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Symposium review: Effects of carbohydrate digestion on feed intake and fuel supply*

M. Oba[1]† and K. Kammes-Main[2]
[1]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5
[2]Department of Animal Science, Michigan State University, East Lansing 48824

ABSTRACT

Carbohydrates are the primary energy source for lactating dairy cows, and dairy diets are usually formulated for certain concentrations of forage neutral detergent fiber (NDF) and starch due to their direct effects on dry matter intake and milk production. Forage NDF exerts greater filling effects in the rumen than other dietary components and can limit maximum voluntary feed intake of lactating dairy cows. Since an analytical method for NDF was developed more than a half century ago, it has been used widely to characterize forages and diets for dairy cows. However, because NDF is a chemical measurement varying in its digestibility, in vitro digestibility measurements were developed as a biological approach to assess forage quality. Research efforts over the last several decades led to the development of forage cultivars or hybrids with enhanced in vitro NDF digestibility, such as brown midrib, and management practices considering differences in NDF digestibility of forages. In addition, in vitro NDF digestibility and undigested NDF are commonly measured in commercial labs, and estimated rates of digestion are used in dynamic models in an effort to improve the accuracy and precision of diet formulation. Starch digestion in the rumen also varies among starch sources, being affected by grain type, extent of processing, and conservation method. The site and rate of starch digestion affect dry matter intake and nutrient partitioning in dairy cows by modifying temporal supply of fuel. In addition, dietary starch content and its fermentability can affect digestion rates of starch itself and NDF in the rumen. Previous research has increased our understanding of dietary carbohydrates, but its application for diet formulations requires integrated approaches accounting for factors affecting the filling effects of forage NDF, starch digestion, and temporal fuel supply.
Key words: DMI, forage NDF, starch, sugar

INTRODUCTION

Carbohydrates are approximately 70% of diets fed to lactating dairy cows and serve as the primary source of energy. The Dairy NASEM (2021) separated carbohydrates into the following 4 fractions based on the difference in digestibility: NDF, starch, neutral detergent soluble fiber, and water-soluble carbohydrates. Starch and NDF were relatively lower in digestibility among them, and the rate of digestion is greatly variable depending on their sources, affecting feed intake, fuel supply, and fuel utilization (NASEM, 2021). Forages are more filling in the rumen than concentrates, and filling effects of forages are related to their NDF content (Van Soest, 1965). Neutral detergent fiber has been used more than 50 years as a quality parameter of forages and diets fed to dairy cows, and dietary NDF content is also used as an independent variable to predict DMI of dairy cows (Mertens, 1987). However, forage NDF greatly varies in its digestion characteristics and NDF alone, as a chemical measurement, is not sufficient to predict DMI responses of lactating dairy cows (Allen, 2000). Starch digestibility is affected by grain type, endosperm type, processing method, and conservation method, and the extent of starch digestion in the rumen can affect DMI (Allen, 2000). The objective of this paper is to review factors affecting filling effects of forage NDF and starch digestibility of grain, and to discuss effects of carbohydrate digestion on feed intake and fuel supply.

FILLING EFFECTS OF FORAGE NDF

Digesta is selectively retained in the rumen depending on its particle size. In early work using sheep or cattle (Evans et al., 1973; Poppi et al., 1980, 1981), the fraction of particles retained on the 1.18-mm sieve was

