

Addition of Sugars to Dairy Rations

Jeffrey L. Firkins¹

Department of Animal Sciences

The Ohio State University

Abstract

Responses to sugars in dry or liquid form vary from study to study. To explain some of this variation and prioritize when sugars are more likely to have a benefit in diets for high producing dairy cattle, microbial function that influences susceptibility to low ruminal pH or a limitation in growth factors needed for efficient ruminal fiber degradation is discussed in this paper. When fed in proper amounts, sugars should not depress ruminal pH, and there is some evidence that they actually help to prevent a drop in pH after consuming large meals of concentrate by maintaining a higher number of lactate-fermenting bacteria. Adding sugars does prioritize the need for rumen degraded protein (**RDP**). However, lactate-fermenting bacteria probably compete against the bacteria that catabolize amino acids as their main energy source, so feeding sugars potentially preserve higher concentrations of peptides and amino acids for the rest of the microbial consortium to degrade fiber or produce microbial protein more efficiently. Sugars tend to increase butyrate or valerate concentration in the rumen, which, besides consolidating 2 moles of acid into one, provides more fuel for rumen epithelial cells. We don't know if this helps to increase surface area and absorptive capacity from the rumen wall in lactating dairy cows, but there is growing evidence that cows that are more likely to resist subacute rumen acidosis tend to have increasing concentrations of these fermentation end-products. Moreover, sugars do not promote the

formation of *trans* fatty acids that are implicated in milk fat depression, and there is some evidence that they might decrease the accumulation of these fatty acids by slowing lipolysis or modifying rates of biohydrogenation. Combined with the potential to reduce sorting behavior against coarse particles, especially in corn silage-based diets, our data with liquid feeds tend to support the same or enhanced milk fat yield, particularly if dry matter intake (**DMI**) is increased.

Introduction

As we all know, sugars are rapidly and extensively fermented. Also, it pretty well established that there is an optimum feeding rate between 2.5 and 5% supplemental sugar (Broderick and Radloff, 2004; Firkins et al., 2008b), but it is not clear in what diets sugars are more effective and in which form to use them. The typical inference is of a double-edged sword in that sugars are providing a burst of energy to “jump start” ruminal processes, but excess sugar intake could cause a burst of acid production that promotes acidosis. Current research complicates these traditional interpretations and blunts both ends of the sword. Let's start with separating rate from amount of fermentation. Nearly all models for ration evaluation or description of rumen function work on a daily interval even though the cow eats multiple meals of varying amounts of feed per meal. Then in a group situation, there is a large variation among cows and even by the same cow over multiple days. Starches are degraded and

¹Contact at: 2029 Fyffe Court, 223 Animal Science Bldg., Columbus, OH 43210-1995, (614) 688-3089, FAX: (614) 292-1515, Email: firkins.1@osu.edu



fermented in the 10 to 20%/hour range, thus taking several hours to degrade and providing a more continuous supply of sugars over the day (among all meals). Fiber sources are typically degraded at about 5%/hour, thus taking something like one day to degrade but still even more gradually and hemicellulose that is used by the entire bacterial community. When sugars are released by polysaccharide hydrolysis or by feeding them directly, they are fermented within about an hour (i.e., they have > 100%/hour fermentation rates). The more frequent the meals are consumed, the daily amount is divided into smaller increments and decreases the opportunity to jump start microbial functions but also to promote acidosis. Thus, TMR feeding and enhancing multiple meals per day through multiple feedings or pushups should reduce these typical explanations for justifying sugars. In contrast, there is a core population of particle-associated bacteria but considerable variation among the structure of the fluid-associated bacteria (Wallace, 2008; Welkie et al., 2010), so sugars likely influence those transient fluid-phase bacterial populations. Because they do not directly compete in the same niche as the adherent fibrolytic populations, certain sugar-using bacteria could still be providing growth factors or helping to control the fluid environment that bathes the fiber-enriched particulate matter. Optimizing the use of sugars probably depends on how well we can predict ruminal carbohydrate degradability and manage meal feeding behavior in groups of cows on farms with varying grain and forage sources. Therefore, how sugars might be optimizing the overall microbial ecosystem for efficient feed (especially fiber) degradation and microbial function will be discussed.

Although a low ratio of effective fiber:rumen-degraded carbohydrate has long been associated with milk fat depression, most studies with sugars are neutral or actually support a higher production of milk fat (see below). In order to understand when and how sugars could increase milk fat yield, we must address some critical mechanisms. One

obviously critical component is enhanced DMI, which obviously increases NE_L intake needed for production of energy-corrected milk (including milk fat), but DMI also is the most critical driving variable positively related to microbial protein synthesis (Oldick et al., 1999) in a variety of dietary conditions and to milk protein yield when cows are fed supplemental fat (Wu and Huber, 1994). Milk fat yield is limited by fatty acid synthesis in the mammary gland, so we must evaluate whether or not sugars will foster ruminal production of *trans* fatty acids that can pass to the intestine and depress milk fat secretion (Jenkins et al., 2008). Finally, these factors might interact with the source and particle length of forage. My objectives are to integrate the ramifications of these factors when considering sources of sugars in dairy rations.

Sugars, Ruminal pH, and Fiber Digestibility

Because we want to efficiently degrade particulate matter before it passes from the rumen, we must optimize bacterial colonization of stems, leaves, and even starch granules. The primary cellulolytic bacteria (they also contribute to hemicellulose degradation) are less tolerant to a low pH, and if we add too much grain to the diet, fiber digestibility can be reduced. This decreased fiber digestibility is important because it could promote bulk fill limitation of voluntary feed intake. Low ruminal pH could be reducing binding by cellulolytics to particulate matter in the rumen, allowing more tolerant bacteria to initially adhere and therefore have a more favorable competition for new feed particles (Mouriño et al., 2001). After initial adhesion to newly ingested particles, bacteria must grow (divide into many more cells) to rapidly and extensively degrade that particle before passage. However, although the latter reference (and much of our thinking) focuses on ruminal pH < 6.0 as the main limitation of fiber digestibility, more current work with molecular techniques has shown that even cows with very low pH can maintain normal populations of cellulolytic bacteria (Palmonari et al.,

2010). Even grain-induced acidosis did not reduce the abundance of cellulolytic bacteria unless it progressed to what was classified as severe acidosis (Khafipour et al., 2009). Thus, because increasing concentrate usually decreases pH, Calsamiglia et al. (2008) varied forage:concentrate while maintaining different constant pH values in continuous culture. Adding acid to systematically decrease pH had a direct effect that was dose-responsive and predictive for many variables, and was much more critical than forage:concentrate. However, while confirming the important response to low pH, these pH values were maintained constantly and were distributed throughout the entire flasks by rapid stirring of pH-controlled buffer with finely ground feed particles. In contrast, pH has been long known to depend on the time after feeding, particle size, and location of those particles stratified and slowly mixed in the rumen. Thus, this model does not consider how variable pH influences the initial attachment and during progressive need for growth factors in the feed particles containing substrate that is limited by surface area.

