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Symposium review: Physical characterization of feeds and development of the physically effective fiber system*

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ABSTRACT

Historical research had shown that forage particle size influences chewing activity, ruminal pH, volatile fatty acid profiles, and milk fat percentage. With this in mind, Mertens in 1997 published one of the most frequently cited papers in the *Journal of Dairy Science* that laid out a comprehensive system for integrating neutral detergent fiber (NDF) and particle size of feeds into one measure: physically effective NDF (peNDF). Based on total chewing time (i.e., eating plus ruminating), peNDF enabled ration formulation to meet the minimum fiber requirements of ruminants to maintain ruminal pH and milk fat. Total chewing time is related to feed NDF content and particle size, so Mertens proposed that peNDF could be determined simply from a chemical measure of NDF and particle size measured as the fraction of dry matter retained on a 1.18-mm sieve with vertical shaking of a dried sample. In the past 2 decades, the peNDF system has been incorporated into nutrition models and is routinely used in ration formulation. Early on, Mertens recognized that starch would affect the minimum peNDF requirements, and his work was the first to demonstrate that starch and fermentation pH affect ruminal fiber degradation kinetics. Subsequently, Mertens's insight into particle size analysis was extended from fibrous feeds to corn silage processing with the development of the commonly used corn silage fragmentation index for assessing starch availability. Participants at the 33rd Discover Conference on fiber in 2017 ranked improved physical description of feeds as a top priority for future research, undoubtedly recognizing the need to carry forward Mertens's pioneering work. Future research will likely focus on improving the physicochemical and biological evaluation of rumen fiber degradation and passage, thereby improving the prediction of animal response. The comprehensive system that David Mertens built for meeting the fiber requirements of ruminants has transformed ration formulation.
Key words: physically effective fiber, starch, particle size, degradation, physical form

INTRODUCTION

An allegorical letter to the editor of *Science* by Forscher (1963) differentiated between scientists as brick makers or builders. Titled *Chaos in the Brickyard*, this letter lamented the proliferation of research data with no clear endpoint in mind (i.e., bricks) at the expense of science, aimed at building systematically on previous research to create useful models (i.e., the buildings comprised of bricks). A year later, Platt (1964) expanded on this topic and termed this systematic method of scientific thinking that results in the most rapid progress, "strong inference." The first, and overarching, theme of this review is that David Mertens has emphatically been a master builder and practitioner of strong inference during his decades-long scientific career. The NDF-Energy Intake System (Mertens, 1987, 1994), the physically effective NDF system (**peNDF**; Mertens, 1997), and the ruminal digestion and sequential passage model (Mertens and Ely, 1979; Mertens, 2011) exemplify his creative, systematic approach to fiber research and its application in the field of ruminant nutrition.

The specific goal of this review is to highlight the contributions of David Mertens to our ability to assess feed physical form and understand how the physical and chemical characteristics of feeds affect animal responses. With a thorough appreciation of historical research in this area, Mertens created a "comprehensive system for meeting the fiber requirements of dairy cattle"—the title, in fact, of his landmark 1997 paper that defined peNDF. Figure 1 is a simplified flowchart of Mertens's major accomplishments in characterizing the physical nature of feeds, with the peNDF system being the crowning achievement and stepping-off point for future research. Figure 1 serves as the outline for this review.

