OPTIMAL USE OF SUGAR IN DIETS FOR DAIRY CATTLE

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There are many different sources of dietary sugar for use in rations for dairy cattle. Common ingredients used to increase the dietary sugar concentration in North America include molasses-based products (beet or cane molasses and beet pulp), citrus products, or byproducts from cheese processing such as whey permeate. While these ingredients contain different types of monosaccharides and disaccharides, current dietary recommendations only pertain to total dietary sugar and total non-structural carbohydrate (**NSC**) concentrations and common analysis do not differentiate sugar type. This paper will review the potential of dietary sugar to modulate dry matter intake, ruminal fermentation and production outcomes for lactating dairy cattle, and will investigate whether identification of disaccharides should be included rather than a single classification system for sugar.

Characterizing Sugar in Diets for Dairy Cattle

Characterization of feed components has greatly improved including the understanding of carbohydrate fractions. Under conventional analytical approaches carbohydrates can be classified as neutral detergent insoluble (neutral detergent fiber) and neutral detergent soluble fractions. The neutral detergent soluble fraction has been of interest as it contains organic acids, simple sugars and disaccharides, oligosaccharides, starch, pectins, and soluble fibre (Hall, 1999; Lanzas et al., 2007). Obviously, the neutral detergent soluble fraction is diverse and the resulting fermentation rates within the rumen for this fraction also differ markedly. For example, according to the Cornell Net Carbohydrate System starch from corn and barley are degraded at 12 and 30%/h, respectively. This compares to rates for hydrolysis for sucrose and lactose of 1311 and 331%/h, respectively and fermentation of glucose and fructose of 521 and 530%/h and that of galactose estimated at 439%/h (Weisbjerg et al. 1998). Thus, it could be expected that the potential for short-chain fatty acid (**SCFA**) production (an hence energy supply) and acidification of the rumen digesta would also differ not only among starch and sugar sources but also between different disaccharides.

Given the rapid rates of hydrolysis and fermentation of disaccharides and monosaccharides, respectively, there is no doubt that increasing the sugar content without a concomitant reduction in starch will result in reduced ruminal pH. In fact, simple sugars such as glucose (Krehbiel et al., 1995; Penner et al., 2009a; Oba et al., 2014) and oligosaccharides (Gressley et al., 2011) have been used to induce ruminal acidosis. That said, a common inclusion strategy for sugar inclusion in diets is through the replacement of dietary starch such that the total dietary NSC does not change. Under such a dietary scenario, sugar inclusion can result in numerous benefits.

Effects of dietary sugar on DMI

Sugar is a palatable component within diets for dairy cattle. Early work had suggested that inclusion of sugar may be one strategy to improve DMI and could represent an opportunity for cows in early lactation (Nombekela et al., 1994; Nombekela and Murphy, 1995). The suggestion for potential to improve DMI in early lactation was supported by Penner and Oba (2009) where cows fed a diet containing 8.7% ethanol soluble carbohydrates (using sucrose) consumed nearly 1 kg/d more during the first 4 wk of lactation than cows not provided with supplemental dietary sugar. It is important to note that sugar was included in the diet in that study as a partial replacement for dietary starch. Broderick and Radloff (2004) evaluated the inclusion rate of dried molasses and reported that as dietary sugar concentration increased from 2.6 to 7.2%, DMI increased linearly. In the same manuscript, the authors also evaluated liquid molasses inclusion and reported a cubic response for DMI where a cows fed a dietary concentration of 4.9% (DM basis) sugar had greatest DMI. DeFrain et al. (2004) reported a tendency (P = 0.09) for a linear increase in DMI (1.6 kg increase) as lactose inclusion increased from showed that DMI tended to increase linearly as lactose increased from 5 to 13% in the diet on a DM basis. In contrast, numerous studies have reported no effect of sugar on DMI (Nobekela and Murphy, 1995; Ordway et al., 2002; DeFrain et al., 2006; Penner et al., 2009; Chibisa et al., 2015) reported no effect of sucrose on DMI. It is not clear why sugar inclusion does not consistently improve DMI, but it should be noted that sugar inclusion not appear that sugar inclusion would reduce DMI as summarized in Figure 1.