In studies investigating the “carbohydrate effect” independent of pH (Piwonka and Firkins, 1996), as documented by adding medium from previous batch culture incubations that were not or were autoclaved (apparently to denature proteins), we discussed the potential for higher glucose supply to antagonize fiber degradation through production of proteinaceous inhibitors. Although these inhibitors could be detrimental in high grain diets, what if some proteinaceous inhibitors provide some benefit in diets with moderate amounts of grain? Some of these proteins inhibit the low abundance/high activity group termed “hyperammonia-producing bacteria” (Walker et al., 2005). Unlike other amylolytic bacteria that have a moderate rate of deamination and that use the carbon skeletons for only a portion of their energy, these obligate amino acid fermenters rapidly reduce the availability of amino acids to stimulate growth of amylolytic or cellulolytic bacteria. Those bacteria that have been cultivated are inhibited

by low pH, but a computer modeling study suggested a more direct antagonism by carbohydrate-fermenting bacteria against the hyper-ammonia producers (Rychlik and Russell, 2000). Thus, moderate provision of grain could be limiting these obligate deaminators and maintaining a more consistent concentration of peptides and amino acids between meals to maintain a more efficient microbial ecosystem involved in fiber degradation. Various additives are being explored for their inhibition against the hyper-ammonia producing bacteria and other microbes, and more work is needed (Calsamiglia et al., 2007).

We need to understand why sugars should not promote acidosis to understand how they could (at least sometimes) actually benefit the bacterial community. Lactic acid is well known to be a much stronger acid than the volatile fatty acids (VFA). That is, at the same molarity, lactic acid will drop the pH about one full pH unit lower compared with the same molarity of any of the VFA. Microbiologists have well characterized how the acid-tolerant microbes can ferment glucose to lactate 5 or more times faster, thus getting more energy even from a less energetically efficient pathway (Nagaraja and Titgemeyer, 2007). However, those authors discussed that, although this potential burst of lactate production can result in acute acidosis, lactic acid concentration rarely increases because its catabolism rate compensates to metabolize more lactate as more is produced until pH progressively declines below 5.5 to inhibit the lactate consumers. Therefore, if we stimulate the lactate consumers through basal sugar feeding, this should provide a ready population to “buffer” against bursts of lactate production, effectively preventing short-term accumulation to concentrations high enough to significantly depress ruminal pH and provide a competitive advantage for the minority populations that escalate lactate production and inhibit fiber degraders. In support, subacute acidosis was associated with reduced bacterial diversity (Khafipour et al., 2009). Moreover, supplementing

sugars could actually increase pH if there is increased production of VFA that are 4 carbons or greater in chain length because these pathways would condense 2 moles of acid into one, thus partially compensating for the high ruminal digestibility of sugars. Although 2 moles of lactate can be converted to 2 moles of propionate, Piwonka and Firkins (1996) added either glucose or lactate to batch cultures. We estimated that lactate was converted to propionate and butyrate in a ratio of about 1 to 2.

Many, but not all, studies with sugars show increases in the molar proportion of butyrate or valerate (Heldt et al., 1999), and a recent molecular analysis of rumen contents from feedlot beef steers (not fed sugars) documented that those with improved feed efficiency had increased butyrate and valerate concentrations (Guan et al., 2008). These are much more important fuel sources for the rumen epithelium than are acetate or propionate (Kristensen, 2005). For sheep fed the same acidosis challenge diets, those grouped as non responders probably had increased rates of VFA absorption in vitro from rumen epithelia samples than those grouped as responders (much lower pH), with correspondingly increased β -hydroxybutyrate concentrations in the blood for the non-responders (Penner et al., 2009). In addition to passive absorption removing a proton from the rumen, acetate can be absorbed as an anion with a corresponding exchange with a bicarbonate anion that would help buffer pH. Regardless of mechanism, these results still document a greater variability among lactating cows fed the same diet and the potential for the need to maintain conditions that resist a decline in pH and lost microbial efficiency for some cows.

In our study (Oelker et al., 2009) and several others we cited, ruminal pH was not decreased by sources of sugars in the diet. Therefore, so long as we maintain a proper environment for microbial populations, feeding less

than 5% sugars rarely decreases ruminal pH and sometimes actually increases it. When 5 cows each were fed a control or a diet with 4.7% sucrose starting on the day after calving, the ruminal pH actually tended ($P = 0.08$) to be higher for sucrose, and there was a numerical ($P = 0.13$) reduction of about 2.5 hours per day in which the pH was below 5.8 (Penner and Oba, 2009). If sugars reduce the time when pH is below a critical threshold and if initially low pH residually limits degradation of newly colonized fiber particles (Mouriño et al., 2001), then there should be efficient colonization of fiber particles ingested after each meal, assuming growth factors are not limiting. Broderick and Radloff (2004) provided evidence from 2 trials as well as from other studies that a moderate amount of sugars in the diet can increase NDF digestibility in dairy cattle.

The ability to consume lactate and stimulate fiber digestibility probably depends on having adequate rumen-degraded protein (**RDP**). Both low pH (Calsamiglia et al., 2008) and low nitrogen per se (Griswold et al., 2003) can decrease proteolysis by bacteria in continuous culture. Many bacteria and protozoa can ferment lactate, but *Megasphaera elsdenii* is most attributed to filling this niche (Nagaraja and Titgemeyer, 2007). A comprehensive metagenomics study confirmed the importance of bacterium to keep lactate concentrations low in dairy cattle fed diets promoting acidosis (Khafipour et al., 2009). Besides *M. elsdenii*, though, increased *Prevotella* spp were associated with maintaining an efficient bacterial population structure in that study. The authors discussed the potential for a *Prevotella* probiotic to reduce the incidence of subacute acidosis. This large phylum is well documented for its starch-degrading and sugar-fermenting niche and also its major capacity to degrade proteins (Walker et al., 2005). Their active protease capacity funnels short peptides and amino acids to other bacteria for uptake and use for protein synthesis or for catabolism. Some strains of *M. elsdenii* have rapid rates of deamination, but not