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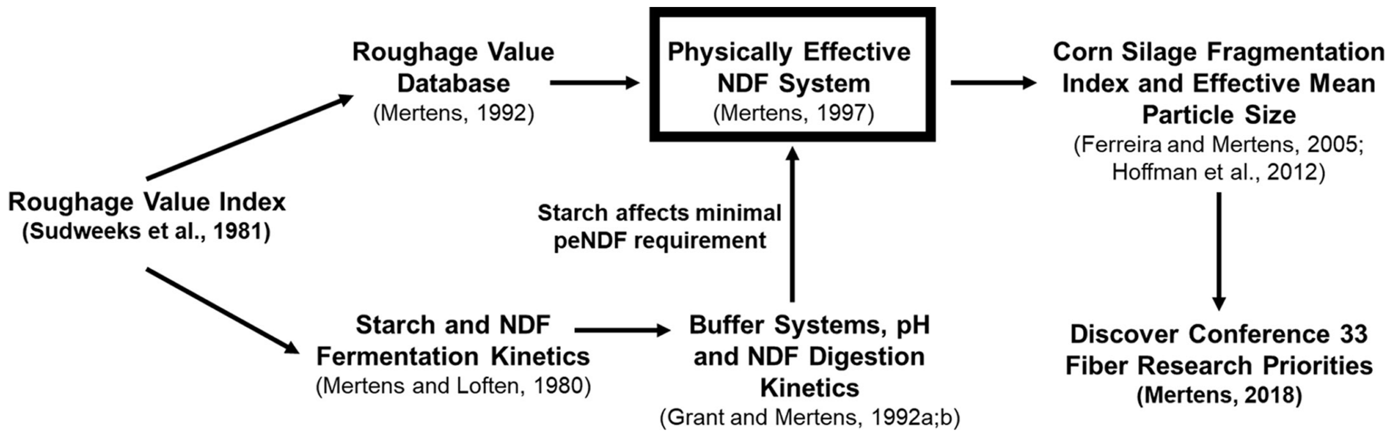

Figure 1. Key research milestones comprising David Mertens's research on how physical characteristics of feeds affect animal responses. Creation of the physically effective NDF system, with associated measurement methodology, and its ability to be incorporated into ration formulation and nutrition models is a key component of Mertens's enduring legacy in ruminant nutrition. His legacy of research provided the foundation for many of the research priorities identified at the 33rd Discover Conference focused on future fiber challenges and solutions.

Specific topics include Mertens's pioneering work on (1) characterizing fiber physical form and development of the peNDF system; (2) understanding how dietary starch and ruminal pH affect fiber degradation kinetics and peNDF requirements; and (3) measuring the physical characteristics of starch sources, notably corn silage and grain. The review concludes with a brief discussion of future fiber research priorities and reflections on Mertens's contributions and enduring legacy.

FROM FIBROUSNESS TO PHYSICAL EFFECTIVENESS: DEVELOPMENT OF THE PHYSICALLY EFFECTIVE NDF SYSTEM

Historical research demonstrated that forage particle size influences chewing activity, ruminal pH, VFA profiles, and milk fat percentage in dairy cattle (Van Soest, 1994). Balch (1971) compiled an extensive database of ruminant chewing responses across a wide range of diets and proposed that total time spent chewing (eating plus ruminating) would be a useful index of dietary fibrousness. Specifically, he defined a roughage index as the total chewing time elicited per kilogram of dietary DM. With Balch's system, roughage indices ranged from less than 20 min/kg of dietary DM for concentrate-based and finely chopped diets to upwards of 190 min/kg of DM for straws and coarse roughages.

Roughage Value Systems

University of Georgia researchers (Sudweeks et al., 1979) published a technical bulletin on the development and application of a roughage value index system for formulating dairy cattle rations built on the fibrousness concept of Balch (1971). This work described the equipment needed to measure chewing, methods to measure roughage values based on total chewing response, and established roughage requirements for lactating cows that could be used in ration formulation. Roughage values ranged from 5 to 15 for concentrate feeds to over 100 for forages depending on type of forage and chop length (for complete list of indices, see Table 2 in Sudweeks et al., 1981). Using the established relationship between the physical nature of feeds and their ability to stimulate chewing and salivary buffering, Mertens developed, for the first time, equations to predict roughage value indices from sieving and chemical data rather than relying solely on tabulated in vivo responses (Sudweeks et al., 1981).