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†Corresponding author: moba@ualberta.ca

proposed as the critical particle size to be selectively retained in the rumen. Maulfair et al. (2011) reported that diet particle size affects rumen digesta particle size for particles retained on ≥3.35-mm sieves, but not for <3.35-mm sieves, and suggested that the critical particle size to be retained in the rumen is likely greater than the particles retained on the 1.18-mm sieve. In high-producing dairy cows, the fraction retained on the 2.36-mm sieve was selected as the threshold for passage based on sieving analysis of duodenal digesta (Voelker Linton and Allen, 2007; Kammes and Allen, 2012b). Another factor affecting retention of rumen digesta is its location relative to the reticulo-omasal orifice. Voelker Linton and Allen (2007) fed diets with corn silage as the primary forage and showed that the rate of passage is much slower for potential digestible NDF (**pdNDF**) compared with indigestible NDF (**iNDF**), and attributed it to the difference in buoyancy. Digestible NDF is associated with fermentation gas, and more buoyant in the rumen and lower in specific gravity, which makes it form the fiber mat in the rumen and away from the reticulo-omasal orifice. Kammes and Allen (2012b) suggested that entrapment by the fiber mat can slow down digesta passage regardless of potential difference in buoyancy or specific gravity for cows fed alfalfa silage or grass silage. As such, particle size reduction does not necessarily mean its passage out of the rumen, but it is considered as a prerequisite to ruminal passage. It is important to understand factors affecting particle size of ruminal digesta as they are related to filling effects of forage NDF.

Particle Size of Forages

Effects of forage particle size on DMI are not consistent; for example, some reported that cows fed forages with short particles increased DMI (Mooney and Allen, 1997; Kononoff and Heinrichs, 2003; Haselmann et al., 2019), whereas others reported no effects of forage particle size (Krause et al., 2002; Beauchemin et al., 2003) or the opposite effects (Krause and Combs, 2003). The inconsistent effects are partly attributed to mastication activity during eating. Schadt et al. (2012) fed hay components that were retained on each screen of the Penn State Particle Separator, and measured particle size of swallowed digesta. They reported mean particle size of the swallowed digesta was similar at 8.1 to 10.8 mm regardless of initial particle size (Schadt et al., 2012), indicating that the differences in forage particle size is substantially reduced by mastication during eating. If the swallowed digesta becomes similar in particle size regardless of the initial differences in the diet, it may not affect digestion kinetics in the rumen. Digestion rate of pdNDF and passage rate of iNDF or pdNDF were not affected by particle size of dietary forage for cows fed alfalfa silage (Kammes et al., 2012) or grass silage (Kammes and Allen, 2012c).

Another possible reason accounting for the inconsistent animal responses in DMI to forage particle size is whether rumen fill is the dominant factor in regulation of DMI. Dado and Allen (1995) showed that rumen fill affected DMI for cows fed a high NDF diet, but not for cows fed a low NDF diet. Beauchemin et al. (1994) reported a significant interaction between dietary forage allocation and forage particle size on DMI, in which greater forage particle size decreased DMI only for cows fed a 65% forage diet, but not for a 35% forage diet. Particle size of forages may not exert consistent effects on particle size of ruminal digesta, filling effects of forage NDF, or DMI.

In Vitro NDF Digestibility

Forages with enhanced in vitro NDF digestibility can increase DMI of lactating dairy cows. Oba and Allen (1999a, 2000) showed that feeding brown midrib corn silage, which is higher in in vitro NDF digestibility than control corn silage, increased DMI of lactating dairy cows. Some recent studies consistently reported positive effects of in vitro NDF digestibility of forages on DMI for cows fed alfalfa hay (Fustini et al., 2017) or corn silage (Miller et al., 2020; Miller et al., 2021). A meta-regression of treatment means from the literature showed a positive relationship between DMI and in vitro NDF digestibility within forage family (i.e., grass or legume; Oba and Allen, 1999b). However, DMI and in vitro NDF digestibility were related negatively across forage family (Oba and Allen, 1999b). Similarly, a recent meta-analysis by Johansen et al. (2018) showed that feeding legumes increased both DMI and milk yield compared with grasses. These findings indicate that in vitro NDF digestibility may be a good indicator of filling effects for comparisons within forage families but cannot be used as an overall indicator of filling effects of forages that works for all comparison of forages.