Effect of sugar inclusion on ruminal fermentation

A common response observed with the inclusion of lactose into diets for ruminants is an increase in the concentration of butyrate in ruminal fluid (DeFrain et al., 2004; Chibisa et al., 2015); however, sucrose does not seem to elicit the same response (Broderick and Radloff, 2004; Vallimont et al., 2004; Penner et al., 2009) except under a challenge model (Oba et al., 2015). The differential response may suggest that pathways of fermentation also differ. Interestingly, when cows were provided with the lactose, sucrose, or corn starch with a dose that would balance the quantity of hexose provided, sucrose increased the short-chain fatty acid (**SCFA**) concentration in the rumen to a greater extent than lactose and corn starch. The differential response between sucrose and lactose suggests that perhaps dietary evaluation and predictive models should consider the type of sugar in addition to the total sugar concentration.

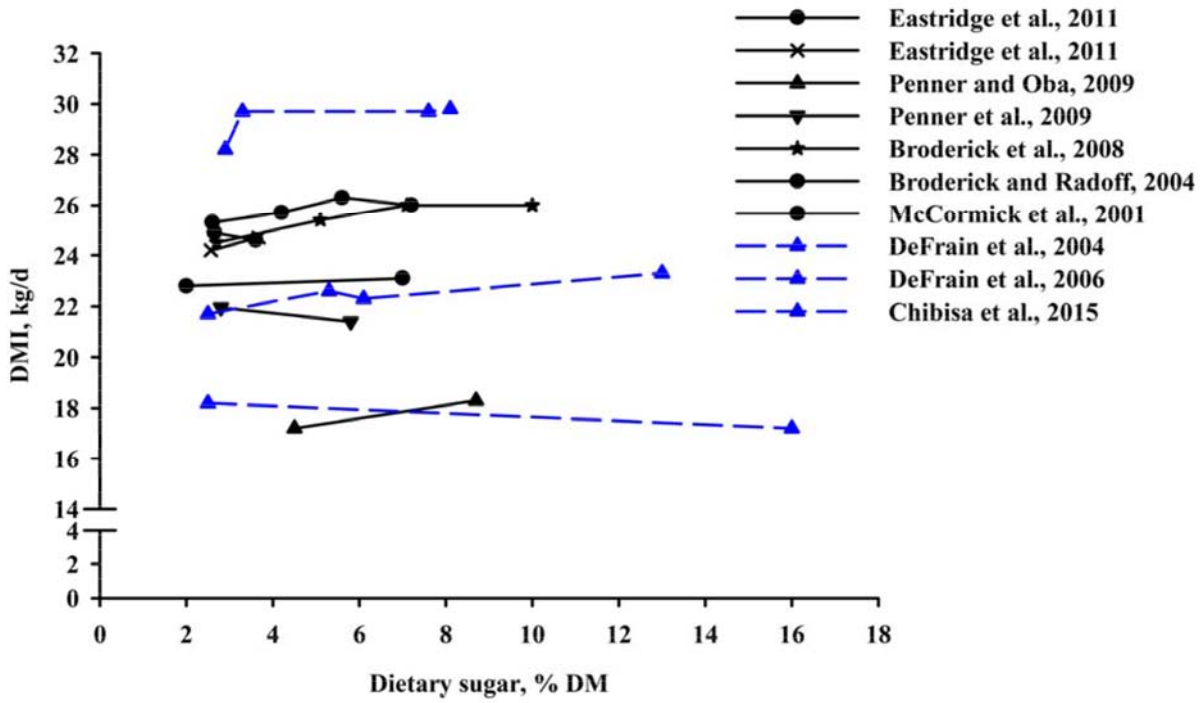

Figure 1. Relationship between dietary sugar concentration and DMI. Data compiled from treatment means from 9 separate studies. Solid lines indicate treatments with sucrose as the primary sugar source and dashed lines indicate treatments with lactose as the primary sugar source.

