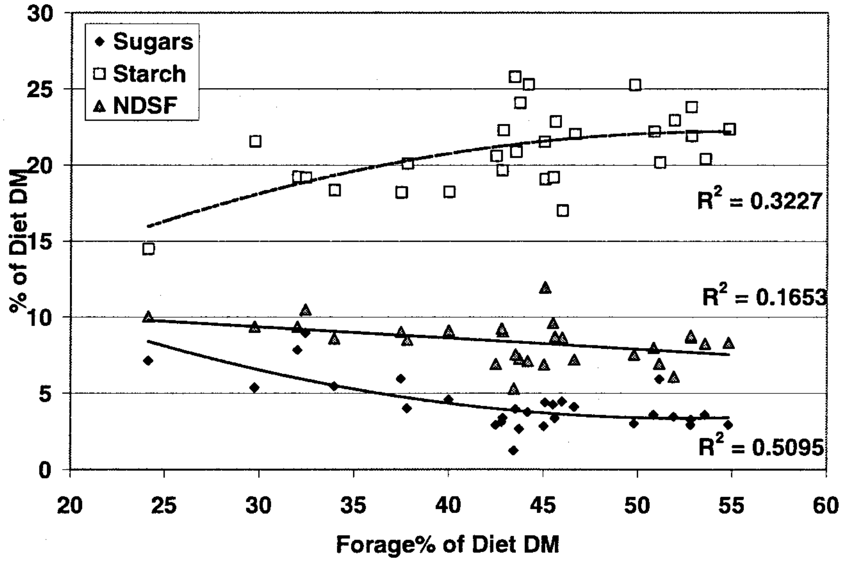


Figure 4. Estimated sugars, starch, and NDSF(soluble fiber) relative to the forage in the diets all as % of diet dry matter. (Hall and Van Horn, 2001).

The relationship between starch and forage in the above graph echoes the recommendations for NFC and NDF feeding offered by the 2001 Dairy NRC (Table 3): as NDF from forage increases, more NFC can be included in the ration. The table is based on the assumptions that the forage is of adequate particle size (to maintain rumination and rumen function) and ground corn is the predominant starch source. If conditions are such that animals consume large meals of grain, sort their feed for grain, slug feed, suffer from heat stress, consume starch sources with very rapid rates of fermentation (high moisture shell corn, finely ground barley or wheat), it might be a good idea to include more NDF and less NFC as a matter of "risk management" to prevent digestive problems.

Table 3. 2001 Dairy NRC recommendations for NDF and NFC formulation.

Minimum NDF from Forage, %	Minimum NDF in Ration, %	Maximum NFC in Ration, %	Minimum ADF in Ration, %
19	25	44	17
18	27	42	18
17	29	40	19
16	331	38	20
15	33	36	21

Thoughts:

- Effective fiber/forage amount consumed by the cows has got to be adequate to maintain rumination and good rumen function no matter what the level of NFC supplementation.
- Use the amount of forage/effective fiber to set the amount of starch to be fed in order to keep the rumen and animal healthy, and then "fill in" with sugars and soluble fiber. The rate of starch fermentation, feeding management, animal management, facilities, etc. should also be considered so that the ration can be formulated to enhance production / decrease risk of feeding.
- Pectins/Soluble Fiber: If they yield less microbial protein, inclusion of a greater proportion of rumen undegradable protein in the ration may be appropriate.
- Sugars: Sugars may yield less microbial protein than starch, but also provide starch ruminally and post-ruminally in the form of microbial glycogen. We do not fully understand what factors determine the microbe, organic acid, or glycogen yields from sugars in the ration. Addition of sugars may improve fiber digestibility if protein is not limiting, but this likely depends upon the amount available in the base diet. It is likely that rumen pH will have some effect. Sugar sources may affect palatability, intake, and rates of passage from the rumen. Again, additional rumen undegradable protein feeding may be useful.
- Starch: Appears to offer the highest microbial crude protein yield, however, feeding high levels of starch have the potential to cause ruminal acidosis and digestive upset. We need to find out the extent to which sugars and starch are interchangeable to deliver a glucose source to the small intestine, and what proportions of soluble fiber, sugars, and total or physically effective NDF to include to offset the potential for ruminal acidosis.