Fragility

The filling effects of forage NDF are affected by fragility of forage particles (Allen, 2000). Forage fragility can be determined by measuring electrical energy required to grind samples (Minson and Cowper, 1974) or the difference in the fraction of particles retained on the 1.18-mm sieve before and after ball milling (Farmer et al., 2014). Fragility should be distinguished from digestibility as ruminal digesta does not need to be completely digested to disappear from the rumen, but its particle size can be also reduced by mastication and detrition to become small enough, allowing for passage. As such, fragility that affects the rate of particle size reduction in the rumen can be an independent factor affecting filling effects of forages. Voelker Linton and Allen (2007) determined fragility by measuring the reduction rate of iNDF from large particles ($\geq$2.36 mm) to small particles (<2.36 mm) in the rumen based on a pool and flux method, where intake, duodenal flow, and rumen pool of iNDF in $\geq$2.36-mm particles were used for the calculation. In their study (Voelker Linton and Allen, 2007), greater dietary forage NDF content (27.3 vs. 19.9% of dietary DM) increased rumen pH (6.00 vs. 5.86), digestion rate of pdNDF (4.74 vs. 3.32%/h), ruminal NDF digestibility (40.1 vs. 29.3%), and rate of particle size reduction (6.92 vs. 3.81%/h), indicating that fragility is related to NDF digestion parameters.

Although in vitro NDF digestibility and iNDF are expected to be related to intrinsic differences in fragility of forages, this may not hold true for comparisons between legume and grass; for example, alfalfa silage had a greater rate of particle size reduction compared with orchardgrass silage (7.16 vs. 4.67%/h), although it was lower in in vitro NDF digestibility (38.3 vs. 53.3%) and higher in iNDF content (23.0 vs. 16.1%; Kammes and Allen, 2012b). However, the digestion rate of pdNDF was higher for cows fed alfalfa silage (7.27 vs. 4.74%/h; Kammes and Allen, 2012a), which is consistent with the faster rate of particle size reduction (Kammes and Allen, 2012b). As discussed above, the positive relationship between rate of NDF digestion and fragility was also shown when forage NDF sources were the same (Voelker Linton and Allen, 2007). These findings collectively indicate that fragility is affected more by the rate of NDF digestion rather than NDF digestibility or pdNDF content. Kammes and Allen (2012b) demonstrated that legume, which is greater in fragility than grass, decreased the ruminal pool of large NDF particles and increased the passage rate of small NDF particles. Fragility may play a direct role in reducing filling effects of forage NDF, and a common analytical approach for fragility measurement needs to be established.

STARCH DIGESTIBILITY OF GRAIN

Over the last 35 years, factors affecting starch digestibility in the rumen and effects of greater starch digestion on DMI have been extensively studied. Grain type affects starch digestibility, and its ruminal degradability is in the order of oats, wheat, barley, corn, and milo, from high to low (Herrera-Saldana et al., 1990). Researchers in Illinois showed that steam-rolled barley is more fermentable in the rumen compared with dry ground corn, and cows fed barley grain decreased DMI by more than 3 kg/d (McCarthy et al., 1989; Overton et al., 1995). Silveira et al. (2007) also reported that cows fed barley grain decreased DMI (21.6 vs. 23.6 kg/d). However, effects of grain type on DMI have not been consistent, and the discrepancies can be attributed to the differences in the level of dietary grain allocation, dietary starch concentration, and availability of physically effective fiber among studies. For example, Grings et al. (1992) and Doepel et al. (2009) reported that grain type did not affect DMI in their studies, but they fed low-starch (<22%) diets.