Although under challenge models it is clear that sugar can be used to reduce ruminal pH (Oba et al., 2015), use of sugar as a partial replacement for starch does not reduce ruminal pH (Chibisa et al., 2015). Past in vitro studies evaluating sugar inclusion in vitro have noted either no effect of sugar on pH of the incubation media (McCormick et al., 2001) or a tendency for increased pH for high sugar compared to low sugar incubations (Vallimont et al., 2004). Supporting the in vitro results, Broderick and Radloff, (2004), Penner et al. (2009), Penner and Oba (2009), and Chibisa et al. (2015) all reported that sugar inclusion did not decrease ruminal pH or tended to increase pH (Figure 2). The mechanisms for why sugar does not depress ruminal pH are not fully understood. However, the finding that pH is not affected in vitro (McCormick et al., 2001; Vallimont et al., 2004) and that pH is not reduced or may be improved in vivo suggests that the underlying mechanisms are likely related to microbial utilization of sugar.

Regarding microbial utilization, it has been shown that sugar inclusion increases the lag time and increased incorporation of C into microbial contents (Hall and Weimer, 2011). While it was suggested that this C incorporation was likely attributed to amino acid synthesis, it is now accepted that microbes, primarily protozoa, will accumulate reserve carbohydrates (Hackmann and Firkins, 2015). In particular, isotrichid protozoa are efficient at converting glucose to glycogen (Hall, 2011). Hall (2011) evaluated glycogen accumulation in response to sugar when incubations were performed under

faunated and defaunated conditions. That study demonstrated that total microbial glycogen accumulation increased with sugar and that protozoal glycogen accumulation represented 51% of the total glycogen recovered. Interestingly, glycogen did not accumulate in protozoa during the defauntated incubation supporting the model and total microbial glycogen accumulation was reduced by nearly 45% relative to the faunated incubations. The accumulation of carbon into microbial reserve carbohydrates could help explain why ruminal pH is not reduced when sugar replaces starch as the total amount of rapidly fermentable carbohydrate that is fermented would be reduced. The storage of carbohydrates by the rumen microbes rather than immediate fermentation may also explain why ruminal ammonia concentrations often increase or are at least not reduced with addition of sugar into diets (Penner et al., 2009; Oba, 2011; Oba et al., 2015). It could be expected that glycogen deposition by ruminal microbes may also diminish some of the potential productivity benefits arising with the inclusion of dietary sugar into diets for dairy cattle and may support microbial maintenance functions.