necessarily high proteolytic activity, and they likely use these amino acids more for energy after glucose or lactate become limiting (Rychlik et al., 2002). However, as explained by those authors, this predominant lactate fermenter could be an important producer of branched chain VFA from their corresponding amino acids, effectively competing against the hyperammonia producers, which consume amino acids but do not ferment lactate or otherwise contribute as much to the balanced consortium. When beef cattle were dosed with pure starch or glucose, lactate only spiked after feeding glucose, and there was a corresponding prolonged butyrate concentration, indicative of a stimulation of a butyrate-producing population (Arroquy et al., 2004b). In a companion study, lactate concentration again spiked when glucose was dosed at an equivalent concentration as starch, but lactate concentration decreased incrementally back to baseline with increasing supply of RDP (Arroquy et al., 2004a). Thus, having adequate RDP might be a prerequisite for allowing the sugar-fermenting/lactate-fermenting populations to “buffer” the ruminal fermentation from bursts of low pH, with the caveat that adding RDP would only be beneficial if peptide concentration is indeed limiting.

Research with isotopically labeled amino acids supports their stimulation of fiber digestibility (Walker et al., 2005). Specialist fibrolytics efficiently degrade native cellulose or hemicellulose, but many generalists can scavenge the short-chain saccharides from enzymatic hydrolysis while supplying growth factors to the fibrolytics. Colonization of both groups is extensively committed within 5 to 15 min and thereafter is a function of subsequent bacterial growth (Edwards et al., 2007). Moreover, protease activity has been proposed to expose more surface area to stimulate rate of fiber degradation (Colombatto and Beauchemin, 2009). Thus, stimulation of proteolytic bacteria, while not stimulating hyperammonia producers, should stimulate ruminal fiber digestibility, whereas over-feeding grain could negate this benefit by reducing pH or reduced

availability of growth factors from proteolytic bacteria.

Rumen-degraded protein does not just provide peptides for bacterial growth; it also is continually degraded to ammonia, the main N source for cellulolytic bacteria. In our study (Oelker et al., 2009) and several others we cited, adding molasses decreased ruminal ammonia concentration. Adding urea to corn silage diets recovered ammonia concentration, but when we fed alfalfa hay (high in RDP), molasses did not influence ammonia concentration. The linear decrease in ammonia concentration with increasing sucrose substitution for starch without an increase in microbial N production is consistent with these responses (Broderick et al., 2008). The net concentration of ruminal ammonia depends on its production from RDP and blood urea N relative to its incorporation into microbial protein. Thus, a net decrease in ammonia concentration can be a sign of more efficient microbial protein synthesis that could be limited by peptide supply, not necessarily ammonia. If we can better understand how sugars influence ammonia production and uptake, we should have a greater opportunity to optimize the conversion of RDP into microbial protein with less need for extra RDP safety factors that promote excessive loss of N in the urine (Firkins et al., 2007). These efforts will require quantification and modeling for improved predictability in dairy rations.

Many modeling efforts have focused on the three well characterized cellulolytic isolates: *Fibrobacter succinogenes*, *Ruminococcus flavefaciens* and *R. albus*. All require branched chain VFA and ammonia as the principal nitrogen source. Because branched-chain VFA are less likely to be limiting for their growth in the rumen compared with ammonia, the CNCPS and CPM models focus on providing adequate ammonia concentration for the cellulolytic populations but focus on peptide supply for the amylolytic bacteria. However, they have focused on the use of pure cultures and have

typically ignored that these cellulolytics work in a consortium and benefit from preformed amino acids (Walker et al., 2005). The lack of interaction between the non-structural carbohydrate bacteria and the structural carbohydrate bacteria in CNCPS/CPM thus might require more empirical consideration or adding constraints to optimize the integration of efficiency of RDP with ruminal carbohydrate degradability and source.

An alternative to fostering enzymatic attack within the rumen is to first expose feed to exogenous enzymes, especially those with fibrolytic activity (Beauchemin et al., 2003). However, even addition of exogenous amylase with insignificant activities against protein or fiber still stimulated NDF digestibility (Kingerman et al., 2009). The authors referenced a proposed mechanism that amylase stimulated non-cellulolytics to cross-feed with cellulolytic bacteria. These results with amylase treatment are in contrast with meta analyses showing decreased ruminal NDF digestibility with increasing starch concentration (Firkins et al., 2001; Nousiainen et al., 2009). Thus, a small amount of sugars could stimulate an optimal development/progression of the consortium needed for efficient degradation of fiber in diets with moderate starch concentration with the caveat for an adequacy of RDP for the consortium.

Both depressed pH and increasing concentrate proportion in diets are well known to potentially depress milk fat, sometimes sporadically among different cows fed the same diet and with shifts in bacterial populations (Weimer et al., 2010). To sort out some of these responses, continuous culture has been used to establish conditions to try to better document a mechanism. Continuously decreasing pH to 5.6 in continuous culture dramatically elevated the outflow of the 18:1 *trans*-10 isomer that is strongly correlated with milk fat depression, and quantitative PCR analysis of biohydrogenating bacterial groups suggested a change in the 18:1 *trans* producing group (Fuentes

et al., 2009). Because pH was maintained at 6.2 in another continuous culture study, the linear decrease in biohydrogenation (which would decrease production of *trans* isomers) associated with increased sucrose addition was attributed to shifts in bacterial populations (Ribeiro et al., 2005). Future efforts should separate the rates of lipolysis from the kinetics of biohydrogenation (Jenkins et al., 2008) and should consider interactions with protozoa, which contribute to lipolysis but only indirectly influence the accumulation of *trans* fatty acids by incorporating unsaturated fatty acids or intermediates such as conjugated linoleic acids (Firkins et al., 2008a). Protozoal populations were changed by molasses and interacted with forage source (Oelker et al., 2009). In that paper, we noted that entodiniomorphid protozoa are prominent starch and fiber degraders but also can metabolize sucrose and lactate.