Conservation method (high-moisture corn vs. dry ground corn) has consistent effects on DMI. Cows fed high-moisture corn had greater starch digestibility in the total-tract (Krause et al., 2002; Krause and Combs, 2003) or in the rumen (Oba and Allen, 2003b; Allen and Ying, 2021b), and all these researchers reported lower DMI for cows fed high-moisture corn. However, it is noteworthy that Oba and Allen (2003a) reported an interaction effect between dietary starch content and conservation method of corn grain, in which high-moisture corn decreased DMI (20.8 vs. 22.5 kg/d) only for cows fed a high-starch (32%) diet but not a low-starch (21%) diet. In their study (Oba and Allen, 2003b), feeding high-moisture corn increased the rate of starch digestion compared with dry ground corn to a greater extent in the high-starch diet (28.2 vs. 14.6%/h) than in the low-starch diet (16.8 vs. 12.2%/h), which is consistent with animal responses in DMI.

Grain processing can increase starch digestibility in the rumen. In steam rolling/flaking, heat and moisture are added to the grain to gelatinize starch and denature protein matrix that protects starch granules, and the extent of processing is indicated by the specific gravity with lower values meaning greater processing. Although greater extent of processing increased total-tract starch digestibility, it did not decrease DMI of lactating dairy cows in the literature (Plascencia and Zinn, 1996; Yu et al., 1998; Yang et al., 2000). Grinding is another common processing method of grain, which increases starch digestibility by increasing the surface area of grain and exposing more of the endosperm for microbial attachment and enzyme access. Fine-grinding increased starch digestibility in the total-tract (Knowlton et al., 1996) or in the rumen (Rémond et al., 2004; Allen et al., 2021b) compared with coarse-grinding, but it did not affect DMI. Dry ground corn is relatively low in ruminal starch digestibility, and even with fine-grinding may not have increased starch digestibility to an extent to affect DMI; it was 58.6% (Rémond et al., 2004) or 50.6% (Allen et al., 2021b), which is far lower than ruminal starch digestibility of steam-rolled barley grain (McCarthy et al., 1989; Overton et al., 1995) or high-moisture corn (Oba and Allen, 2003b; Allen and Ying, 2021b)

Endosperm type of corn grain (floury vs. vitreous) also affects starch digestibility in the rumen (Taylor and Allen, 2005; Allen et al., 2021b) or in the total-tract (Allen and Ying, 2021b), but has less consistent effects on DMI. Feeding floury corn did not affect DMI in one study (Allen and Ying, 2021a), tended to decrease DMI in another study (Allen et al., 2021a), and decreased DMI only for cows fed corn silage with lower in vitro NDF digestibility in the other study (Taylor and Allen, 2005). Other dietary factors such as primary forage source or starch source might have exerted greater effects on rumen fermentation, masking effects of endosperm type of grain.

EFFECTS OF FEEDING SUGAR

Sugar (water-soluble carbohydrate) is another carbohydrate fed in the diet of lactating dairy cows, and ferments faster than starch in general (Oba, 2011). Although replacing dietary starch with sugar is expected to increase ruminal fermentation, it often increases rumen pH (Chamberlain et al., 1993; Heldt et al., 1999; Penner and Oba, 2009). It is partly because sugar provides approximately 10% less carbon than starch per unit of mass due to less glycosidic bonds (Hall and Herejk, 2001). In addition, sugar fermentation in the rumen increases butyrate production rather than propionate (Vallimont et al., 2004; Ribeiro et al., 2005; Gao and Oba, 2016), leading to less fermentation acid production per unit of fermented hexose (Oba, 2011) and faster absorption (Dijkstra et al., 1993). Furthermore, sugar would decrease fermentation acid production in the rumen if it is used for microbial glycogen storage (Hall and Weimer, 2007).

Although sugar ferments quickly in the rumen, feeding sugar in place of starch often increased DMI of dairy cows possibly due to preference for sweet taste (Nombekela et al., 1994) or decreasing propionate flux to the liver (Oba, 2011). Broderick et al. (2008) fed experimental diets where corn starch was replaced by sucrose at 4 increments (0, 2.5, 5.0, and 7.5% of dietary DM), and reported that DMI increased linearly from 24.5 to 26.0 kg/d as dietary sugar contents increased from 2.7 to 10.0%. Penner and Oba (2009) also found that sucrose supplementation at 4.7% of dietary DM increased DMI of fresh cows (18.3 vs. 17.2 kg/d). Gao and Oba (2016) reported feeding sucrose or lactose at 5.5% of dietary DM in place of corn grain increased DMI (27.5 vs. 26.2 kg/d).