Mertens observed that, for long and coarsely chopped forages, the roughage value index, based on chewing per kilogram of feed DM, was also highly correlated with feed NDF content. Consequently, chewing activity could be related usefully to the NDF content of feeds. The detergent system of feed analysis (thoroughly described by Van Soest, 2015) was relatively new at this point (1970s and 1980s), and the recognition that NDF could be used to improve ration formulation was groundbreaking. Specifically, Mertens noted that the structural carbohydrates measured as NDF typically required chewing during eating and ruminating for particle size reduction and passage from the rumen. Therefore, he proposed that total chewing time per kilogram of NDF could be used as an adjustment factor to account for differences among feeds in particle size (Mertens, 1992). That was a novel insight, and it paved the way for eventual development of the peNDF system.

In the 1992 edition of Large Dairy Herd Management, Mertens elaborated on his NDF-based system. In this system, a hypothetical, standard feed containing 100% NDF in long form was assigned a roughage value of 100. Other feeds were ranked relative to this standard of 100 based on their NDF content and particle size (Mertens, 1992). A roughage value was calculated as the product of NDF content × fraction of particles retained on a 1.18-mm sieve with dry sieving (see Table 25.2 in Mertens, 1992). The roughage value system assumed that all fiber particles retained on the ≥1.18-mm sieve elicited the same chewing response regardless of source or fragility—a key assumption of the peNDF system as well.

An extensive table of standardized roughage value adjustment factors for converting NDF to roughage value units was provided by Mertens (1992) for a wide range of 103 feeds, and it was proposed that these values could be used to incorporate fiber content and particle size into a practical and quantitative system for formulating dairy rations. To ensure sufficient dietary roughage value, Mertens (1992) recommended that diets contain at least 21% roughage value, as a percentage of ration DM, to maintain normal ruminal health and milk fat percentage. The roughage value units and roughage value-adjusted NDF described and tabulated by Mertens (1992) served as precursors to the physical effectiveness factor (**pef**) and peNDF.

Introduction of the Physically Effective NDF System

A symposium was held at the 1995 ADSA annual meeting entitled "Meeting the fiber requirements of dairy cows." Five presentations covered the following topics: measuring effectiveness of fiber with animal response trials (Armentano and Pereira, 1997); effect of nonforage sources of fiber and starch on site of fiber digestion (Firkins, 1997); interactions between forage and nonforage sources of fiber (Grant, 1997); relationships between fermentation acid production and the requirement for peNDF (Allen, 1997); and the capstone paper "Creating a system for meeting the fiber requirements of dairy cows" (Mertens, 1997). This 1997 paper has become the 11th most cited paper in the *Journal of Dairy Science*. In it, Mertens systematically laid out how chemical and physical properties of fiber can be combined into a single peNDF measure, with total chewing activity as the cow response, allowing formulation of rations to meet the minimum fiber requirement of ruminants to maintain ruminal function, health, productivity, and welfare. Importantly, this paper also described a simple laboratory method to measure pef and peNDF from chemical and particle size measures so that it could be readily adopted in the field.

Mertens (1997) also clarified the difference in meaning between peNDF and effective NDF (**eNDF**), which had been commonly used to describe the ability of a feed to replace roughage and maintain milk fat percentage. At this time, these 2 terms were sometimes used interchangeably, which created confusion. Unlike peNDF, eNDF reflected nonfiber as well as fiber characteristics of a feed that affect milk fat such as lipids, sugars, or intrinsic buffering capacity. Consequently, eNDF could be either greater or lesser than peNDF depending on the feed and its effect on milk fat synthesis and ruminal fermentation. Mertens (1997) concluded that the insensitivity of milk fat to ration changes that sometimes occurs and the typically larger coefficient for eNDF made it a less sensitive indicator of true fiber effectiveness than peNDF.

At the time of this symposium, despite the advances in defining roughage value of feeds, the conventional paradigm regarding fiber recommendations was that, to maintain normal ruminal function and milk fat percentage, a substantial portion of the ration fiber needed to come from coarse forage (Varga et al., 1998). The NRC (1989) recommended a minimum of 25 to 28% NDF with 75% supplied from coarse forage. Although the subsequent NRC (2001) acknowledged peNDF, it did not adopt this system citing a lack of validation. Similarly, the latest NASEM (2021) did not recommend use of peNDF, opting instead to focus on percentage of forage NDF. Nonetheless, the peNDF concept has been implemented in widely used nutrition models, notably the Cornell Net Carbohydrate and Protein System model (Sniffen et al., 1992) whose biology alone is used in over 20 countries and the feeding of >3 million cows (Chase, 2014).