Sugars in Moderate Starch Diets

After surveying numerous studies with sugars, I have concluded that they are most efficacious when they can stimulate total DMI (Firkins et al., 2008b). Propionate is the principal gluconeogenic precursor for glucose production, which occurs in the kidney but primarily in the liver. I subscribe to the theory that glucose demand by the mammary gland for milk synthesis rate-limits milk production (Lesmosquet et al., 2009). That is, as the cow produces more milk volume (and lactose), this increases the need for the liver to supply that glucose; in contrast, increasing glucose supply by the liver will not necessarily increase production of milk lactose. Therefore, when propionate supply to the liver exceeds its needs for glucose release to the mammary gland, the propionate then can send a feedback loop to reduce feed intake (Allen et al., 2009). As stated previously, sugars tend to increase the ruminal concentration of butyrate and sometimes valerate (Heldt et al., 1999; Ribeiro et al., 2005), but typically not propionate. When purified corn starch was replaced with sucrose, propionate or

butyrate concentrations were not affected, but valerate and the branched chain VFA maximized at an intermediate sugar concentration ($P < 0.05$ quadratic response; Broderick et al., 2008). As the authors discussed, acetate and propionate condense to produce valerate; thus sugars could also help suppress the net propionate absorption even if for a limited degree. Both DMI and milk fat yield increased linearly ($P < 0.05$) with increasing sucrose substitution for starch. In contrast with feeding sugars, increasing supply of highly degraded starch sources should increase propionate production (Firkins et al., 2006). In a recent paper (Gencoglu et al., 2010), decreasing starch concentration from 27 to 22% (2/3 of the forage was corn silage) increased DMI unless a commercial amylase was added to the lower starch diet (Table 1). The amylase should have increased the starch availability in the rumen while not increasing the measured concentration of dietary sugars. Interestingly, decreasing the starch concentration (with or without amylase) increased total tract NDF digestibility because those authors added more highly degradable NDF from soyhulls. The authors stressed the improved efficiency of milk production with decreased DMI for the amylase treatment, but the response was attributed to increased protein and NDF digestibility, not to starch, compared with the same diet without amylase. However, other studies with amylase did not decrease DMI and sometimes increased it (Kingerman et al., 2009). In those cases, propionate feedback probably did not limit DMI.

The relationship between nonstructural carbohydrates and milk fat yield probably depends on forage source. Recently, Weiss et al. (2009) documented an important interaction between dietary starch concentration and the ratio of alfalfa silage:corn silage for milk fat yield. With increasing alfalfa silage:corn silage, increasing dietary starch concentration tended to increase milk fat yield. However, with decreasing ratio of alfalfa silage:corn silage (i.e., more corn silage), increasing dietary

starch above about 25% was associated with decreasing milk fat yield. This relationship to forage source is consistent with the greater potential to depress milk fat when Rumensin is added to high starch diets in which corn silage is the main forage (Oelker et al., 2009). In the study of Penner and Oba (2009), replacing corn grain with sucrose increased DMI ($P < 0.05$) and milk fat yield ($P < 0.10$) and decreased ($P < 0.05$) the concentration of the 18:1 *trans*-10 fatty acid isomer that is strongly associated with milk fat depression. I am not suggesting that adding sugars can prevent milk fat depression in diets with excess fermentable carbohydrate, and in fact seem to work better in lower starch diets (Firkins et al., 2008b). Still, sugars should not be increasing risk of milk fat depression and could be reducing this risk if kept at appropriate levels ($< 5\%$ added sugar).

Whey provides a moderate amount of RDP and is a good source of lactose, which is extensively used by ruminal microbes. Consistent with previous discussion, feeding whey to replace starch increased DMI, milk fat % (with a numerical trend for increased yield), and butyrate percentage (Charbonneau et al., 2006). This expected increase in lactose fermentation to butyrate was proposed to increase ruminal papillae conversion of butyrate to beta-hydroxybutyrate (**BHBA**) for fuel, whereas the released BHBA was suggested to stimulate hepatic gluconeogenesis from propionate and reduce hepatic lipid infiltration in transition cows (DeFraire et al., 2006). Butyrate's role in papillae regeneration for transition cows (after high forage diets are fed to reduce incidence of displaced abomasum) needs further corroboration, but there is some indication that some cows reduce their susceptibility to acidosis by having a faster rate of VFA absorption (Khafipour et al., 2009). The classical work of Palmquist et al. (1969) demonstrated that BHBA only contributes carbon for the priming unit (the first four carbons) of synthesized fatty acids; because acetate is needed for subsequent fatty acid elongation, BHBA contributed a maximum of 8%

of the fatty acid carbon. Despite several references to this role for butyrate, increased BHBA supply to the mammary gland should not provide a direct explanation on the increased milk fat often associated with feeding sugars.

Sugars and Feedbunk Management

We are all acutely aware of the need for optimize the amount of energy intake through concentrates containing starch (as diluted by fibrous byproducts) while maintaining at least a minimum amount of forage NDF. I will refer readers to a recent article relating physically effective NDF (**peNDF**) to rumen-degraded starch percentages for useful application of the Penn State separator to optimize this ratio to at least 1.45:1 (Zebeli et al., 2010). Moreover, based on the previous discussion, I will stress that diets primarily composed of corn silage as the forage sources are more likely to cause milk fat depression. Zebeli et al. (2009) chopped corn silage (kernel processed) to three theoretical lengths of cut (approximately 0.55, 0.32, and 0.22 inches, respectively; Figure 1). Particle length was related quadratically ($P = 0.08$) to number of meals per day but linearly ($P = 0.09$) to the amount of feed consumed per meal. The diets were mixed as TMR and offered at 7:30 a.m. Interestingly, in the daytime, cows consumed more of the TMR, and the medium-sized silage had the highest number of meals (explaining the quadratic response). However, during the evening, there was no difference in meal numbers, but the cows fed the corn silage with the shortest particle length still consumed more feed per meal. Thus, the coarsest corn silage probably limited ($P < 0.05$) DMI from bulk fill (45.1 lb/day) compared with the other two treatments; those fed the medium silage increased DMI (48.0 lb/day) because, on average, they ate more meals, but those fed the short silage (48.4 lb/day) ate more feed per meal, primarily in the evening. As particle length of corn silage increased, cows linearly increased ($P < 0.01$) their preference for particles retained on the 1.18-mm screen as well as those