Evaluation

No matter what the rations say, the cows are the ones who determine what is or is not a healthy ration. Evaluation of animal performance needs to take a variety of forms. Body condition, incidence of health disorders, rumination, lameness, milk production, feed efficiency, milk components, reproductive performance, manure consistency and particle size, and any other factors that reflect the effect of the diet on the animal should be examined. If acceptable goals for these elements are not being met, review of the ration, ration management, feeds, facilities, cow comfort, and herd management should be appraised to determine what changes should be considered.

References

Aldrich, J. M., L. D. Muller, G. A. Varga, and L. C. Griel, Jr. 1993. Nonstructural and carbohydrate effects on rumen fermentation, nutrient flow, and performance of dairy cows. J. Dairy Sci. 76:1091-1105.

Broderick, G. A., N. D. Luchini, W. J. Smith, S. Reynal, G. A. Varga, and V. A. Ishler. 2000. Effect of replacing dietary starch with sucrose on milk production in lactating dairy cows. J. Dairy Sci. 83(Suppl. 1):248 (Abstr.).

DeFrain, J. M., A. R. Hippen, K. F. Kalscheur, and D. J. Schingoethe. 2004. Feeding lactose increases ruminal butyrate and plasma β-hydroxybutyrate in lactating cows. J. Dairy Sci. 87:2486-2494.

Galyean, M. L., D. G. Wagner, and F. N. Owens. 1981. Dry matter and starch disappearance of corn and sorghum as influenced by particle size and processing. J. Dairy Sci. 64:1804-1812.

Hall, M. B. 2000. Neutral detergent-soluble carbohydrates: nutritional relevance and analysis, a laboratory manual. University of Florida Extension Bulletin 339, April, 2000.

Hall, M. B., A. N. Pell, and L. E. Chase. 1998. Characteristics of neutral detergent-soluble fiber fermentation by mixed ruminal microbes. Animal Feed Sci. Technol. 70:23-29.

Hall, M. B., and C. Herejk. Differences in yields of microbial crude protein from in vitro fermentation of carbohydrates. J. Dairy Sci.84:2486-2493.

Hall, M. B., and H. H. Van Horn. 2001. How Should We Formulate For Non-NDF Carbohydrates? Proc. 12th Annual Florida Ruminant Nutrition Symposium, Gainesville, FL. pp. 44-50.

Hatfield, P. G., J. A. Hopkins, W. S. Ramsey, and A. Gilmore. 1998. Effects of level of protein and type of molasses on digesta kinetics and blood metabolites in sheep. Small Ruminant Research. 28:161-170.

Heldt, J. S., R. C. Cochran, G. L. Stokka, C. G. Farmer, C. P. Mathis, E. C. Titgemeyer, and T. G. Nagaraja. 1999. Effects of different supplemental sugars and starch fed in combination with degradable intake protein on low-quality forage use by beef steers. J. Anim. Sci. 77:2793-2802.

Herrera-Saldana, R.E., J. T. Huber, and M. H. Poore. 1990. Dry matter, crude protein, and starch degradability of five cereal grains. J. Dairy Sci. 73:2386-2393.

Holtshausen, L. and M. B. Hall. 2002. Effect of medium pH on microbial crude protein yield, pH, and neutral detergent fiber digestion from fermentation of neutral detergent fiber and sucrose in vitro. J. Dairy Sci. 85(Suppl. 1):182 (Abstr.).

Jones, B. A., R. D. Hatfield, and R. E Muck. Effect of fermentation and bacterial inoculation on lucerne cell walls. J. Sci. Food Agric. 60: 147-153.