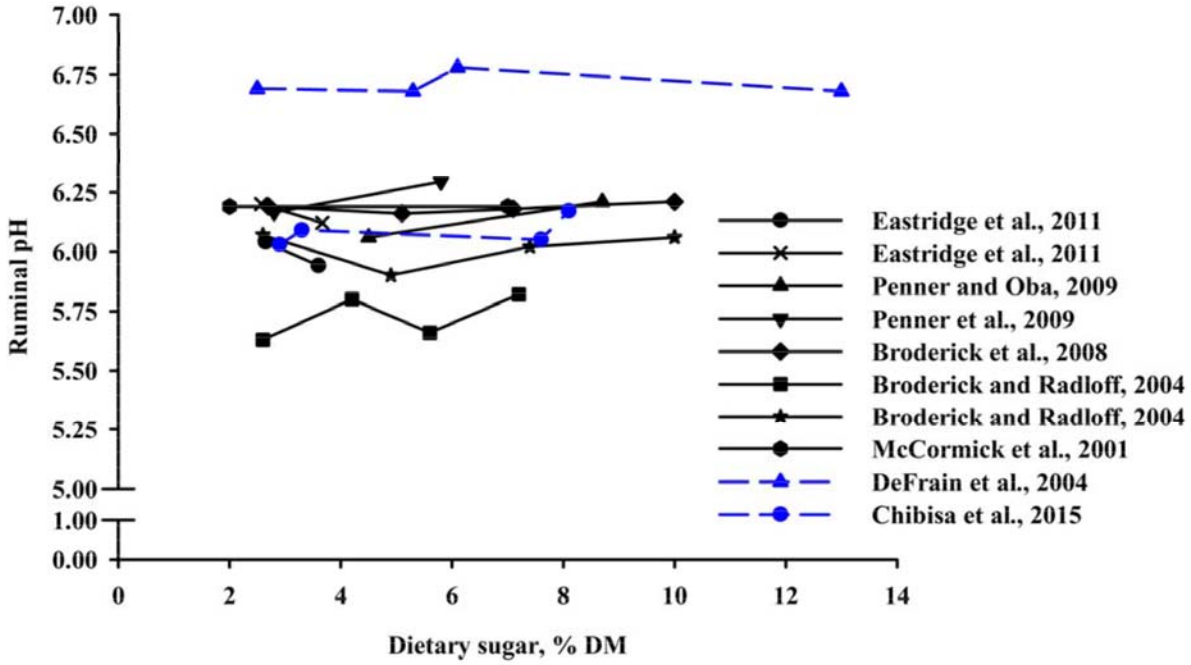

Figure 2. Relationship between dietary sugar concentration and ruminal pH. Data compiled from treatment means from 9 separate studies. Solid lines indicate treatments with sucrose as the primary sugar source and dashed lines indicate treatments with lactose as the primary sugar source.

While the ruminal pH response associated with dietary sugar inclusion is consistent between in vitro and in vivo studies, recent studies have indicated that presence of sugars in the diet may up regulate sugar transport (Moran et al., 2014). Another possible reason or the positive effect of sugar on rumen pH may be related to SCFA transport across the rumen epithelium. The mechanisms involved in SCFA

transport across the rumen epithelium have been described by Aschenbach et al. (2011) and primarily include passive diffusion, $SCFA^-$/ HCO_3^-exchange. Passive diffusion of SCFA may not result in complete proton removal from the rumen as a significant proportion of the protons can be recycled back into the rumen contents through the action of Na^+/H^+ exchangers. In contrast, absorption of SCFA via the $SCFA/HCO3^-$ exchange will result in the neutralization of a proton as $HCO3^-$ reacts with H^+ in the carbonic anhydrase reaction. In a study at the University of Saskatchewan, 4 cows were used in a Latin square design comparing low (2.6%) vs. high (8%) sugar diets (lactose as a sugar source) when the basal concentrate was corn or barley. While DMI did not differ averaging 29.5 kg/d, cows fed the high sugar diet had a greater reliance on $SCFA^-$/ $HCO3^-$ exchange than cows fed the low sugar diets. This suggests that sugar may not only affect the rumen microbial community and function but may also affect epithelial function.

A second study was conducted at the University of Saskatchewan to further evaluation the effect of sugar inclusion and sugar type on ruminal epithelial function (Penner et al., unpublished). A total of 18 lambs were fed a diet that contained no added sugar (2.6% sugar) or diets where either dried whey permeate or dried molasses were used to increase dietary sugar to 6%. As with previous work, sugar inclusion and sugar type did not affect ruminal pH and ruminal SCFA concentrations were not affected. Despite these findings, serum BHBA was greater for lambs fed lactose than sucrose and the total flux of acetate was reduced for lambs fed sugar compared to the control. However, total propionate flux tended to be greater for lambs fed lactose than those fed sucrose and the reliance on bicarbonate-dependent transport of SCFA was greater for lactose than sucrose for propionate (P = 0.043) and tended to be greater (P 0.10) for butyrate. While not commonly investigated, this study also showed that glucose uptake by the ruminal epithelium was twice as great for lambs fed diets with added sugar than the control and the SGLT-1 dependent portion of glucose uptake also tended to increase (P = 0.09). This supports work evaluating the inclusion of artificial sweeteners on glucose uptake by the intestinal epithelium (Moran et al., 2014). However, the quantitative importance of glucose uptake by the ruminal epithelium is not known.