particles passing through that screen but recovered in the pan. In the study of Penner and Oba (2009), adding dry sucrose promoted selection for the particles recovered in the pan (presumably with a higher concentration of added dry sucrose), especially in the first week after calving. In contrast, in our study (Oelker et al., 2009), liquid molasses added to the corn silage-based diet increased measured particle size because small particles were conglomerated and therefore not recovered in the pan. Although these were individually fed cows, molasses seemed to reduce sorting behavior in corn silage diets but not in alfalfa hay diets; we attributed the latter response to adding water to the dry hay TMR immediately prior to mixing in liquid molasses (which would not coat the wet alfalfa hay particles). In contrast with their hypothesis (and the prevailing wisdom), a recent report suggested that water addition to haylage/corn silage diets actually increased sorting behavior (Miller-Cushon and DeVries, 2009). In our study, we anecdotally noted that water softened dry hay particles and consistently improved DMI, and I would suspect a similar response in field conditions, but it does not automatically follow that water will reduce sorting against long particles for all types of diets. When applied to the TMR, liquid feeds should reduce sorting for small particles and against long particles, decreasing slug feeding of grain and providing an additive benefit to the effect of sugars per se on the ruminal fermentation. Sugars in liquid feeds could allow the use of slightly coarser corn silage to help reduce milk fat depression with less risk of this response being partially negated by cows sorting, especially in group situations. Moreover, in addition to a more consistent intake of forages and grain from reduced sorting, sugars make diets more acceptable to dairy cows (Murphy et al., 1997). Even if nutrient demand by the mammary gland is driving total voluntary DMI, greater acceptability could be attracting cows back to the feedbunk more frequently and better spacing out the inter-meal frequency. More work is needed to verify this contention.

OSU Production Responses with Liquid Feeds

Firkins et al. (2008b) described data from individually fed Holstein cows for three lactation trials with different liquid feeds (Table 2). When liquid feed was added to diets containing 40% non-fiber carbohydrate (NFC), DMI and milk production were not affected. However, when NFC was reduced to 37%, milk fat yield increased ($P < 0.08$) and DMI tended to increase. When doubling the inclusion rate of liquid feed, DMI increased compared with control unless Rumensin was added. As in many other cases, Rumensin maintained milk fat yield with decreased DMI, and the combination did not depress milk fat secretion. Another trial in that publication showed that adding liquid feeds as the last ingredient of the TMR maintained DMI even when fat also was added, and the combination increased milk fat production.

We just analyzed another trial with liquid feeds replacing corn that was either finely ground or coarsely ground and compared those data to a control with steam-flaked corn (Table 3). In this trial, though, NFC was maintained at about 36% in diets with forage NDF maintained between 20 and 21%. Cows fed the steam-flaked corn diets had the lowest milk fat yield. Despite the higher butyrate and valerate molar percentages for liquid feeds, there apparently was not enough difference in particle size of ground corn for liquid feeds to interact for milk fat yield. Decreasing rumen degradable starch in the previous trial (Table 2) was associated with an increase in DMI and milk fat yield. In the current trial, grinding corn more finely increased the soluble dry matter but did not affect the rate of DM degradation of the potentially degradable pool (data not shown), and NDF digestibilities (51.8 to 56.8%) were not affected by treatment. Thus, these data support previous discussions that sugars do not increase the likelihood for milk fat depression, but our expectation to improve milk fat more with addition of liquid feed to coarsely ground corn than

to finely ground corn (a statistical interaction) was not realized. Perhaps the lack of change in DMI was associated with different dietary conditions in which DMI was not limited by a metabolic response or else non-nutritional benefits of liquid feeds were not realized under the conditions of the current trial.

Conclusions

Sugars at 2.5 to 5% offer potential benefits that should be considered when formulating dairy rations. Based on current information, I recommend keeping NFC $\leq 37\%$ in corn silage-based diets but perhaps $\leq 40\%$ in alfalfa-based diets; starch should be $< 25\%$ but perhaps 25 to 28%, respectively. When NFC and especially rumen-degraded starch are kept at these moderate concentrations, sugars are more likely to stimulate DMI, NDF digestibility, and milk fat production. Adding sugars to diets with Rumensin has no indication for adding to risk of milk fat depression. Moreover, particularly when in the form of liquid feeds applied to the TMR, sugars should help reduce sorting both against forage and for the fines. Ruminal and post-ruminal effects plus feedbunk management for group-fed cows apparently can aggregate for an overall potential benefit in milk production and efficiency.

References

- Allen, M.S., B.J. Bradford, and M. Oba. 2009. Board invited review: The hepatic oxidation theory of the control of feed intake and its application to ruminants. *J. Anim. Sci.* 87:3317-3334.
- Arroquy, J.I., R.C. Cochran, M. Villarreal, T.A. Wickersham, D.A. Llewellyn, E.C. Titgemeyer, T.G. Nagaraja, D.E. Johnson, and D. Gnad. 2004a. Effect of level of rumen degradable protein and type of supplemental non-fiber carbohydrate on intake and digestion of low-quality grass hay by beef cattle. *Anim. Feed Sci. Technol.* 115:83-99.