Leiva, E., M. B. Hall, and H. H. Van Horn. 2000. Performance of dairy cattle fed citrus pulp or corn products as sources of neutral detergent-soluble carbohydrates. J. Dairy Sci. 83:2866-2875.

Mansfield, H. R., M. D. Stern, and D. E. Otterby. 1994. Effects of beet pulp and animal by-products on milk yield and in vitro fermentation by rumen microorganisms. J. Dairy Sci. 77:205-216.

Matheron, C., A.-M. Delort, G. Gaudet, T. Liptaj, and E. Forano. 1999. Interactions between carbon and nitrogen metabolism in *Fibrobacter succinogenes* S85: a ^{1}H and ^{13}C nuclear magnetic resonance and enzymatic study. Appl. Environ. Microbiol. 65:1941-1948.

Mertens, D. R., G. A. Broderick, and R. Simons. 1994. Efficacy of carbohydrate sources for improving utilization of N in alfalfa silage. J. Dairy Sci. 77(Suppl. 1):240 (Abstr.).

National Research Council. 2001. Nutrient requirements of dairy cattle, 7th rev. ed. National Academy Press, Washington, DC.

Nocek, J. E. 1997. Bovine acidosis: implications on laminitis. J. Dairy Sci. 80:1005-1028.

Oba, M., and M. S. Allen. 2003. Effects of corn grain conservation method on ruminal digestion kinetics for lactating dairy cows at two dietary starch concentrations. J. Dairy Sci. 86:184-194.

Pate, F. M. 1983. "Molasses in beef nutrition, *In* "Molasses in Animal Nutrition". National Feed Ingredients Assoc., West Des Moines, IA.

Piwonka, E. J., J. L. Firkins, and B. L. Hull. 1994. Digestion in the rumen and total tract of forage-based diets with starch or dextrose supplements fed to Holstein heifers. J. Dairy Sci. 77:1570-1579.

Piwonka, E. J., and J. L. Firkins. 1996. Effect of glucose fermentation on fiber digestion by ruminal microorganisms in vitro. J. Dairy. Sci. 79:2196-2206.

Sannes, R. A., M. A. Messman, and D. B. Vagnoni. 2002. Form of rumen-degradable carbohydrate and nitrogen on microbial protein synthesis and protein efficiency of dairy cows. J. Dairy Sci. 85:900-908.

Smith, D. 1983. Page 1 *in* Removing and analyzing total nonstructural carbohydrates from plant tissue. 2nd ed. University of Wisconsin-Madison, Madison, WI.

Solomon, R., L. E. Chase, D. Ben-Ghedalia, and D. E. Bauman. 2000. The effect of nonstructural carbohydrate and addition of full fat extruded soybeans on the concentration of conjugated linoleic acid in the milk fat of dairy cows. J. Dairy Sci. 83:1322-1329.

Strobel, H. J. and J. B. Russell. 1986. Effect of pH and energy spilling on bacterial protein synthesis by carbohydrate-limited cultures of mixed rumen bacteria. J. Dairy Sci. 69:2941-2947.

Sutton, J. D., J. A. Bines, S. V. Morant, D. J. Napper, and D. I. Givens. 1987. A comparison of starchy and fibrous concentrates for milk production, energy utilization and hay intake by Friesian cows. J. Agric. Sci. (Camb.) 109:375-386.

Thivend, P., and M. A. Ehousinou. 1977. Digestion of lactose in the rumen of sheep. Proc. Nutr. Soc. 36:73A.

Thoefner,M. B., C. C. Pollitt, A. W. van Eps, G. J. Milinovich, D. J. Trott, O. Wattle, and P. H. Anderson. 2004. Acute bovine laminitis: a new induction model using alimentary oligofructose overload. J. Dairy Sci. 87:2932-2940.

Thomas, G. J. 1960. Metabolism of the soluble carbohydrates of grasses in the rumen of the sheep. J. Agric. Sci. 54:360-372.