Defining Physically Effective NDF

Mertens's peNDF system focused squarely on total chewing time as the best biological response to measure effectiveness of fiber to maintain ruminal health and function. Specifically, peNDF was defined by Mertens (1997) as the physical properties of a feed (most importantly particle size) that stimulate total chewing activity (eating and ruminating) and create the biphasic stratification of ruminal digesta. Chewing response, amount of saliva produced, and buffering capacity are all sensitive to dietary peNDF.

Mertens developed a practical, field-applicable system for calculating peNDF as feed NDF content × pef (see page 1,473 in Mertens, 1997). The pef refers to the fraction of particles that are retained on the ≥1.18-mm sieve with dry vertical sieving (theoretical scale from 0 to 1). This "physically effective" fraction of forage or feed particles is resistant to passage from the rumen, requires rumination for passage, and comprises the longer, more buoyant particles that form the ruminal digesta mat (Poppi et al., 1985; Mertens, 1997).

The biological definition of peNDF has proven deceptively simple, and the importance of considering both eating and ruminating responses remains an important insight of Mertens because cows tend to chew many forages to a uniform particle size before swallowing during eating. In fact, it is possible to vary eating time of dairy cattle by over 1 h/d by manipulating forage peNDF content and NDF degradability (Grant and Ferraretto, 2018). Research has shown that when dairy cows consume ryegrass hay, corn silage, grass silage, or TMR with particle size ranging from 12.0 to 43.5 mm, the swallowed bolus of feed is uniformly 8.1 to 12.5 mm (Schadt et al., 2012). Consequently, focusing exclusively or even primarily on rumination may result in inaccurate estimates of peNDF and its effect on rumen function and milk fat for at least some forage sources.

Implementing the Physically Effective NDF System

Mertens (1997) compiled relevant particle size research into 1 database comprising 45 experiments to develop relationships between NDF, peNDF, and total chewing. Correlations between observed and predicted chewing time using standardized peNDF were only modest ($R^2 = 0.47$ to 0.54; see Mertens, 1997 for details on standardization). However, when correcting for outliers and experiment, the R^2 increased to 0.76 to 0.81. To establish requirements for peNDF, Mertens (1997) theorized that ruminal pH reflected the animal's chewing behavior, linked with salivary buffer secretion. He found that dietary peNDF content and ruminal pH were positively related ($R^2 = 0.71$), and that to maintain a ruminal pH of 6.0, the dietary peNDF content needed to be approximately 22% of ration DM. Similarly, milk fat percentage was related to dietary peNDF concentration with a $R^2 = 0.63$ and, to maintain 3.4% milk fat, a peNDF content of approximately 20% of the dietary DM was required.

The current peNDF system and the associated methodology rest on 3 main assumptions, as follows: (1) NDF is uniformly distributed across all particle sizes; (2) chewing activity is equal for all particles retained on the 1.18-mm sieve; and (3) fragility (ease of particle size reduction) does not differ among sources of NDF. Mertens (1997) provided experimental approaches to address the validity of each of these assumptions for any given feed or forage. He also concluded that other potentially important physical and chemical characteristics of feeds, such as fragility, density, or buoyancy, may need to be evaluated to potentially improve predictions of chewing and ruminal function.