- Arroquy, J.I., R.C. Cochran, T.A. Wickersham, D.A. Llewellyn, E.C. Titgemeyer, T.G. Nagaraja, and D.E. Johnson. 2004b. Effects of type of supplemental carbohydrate and source of supplemental rumen degradable protein on low quality forage utilization by beef steers. *Anim. Feed Sci. Technol.* 115:247-263.
- Beauchemin, K.A., D. Colombatto, D.P. Morgavi, and W.Z. Yang. 2003. Use of exogenous fibrolytic enzymes to improve feed utilization by ruminants. *J. Anim. Sci.* 81(E. Suppl. 2):E37-E47.
- Broderick, G.A., N.D. Luchini, S.M. Reynal, G.A. Varga, and V.A. Ishler. 2008. Effect on production of replacing dietary starch with sucrose in lactating dairy cows. *J. Dairy Sci.* 91:4801-4810.
- Broderick, G.A., and W.J. Radloff. 2004. Effect of molasses supplementation on the production of lactating dairy cows fed diets based on alfalfa and corn silage. *J. Dairy Sci.* 87:2997-3009.
- Calsamiglia, S., M. Busquet, P.W. Cordozo, L. Castillejos, and A. Ferret. 2007. Invited Review: Essential oils as modifiers of rumen microbial fermentation. *J. Dairy Sci.* 90:2580-2595.
- Calsamiglia, S., P.W. Cardozo, A. Ferret, and A. Bach. 2008. Changes in rumen microbial fermentation are due to a combined effect of type of diet and pH. *J. Anim. Sci.* 86:702-711.
- Charbonneau, E., P.Y. Chouinard, G. Allard, H. Lapierre, and D. Pellerin. 2006. Milk from forage as affected by carbohydrate source and degradability with alfalfa silage-based diets. *J. Dairy Sci.* 89:283-293.
- Colombatto, D., and K.A. Beauchemin. 2009. A protease additive increases fermentation of alfalfa diets by mixed ruminal microorganisms in vitro. *J. Anim. Sci.* 87:1097-1105.
- DeFrain, J.M., A.R. Hippen, K.F. Kalscheur, and D.J. Schingoethe. 2006. Feeding lactose to increase ruminal butyrate and the metabolic status of transition dairy cows. *J. Dairy Sci.* 89:267-276.
- Edwards, J.E., S.A. Huws, E.J. Kim, and A.H. Kingston-Smith. 2007. Characterization of the dynamics of initial bacterial colonization of nonconserved forage in the bovine rumen. *FEMS Microbiol. Ecol.* 62:323-335.
- Firkins, J.L., M.L. Eastridge, N.R. St-Pierre, and S.M. Nofstger. 2001. Effects of grain variability and processing on starch utilization by lactating dairy cattle. *J. Anim. Sci.* 79(E. Suppl.):E218-E238.
- Firkins, J.L., A.N. Hristov, M.B. Hall, G.A. Varga, and N.R. St-Pierre. 2006. Integration of ruminal metabolism in dairy cattle. *J. Dairy Sci.* 89(E. Suppl.):E31-E51.
- Firkins, J.L., S.K.R. Karnati, and Z. Yu. 2008a. Linking rumen function to animal response by application of metagenomics techniques. *Aust. J. Exp. Agric.* 48:711-721.
- Firkins, J.L., B.S. Oldick, J. Pantoja, L.E. Gilligan, and L. Carver. 2008b. Efficacy of liquid feeds varying in concentration and composition of fat, non-protein nitrogen, and non-fiber carbohydrates for lactating dairy cows. *J. Dairy Sci.* 91:1969-1984.
- Firkins, J.L., Z. Yu, and M. Morrison. 2007. Ruminal nitrogen metabolism: Perspectives for integration of microbiology and nutrition for dairy. *J. Dairy Sci.* 90(E. Suppl.):E1-E16.
- Fuentes, M.C., S. Calsamiglia, P.W. Cardozo, and B. Vlaemink. 2009. Effect of pH and level of concentrate in the diet on the production of biohydrogenation intermediates in a dual-flow continuous culture. *J. Dairy Sci.* 92:4456-4466.

- Gencoglu, H., R.D. Shaver, W. Steinberg, J. Ensink, L.F. Ferraretto, S.J. Bertics, J.C. Lopes, and M.S. Akins. 2010. Effect of feeding a reeduced-starch diet with or without amylase addition on lactation performance in dairy cows. *J. Dairy Sci.* 93:723-732.
- Griswold, K.E., G.A. Apgar, J. Bouton, and J.L. Firkins. 2003. Effects of urea infusion and ruminal degradable protein concentration on microbial growth, digestibility, and fermentation in continuous culture. *J. Anim. Sci.* 81:329-336.
- Guan, L.L., J.D. Nkrumah, J.A. Basarab, and S.S. Moore. 2008. Linkage of microbial ecology to phenotype: correlation of rumen microbial ecology to cattle's feed efficiency. *FEMS Microbiol. Lett.* 288:85-91.
- 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.
- Jenkins, T.C., R.J. Wallace, P.J. Moate, and E.E. Mosley. 2008. Board-Invited Review: Recent advances in biohydrogenation of unsaturated fatty acids within the rumen microbial ecosystem. *J. Anim. Sci.* 86:397-412.
- Khafipour, E., S. Li, J.C. Plaizier, and D.O. Krause. 2009. Rumen microbiome composition determined using two nutritional models of subacute ruminal acidosis. *Appl. Environ. Microbiol.* 75:7115-7124.
- Kingerman, C.M., W. Hu, E.E. McDonell, M.C. DerBedrosian, and L. Kung, Jr. 2009. An evaluation of exogenous enzymes with amylolytic activity for dairy cows. *J. Dairy Sci.* 92:1050-1059.
- Kristensen, N.B. 2005. Splanchnic metabolism of volatile fatty acids in the dairy cow. *Anim. Sci.* 80:3-10.
- Lesmosquet, S., G. Raggio, G.E. Lobley, H. Rulquin, J. Guinard-Flament, and H. Lapierre. 2009. Whole-body glucose metabolism and mammary energetic nutrient metabolism in lactating dairy cows receiving digestive infusions of casein and propionic acid. *J. Dairy Sci.* 92:6068-6082.
- Miller-Cushon, E.K., and T.J. DeVries. 2009. Effect of dietary dry matter concentration on the sorting behavior of lactating dairy cows fed a total mixed ration. *J. Dairy Sci.* 92:3292-3298.
- Mouriño, F., R. Akkarawongsa, and P.J. Weimer. 2001. Initial pH as a determinant of cellulose digestion rate by mixed ruminal microorganisms in vitro. *J. Dairy Sci.* 84:848-859.
- Murphy, M.R., A.W.P. Geijssels, E.C. Hall, and R.D. Shanks. 1997. Dietary variety via sweetening and voluntary feed intake by lactating dairy cows. *J. Dairy Sci.* 80:894-897.
- Nagaraja, T.G., and E.C. Titgemeyer. 2007. Ruminal acidosis in beef cattle: The current microbiological and nutritional outlook. *J. Dairy Sci.* 90(E. Suppl.):E17-E38.
- Nousiainen, J., M. Rinne, and P. Huhtanen. 2009. A meta-analysis of feed digestion in dairy cows. 1. The effects of forage and concentrate factors on total diet digestibility. *J. Dairy Sci.* 92:5019-5030.
- Oelker, E.R., C. Reveneau, and J.L. Firkins. 2009. Interaction of molasses and monensin in alfalfa hay- or corn silage-based diets on rumen fermentation, total tract digestibility, and milk production by Holstein cows. *J. Dairy Sci.* 92:270-285.
- Oldick, B.S., J.L. Firkins, and N.R. St-Pierre. 1999. Estimation of microbial nitrogen flow to the duodenum of cattle based on dry matter intake and diet composition. *J. Dairy Sci.* 82:1497-1511.