PREDICTION OF DMI

Allen et al. (2019) developed the following equation to predict DMI of lactating dairy cows from filling effects of diets, which was adopted by Dairy NASEM (2021):

$$\begin{gathered}\text{DMI (kg/d)} = 12.0 - 0.107 \times \text{forage NDF} \\ + 8.17 \times \text{ADF/NDF} + 0.0253 \\ \times \text{in vitro or in situ forage NDF digestibility} \\ (\textbf{FNDFD}) - 0.328 \times (\text{ADF/NDF} - 0.602) \\ \times (\text{FNDFD} - 48.3) + 0.225 \times \text{milk yield} + 0.00390 \\ \times (\text{FNDFD} - 48.3) \times (\text{milk yield} - 33.1).\end{gathered}$$

The equation contained dietary forage NDF content, forage type indicated by the ADF/NDF ratio (0.8 for legumes, 0.6 for grasses), and FNDFD along with its interactions with forage type and milk yield. Total dietary NDF content was not included in the DMI prediction equation as effects of non-forage NDF on DMI have not been consistent in the literature. Animal responses to non-forage NDF are likely affected by type of feedstuffs replaced by non-forage NDF sources (Allen, 2000). For example, effects of feeding soyhulls, a common non-forage NDF source, on DMI are different when it replaces grain or forage in the diet (Ipharraguerre and Clark, 2003). In addition, non-forage NDF sources vary in neutral detergent soluble fiber and water-soluble carbohydrate contents, which confound effects of non-forage NDF on DMI.

Some interactions affect the filling effects of forage NDF; for instance, higher producing cows respond more positively to legume (Voelker Linton and Allen, 2008; Kammes and Allen, 2012a) or a forage with greater in vitro NDF digestibility (Oba and Allen, 1999a). In addition, animal responses to enhanced in vitro NDF digestibility are more positive in grass than legume (Allen et al., 2019). These findings are also reflected in the DMI prediction equation of Dairy NASEM (2021).

Several research groups measure undigested NDF after 240-h in vitro incubation (**uNDF**) for forages and other feedstuffs and use it as a diet formulation parameter related to NDF digestion characteristics (Cotanch et al., 2014). In vitro NDF digestibility and uNDF are negatively related within forage families; specifically, forages higher in 24-h in vitro NDF digestibility were lower in uNDF for comparison within alfalfa hay (Fustini et al., 2017) or corn silage (Miller et al., 2021). The uNDF has several advantages compared with in vitro NDF digestibility as a quality parameter of forages. As uNDF is an end-point measurement, it is associated with fewer analytical errors, and less variation is expected even when the same sample is analyzed in multiple commercial labs. In addition, dietary uNDF is easily calculated by the sum of uNDF content of individual feedstuffs.

However, uNDF may not be a good indicator of filling effects of forage NDF. As it is an end-point measurement, it does not tell how NDF is digested nor indicate digestion rate or fragility, which has a direct effect on the filling effects of forage NDF. Fustini et al. (2017) fed alfalfa hay differing in in vitro NDF digestibility at 2 dietary uNDF contents, and reported that DMI was greater for cows fed the hay with greater in vitro NDF digestibility, but was not affected by dietary uNDF content. In addition, legume is greater in uNDF content than grass, but it is more fragile and less filling in the rumen (Kammes and Allen, 2012b). As such, uNDF content may not be a good overall parameter related to filling effects of forage that works across different forage types. Development of an integrated system universally accounting for filling effects of forage NDF is warranted.