Since Mertens (1997), meta-analyses have been published that assess the effect of peNDF on various cow responses. Most notably, Zebeli and coworkers have published a series of papers that support the importance of peNDF in maintaining an optimal rumen environment and production of FCM (e.g., Zebeli et al., 2008, 2012). Their database is comprised of papers that used multiple sieving methods on dry and as-fed samples to characterize pef, some of which provide pef values that differ markedly from the vertical dry sieving method that underpins the original peNDF system. Based on their data set, Zebeli et al. (2008) recommended an optimal peNDF range of 30 to 33% of ration DM to maintain ruminal pH and milk fat percentage. Furthermore, with a ration peNDF content of 31.2% of DM, the DMI (20 versus 25 kg/d) and rumen degradable starch (14 versus 22% of ration DM) interacted to determine the risk of rumen pH less than 5.8. This recommended range in peNDF is much inflated over the original value of 20 to 22% of ration DM determined by Mertens (1997). A more recent meta-analysis (Khorrami et al., 2021) found that ration peNDF measured using the 8-mm sieve of the Penn State Particle Separator should range between 15 and 18% of DM to prevent rumen pH less than 5.8 with diets containing between 20 and 25% starch.

Use of the Penn State Particle Separator to measure pef with various combinations of the 19-, 8-, and 1.18-mm sieves may either inflate or reduce pef values, compared with the standard dry sieving method, resulting in poor relationships between peNDF, total chewing time, and ruminal pH (Grant and Cotanch, 2005). However, it is possible that an as-fed, on-farm pef value can be determined using the Penn State Particle Separator adapted with a 4-mm sieve that provides pef values similar to the standard dry sieving method, although more work is needed (Schuling et al., 2015). In this report, an R^2 of 0.93 was reported between pef measured using the 1.18-mm sieve with dry vertical sieving, and the Penn State Particle Separator using a 4.0-mm sieve and horizontal shaking of as-fed samples of corn silage, alfalfa silage, and TMR. Overall, it is evident that to effectively formulate rations using peNDF as created by Mertens (1997), and as currently implemented within the dairy industry, requires pef values derived from dry vertical sieving or a system that yields similar pef. Attempts to evaluate the peNDF system need to use the particle sieving methodology described by Mertens (1997) to be valid.

Recently, White et al. (2017a,b) have re-evaluated the concept of peNDF and proposed the use of NDF and particle size descriptors along with other physical and chemical dietary characteristics to predict DMI, rumination time, and ruminal pH in lactating dairy cows. They have termed this measure physically adjusted NDF (**paNDF**) and the newly released Nutrient Requirements of Dairy Cattle (8th ed.; NASEM, 2021) proposes paNDF as the preferred measure of the adequacy of a diet to maintain a given ruminal pH. The paNDF system relies on a measure of particle size (19-mm sieve of the Penn State Particle Separator) and its interaction with dietary NDF, forage NDF, starch, and forage percentage (NASEM, 2021). As stated in the NASEM (2021) publication, the paNDF system is not intended to be used in ration formulation but rather to illustrate how dietary composition and particle size affect rumen pH and to assist with ration evaluation.

This system has not been field tested, and it remains to be seen whether paNDF will enhance our ability to feed fiber to dairy cattle, but it does differ from peNDF in at least the following 3 major ways, which must be understood and appreciated: (1) focus is on rumination rather than total chewing so contributions of eating are excluded; (2) Penn State Particle Separator is used to measure particle size on as-fed samples rather than dry vertical sieving (though results are expressed on a DM basis which may be challenging for on-farm use); and (3) focus is on ruminal pH rather than chewing response. A focus on ruminal pH (similar to milk fat in earlier work on effective fiber) may prove to be problematic from a ration formulation perspective because pH and milk fat can be influenced by non-fiber factors, both chemical and physical. In contrast, peNDF is related to total chewing activity that largely determines the structure of the biphasic digesta mat, salivary buffering, and ultimately dynamics of particle passage and digestion. In the future, dairy nutritionists may continue to rely on peNDF or a similar system for ration formulation and find usefulness in paNDF or some similar approach to assess rations on farm and guide their formulation strategy.