- Palmonari, A., D.M. Stevenson, D.R. Mertens, C.W. Cruywagen, and P.J. Weimer. 2010. pH dynamics and bacterial community composition in the rumen of lactating dairy cows. *J. Dairy Sci.* 93:279-287.
- Palmquist, D.L., C.L. Davis, R.E. Brown, and D.S. Sachan. 1969. Availability and metabolism of various substrates in ruminants. V. Entry rate into the body and incorporation into milk fat of D(-)-b-hydroxybutyrate. *J. Dairy Sci.*-633.
- Penner, G.B., J.R. Aschenbach, G. Gäbel, R. Rackwitz, and M. Oba. 2009. Epithelial capacity for apical uptake of short chain fatty acids is a key determinant for intraruminal pH and the susceptibility to subacute ruminal acidosis in sheep. *J. Nutr.* 139:1714-1720.
- Penner, G. B., and M. Oba. 2009. Increasing dietary sugar concentration may improve dry matter intake, ruminal fermentation, and productivity of dairy cows in the postpartum phase of the transition period. *J. Dairy Sci.* 92:3341-3353.
- 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.
- Ribeiro, C.V.D. M., S.K.R. Karnati, and M.L. Eastridge. 2005. Biohydrogenation of fatty acids and digestibility of fresh alfalfa or alfalfa hay plus sucrose in continuous culture. *J. Dairy Sci.* 88:4007-4017.
- Rychlik, J.L., R. LaVera, and J.B. Russell. 2002. Amino acid deamination by ruminal *Megasphaera elsdenii* strains. *Curr. Microbiol.* 45:340-345.
- Rychlik, J.L., and J.B. Russell. 2000. Mathematical estimations of hyper-ammonia producing ruminal bacteria and evidence for bacterial antagonism that decreases ruminal ammonia production. *FEMS Microbiol. Ecol.* 32:121-128.
- Walker, N.D., C.J. Newbold, and R.J. Wallace. 2005. Nitrogen metabolism in the rumen. Pages 71-115 in *Nitrogen and Phosphorus Nutrition of Cattle*. E. Pfeffer and A. Hristov, eds. CABI Publishing, Cambridge, MA.
- Wallace, R.J. 2008. Gut microbiology - broad genetic diversity, yet specific metabolic niches. *Animal* 2:661-668.
- Weimer, P.J., D.M. Stevenson, and D.R. Mertens. 2010. Shifts in bacterial community composition in the rumen of lactating dairy cows under milk fat-depressing conditions. *J. Dairy Sci.* 93:265-278.
- Weiss, W.P., N.R. St-Pierre, and L.B. Willett. 2009. Varying type of forage, concentration of metabolizable protein, and source of carbohydrate affects nutrient digestibility and production by dairy cows. *J. Dairy Sci.* 92:5595-5606.
- Welkie, D.G., D.M. Stevenson, and P.J. Weimer. 2010. ARISA analysis of ruminal bacterial community dynamics in lactating dairy cows during a feeding cycle. *Anaerobe Ahead of print*.
- Wu, Z., and J.T. Huber. 1994. Relationship between dietary fat supplementation and milk protein concentration in lactating cows: A review. *Livest. Prod. Sci.* 39:141-155.
- Zebeli, Q., B.N. Ametaj, B. Junck, and W. Drochner. 2009. Maize silage particle length modulates feeding patterns and milk composition in loose-housed lactating Holstein cows. *Livest. Sci.* 124:33-40.
- Zebeli, Q., D. Mansmann, H. Steingass, and B.N. Ametaj. 2010. Balancing diets for physically effective fibre and ruminally degradable starch: A key to lower the risk of sub-acute rumen acidosis and improve productivity of dairy cattle. *Livest. Sci.* 127:1-10.

Table 1. Effects of decreasing starch concentration with or without amylase on animal performance and total tract digestibilities.¹

	Starch, %			SE
	27	22	21	
DMI, lb/day	58.7 ^b	64.0 ^a	57.0 ^b	1.5
Milk, lb/day	110	112	111	2
Milk fat, lb/day	3.34 ^b	3.70 ^a	3.59 ^{ab}	0.09
Milk protein, lb/day	3.34	3.34	3.39	0.09
Starch digestibility, %	94.9 ^b	97.2 ^a	97.6 ^a	0.3
NDF digestibility, %	39.4 ^c	54.1 ^b	57.8 ^a	1.3
Protein digestibility, %	64.9 ^c	68.8 ^b	73.0 ^a	1.0

¹Data are from Gencoglu et al. (2010).

^{a,b,c}Means in the same row lacking a common superscript differ ($P \leq 0.05$).

Table 2. Lactation performance by dairy cattle fed diets containing different concentrations of nonstructural carbohydrates without or with Rumensin[®].¹

Item	40% NFC		37% NFC			SE	P
	Control	3.25% LF	3.25% LF	6.5% LF	6.5% LF+R		
DMI, lb/day	52.6 ^b	52.6 ^b	55.4 ^{ab}	57.0 ^a	53.9 ^b	1.5	0.08
Milk, lb/day	87.3	87.8	91.5	89.5	88.7	2.0	NS
Milk protein, %	2.93 ^a	2.82 ^b	2.85 ^b	2.85 ^b	2.83 ^b	0.02	0.01
Milk protein, lb/day	2.55	2.49	2.60	2.55	2.51	0.07	NS
MUN, mg/dL	12.3 ^{bc}	11.8 ^c	12.8 ^b	13.8 ^a	13.5 ^a	0.5	0.08
Milk fat, %	3.31	3.42	3.34	3.29	3.31	0.07	NS
Milk fat, lb/day	2.88 ^b	2.82 ^b	3.06 ^a	2.93 ^b	2.90 ^b	0.07	0.08
BW change, lb/day	1.12	0.62	0.73	1.28	1.01	0.20	0.13
BCS	2.88	2.74	2.95	2.87	2.76	0.07	NS

¹NFC = nonfiber carbohydrates, LF = liquid feed (Quality Liquid Feeds, Dodgeville, WI), R = Rumensin[®] (11 g/ton; Elanco Animal Health, Greenfield, IN), DMI = dry matter intake, MUN = milk urea nitrogen, BW = body weight, and BCS = body condition score. Data are from Firkins et al. (2008).

^{a,b,c}Means in the same row lacking a common superscript differ according to the P -value shown if $P \leq 0.10$.

NS = not significant ($P > 0.20$).