Factors affecting starch digestibility of grain do not have consistent effects on DMI, as summarized in this review. The lack of consistent effects on DMI indicates that DMI is not affected by starch digestibility per se, but affected by a variable associated with starch digestibility, such as propionate metabolism in the liver (Allen et al., 2009). Positive effects of feeding sugar on DMI also suggest that greater ruminal fermentation per se does not necessarily decrease DMI. Dairy NASEM (2021) did not include starch digestion characteristics or dietary sugar content in the DMI prediction equation, and more research is warranted to accurately predict DMI from digestion characteristics of carbohydrates.

DIGESTIBILITY AND FUEL SUPPLY

It is not appropriate to use in vitro NDF digestibility to estimate in vivo NDF digestibility of forages. As discussed above, higher in vitro NDF digestibility is related to greater fragility, which reduces the ruminal pool of large NDF particles and decreases the retention time of ruminal digesta. This may contribute to greater DMI, but decreases NDF digestion in the rumen. Recent meta-analyses showed that greater DMI decreases the total-tract NDF digestibility (White et al., 2017; de Souza et al., 2018). In addition, in vitro NDF digestibility is to be measured under an optimal condition where concentrations and activities of enzymes do not limit the digestion process, whereas NDF digestion in the rumen often occurs at a suboptimal environment for fibrolytic microbes. Daily mean rumen pH is positively related to digestion rate of pdNDF in the rumen (Oba and Allen, 2003b), and cows fed high starch diets have lower NDF digestibility (Ferraretto et al., 2013; de Souza et al., 2018). To account for these negative effects on in vivo NDF digestibility, Dairy NASEM (2021) discounts NDF digestibility when DMI exceeds 3.5% of BW and when dietary starch content exceeds 26% of dietary DM.

Greater dietary starch content may increase ruminal starch digestibility via greater amylolytic enzyme activity (Oba and Allen, 2003b; Voelker and Allen, 2003), but decrease the total-tract starch digestibility due to faster passage and limited capacity of intestinal digestion (de Souza et al., 2018). Greater DMI also decreases total-tract starch digestibility (Ferraretto et al., 2013; de Souza et al., 2018). Dairy NASEM (2021) discounts starch digestibility when DMI exceeds 3.5% of BW, but no adjustments with dietary factors are made for starch digestibility due to insufficient data.

The type of absorbed fuels is affected by carbohydrate digestion. Carbohydrate type affects fermentation end products (Murphy et al., 1982); particularly, fiber digestion increases absorption of fuel as acetate, whereas fermentation of starch and sugar in the rumen increases absorption of propionate and butyrate, respectively. In addition, site of starch digestion affects the type of absorbed fuel. When a slowly fermentable starch source, such as dry ground corn, is fed to dairy cows, ruminal starch digestibility is decreased substantially but total-tract starch digestibility is not affected as much due to partial compensatory digestion in the intestines (Oba and Allen, 2003b), indicating that substantial amounts of starch are digested in the intestines. If starch is digested enzymatically in the small intestine, it is absorbed as glucose, which increases glucose or lactate flux to the liver (Allen, 2000). Type of absorbed fuels (propionate, glucose, or lactate) affects the extent of hepatic oxidation and feed intake (Allen et al., 2009). As such, temporal pattern of fuel supply from carbohydrate digestion needs to be integrated in predictions of DMI and fuel metabolism.

CONCLUSIONS

The filling effects of forage NDF are affected by in vitro NDF digestibility, fragility, and forage type. Starch digestibility is affected by grain type, processing method, conservation method, and endosperm type. Type of carbohydrate and its digestive characteristics can affect DMI and absorbed fuels. Previous research has increased our understanding of dietary carbohydrates, but its application for diet formulation requires integrated approaches accounting for factors affecting filling effects of forage NDF, starch digestion, and temporal fuel supply.

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ORCIDS

M. Oba https://orcid.org/0000-0001-8057-3500