Effect of dietary sugar on milk yield and composition

As with the effects of sugar on DMI, the results of dietary sugar inclusion on milk yield and milk composition are mixed (Figure 3). For example, Broderick and Radloff (2004) reported a cubic response for milk yield with increasing dry molasses inclusion resulting in dietary sugar values ranging between 2.6 and 7.2%, and with liquid molasses inclusion resulting in dietary sugar concentrations ranging between 2.6 to 10%. That work suggested that the optimal sugar concentration to induce both positive effects on DMI and milk yield was 5.9%. However, that study also noted that as dietary sugar concentration increased, there was a linear decrease in FCM. Most other studies have reported no effect of dietary sugar on milk yield or milk composition (DeFrain et al., 2006; Broderick et al., 2008; Penner and Oba, 2009; Penner et al., 2009; Chibisa et al., 2015). Collectively, it appears that sugar inclusion does not result in improved milk yield

or altered milk composition.

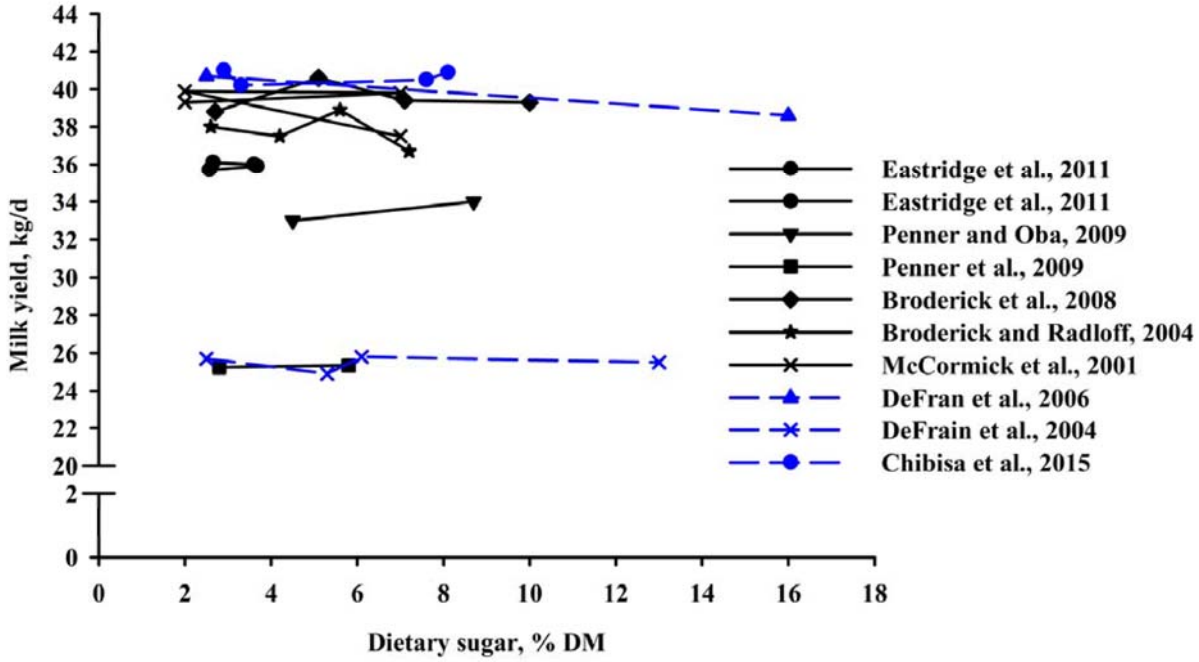

Figure 3. Relationship between dietary sugar concentration and milk yield. Data compiled from treatment means from 9 separate studies. Solid lines indicate treatments with sucrose as the primary sugar source and dashed lines indicate treatments with lactose as the primary sugar source.

CONCLUSION

Although there are studies that show a positive response of increasing dietary sugar, overall it does not appear that dietary sugar affects DMI, milk yield, or milk composition. Interestingly, inclusion of sugar as a partial replacement for starch does not negatively affect ruminal pH which is likely related to an increase lag time in the rapidly fermentable carbohydrate, increased glycogen accumulation by mixed microbes, and increased bicarbonate- dependent SCFA transport and potentially increased glucose uptake. Benefits of including sugar in diets for lactating cows may be limited to situations where sugar inclusion is cost-competitive on a hexose unit basis with starch.

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