Table 3. Fermentation and lactation performance by cows fed different sources of grain without or with liquid feed.¹

	SFC	-LF		+LF		SFC vs. Rest		-LF vs. +LF		FGC vs. CGC		Interaction
		FGC	CGC	FGC	CGC	Rest	SE	Rest	SE	Rest	SE	
Digestion Trial												
NH ₃ , mg/dL	9.3	10.2	12.3	11.2	11.5	1.7	<0.01	NS	0.04	0.04	0.14	
Mean pH	6.03	6.04	6.20	5.94	6.12	0.11	NS	NS	0.03	0.03	NS	
Total VFA, mM	145	145	140	150	143	5	NS	NS	NS	NS	NS	
Ac:Pr	3.17	3.24	3.46	3.34	3.42	0.18	0.05	NS	0.09	0.09	NS	
Butyrate, mol%	10.9	10.4	11.0	11.7	11.2	0.2	NS	<0.01	NS	NS	<0.01	
Valerate, mol%	1.40	1.33	1.34	1.42	1.38	0.04	NS	0.02	NS	NS	NS	
BCVFA	1.98	1.89	2.02	1.89	2.00	0.20	NS	NS	0.10	0.10	NS	
Production Trial												
DMI, lb/day	57.8	55.7	56.8	57.5	56.1	1.2	NS	NS	NS	NS	NS	
Milk, lb/day	85.1	88.2	85.6	89.9	88.4	1.8	0.14	NS	NS	NS	NS	
MUN, mg/dL	12.0	13.3	12.9	12.9	13.2	0.5	0.04	NS	NS	NS	NS	
Milk protein, %/day	2.90	2.90	2.90	2.81	2.80	0.04	NS	<0.01	NS	NS	NS	
Milk protein, lb/day	2.54	2.58	2.53	2.50	2.54	0.04	NS	NS	NS	NS	NS	
Milk fat, %	3.22	3.61	3.45	3.40	3.38	0.11	0.06	NS	NS	NS	NS	
Milk fat, lb/day	2.84	3.19	3.04	3.01	3.08	0.11	0.01	NS	NS	NS	NS	

¹SFC = steam-flaked corn, FGC = fine-ground dry shelled corn (mean particle size = 0.8 mm), CGC = coarse ground dry shelled corn (mean particle size = 1.9 mm), and LF = liquid feed (3.5% of DM; Quality Liquid Feeds, Dodgeville, WI), VFA = volatile fatty acid, Ac:Pr = acetate:propionate, and BCVFA = branched chain VFA.

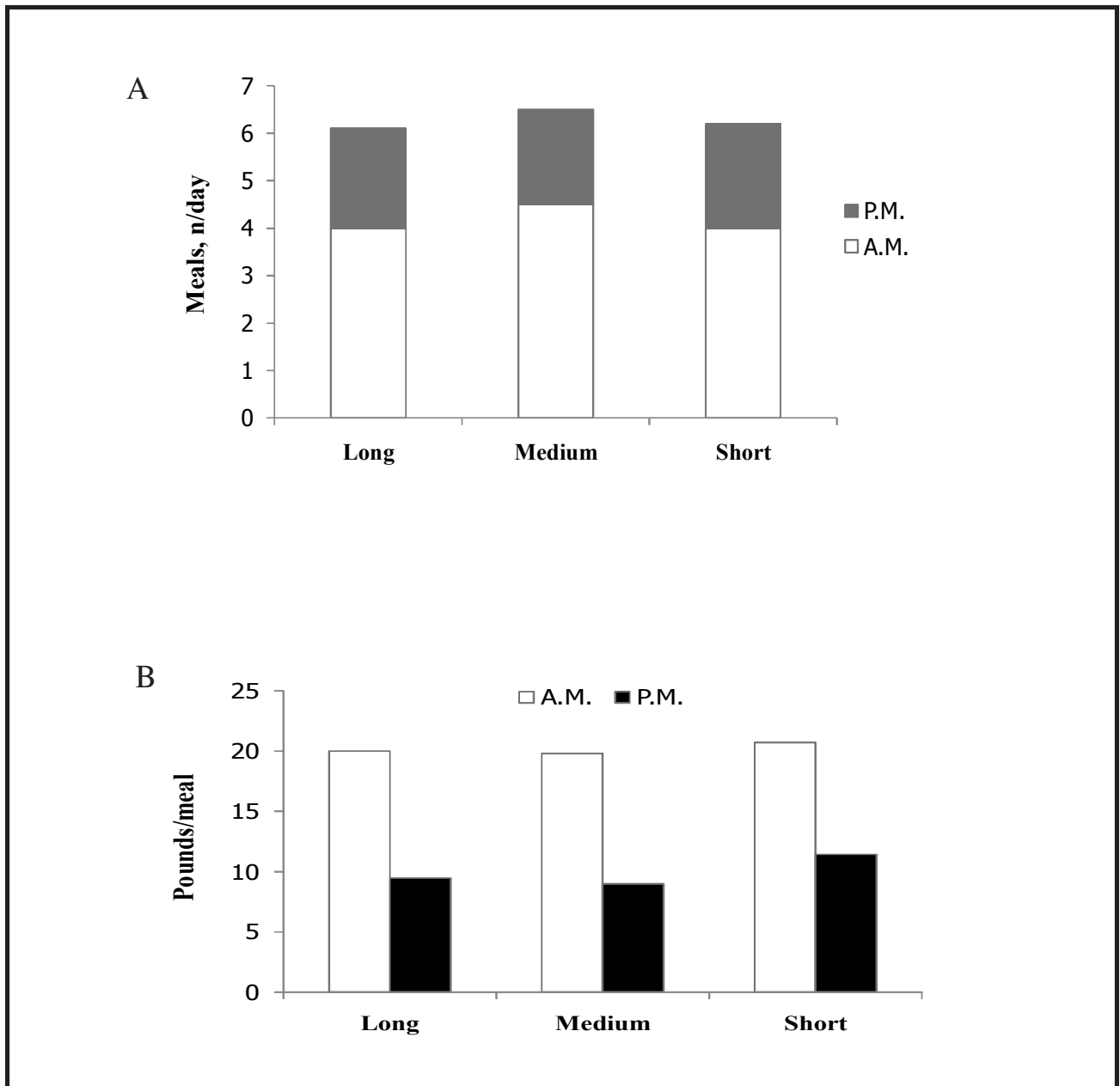


Figure 1. Chopping length of kernel-processed corn silage influences the eating behavior of dairy cows fed TMR containing 40% corn silage, 10% grass hay, and 50% concentrate. Panel a: the number of meals were quadratically related to particle length during the day (A.M., $P < 0.05$) and cumulative responses (A.M. + P.M., $P < 0.08$). Panel b: the as fed amount of feed consumed per meal was linearly ($P < 0.05$) and quadratically ($P < 0.08$) affected by particle length in the evening (P.M.) and linearly ($P < 0.09$) when the A.M. plus P.M. meals were averaged (not shown). Data are from Zebeli et al. (2009).