PHYSICALLY EFFECTIVE NDF AND STARCH

Physically effective NDF was developed to meet minimum fiber requirements and, early on, Mertens recognized that dietary starch would affect these requirements. The significance of the interaction between dietary starch content and fermentability versus buffering elicited by peNDF was highlighted as part of the 1995 ADSA Fiber Symposium by Allen (1997), Firkins (1997), and Mertens (1997). More recently, Zebeli et al. (2010) have modeled the interaction between peNDF and ruminally degradable starch to minimize subacute ruminal acidosis and optimize dairy cattle productivity. Although the biological concepts in their model pertaining to the interaction between dietary starch and NDF are sound, as previously explained, several methods were used to calculate pef in their database and so quantitative implementation within the context of the original peNDF system is difficult.

Mertens and Loften (1980) were the first to demonstrate that starch affects the degradation kinetics of fiber, independent of ruminal pH. In this foundational paper, addition of purified wheat and corn starch to in vitro fermentations of alfalfa, orchardgrass, fescue, and Coastal bermudagrass resulted in linear increases in lag time before fiber degradation with no effect on fractional rate of fiber degradation. Importantly, these in vitro fermentations were conducted at pH 6.8 over 96 h, so responses in NDF degradation kinetics were due to starch addition and not pH.

Taking the next step, Grant and Mertens (1992a) developed an in vitro buffering system capable of pH control within the physiological range of 5.8 and 6.8. When alfalfa, bromegrass, and corn silage were fermented at pH 5.8 or 6.8 for 96 h, the lower pH resulted in a substantial increase in digestion lag time. Subsequently, Grant and Mertens (1992b) assessed the effect of pH 5.8, 6.2, and 6.8 on in vitro degradation kinetics of bromegrass, corn silage, and alfalfa when combined with raw corn starch to approximate a 30% NDF diet. They concluded that low fermentation pH reduces NDF degradation rate and extends lag time, and that starch accentuates the negative effect of low pH. Other in vitro research (Grant and Weidner, 1992; Grant, 1994) has shown that source of starch and its ruminal fermentability influence lag and fractional rate of NDF degradation differentially between pH 6.8 and 5.5. Overall, Mertens's body of research shows that low pH exerts its negative effect between 6.2 and 5.5, primarily by increased lag time and secondarily by a reduction in fractional rate of NDF degradation dependent on forage type. As with peNDF, the NDF degradation kinetics as affected by pH and starch have been incorporated into the Cornell Net Carbohydrate and Protein System model (Pitt et al., 1996).

In vivo experiments have shown that ruminal pH may be quite low in lactating dairy cows fed highly digestible rations. As an example, Robinson et al. (1986) fed dairy cows a diet containing 32% starch and observed that pH was below 6.2 for 70 to 80% of each day. A lingering question for dairy cattle nutritionists has been how dairy cattle derive sufficient energy from NDF when pH may be depressed for significant portions of the day. Providing a possible answer, Mouriño et al. (2001) proposed a model of ruminal cellulose degradation in which the rate of degradation is determined mainly by the pH at which fermentation is initiated. Their work showed that in vitro fermentation pH influences digestion lag with no effect on fractional rate. This response agrees with the earlier work by Grant and Mertens (1992a) that had also found extended lag times with low in vitro fermentation pH. The model of Mouriño et al. (2001) presumes that the percentage of time that ruminal pH is below 6.0 will be less important for cellulose degradation than the pH when microbial attachment to the fiber particle occurs. This model suggests needed research on the relative importance of initial chewing, bolus ensalivation, and successive rumination cycles in raising the pH within the feed bolus, thereby increasing bacterial adhesion to particles. In any event, this contemporary model agrees well with the original kinetic work from Mertens's group in the 1970s and 1980s.

Early on, Mertens (1992) wrote extensively on the interaction between fiber and NFC, recognizing that this interaction would affect the minimum requirements for roughage value-adjusted NDF. To date, incorporation of starch (more broadly ruminally fermentable carbohydrates) into the peNDF system remains a work-in-progress and a priority for further research.

PHYSICAL FORM: FROM FIBER TO STARCH

Decades-long interest in the interactions between peNDF and starch stimulated Mertens to conduct research on the effects of feed physical form on starch digestibility. This line of research mirrored his groundbreaking work on physical properties of fibrous feeds. Recognizing that corn silage is the predominant forage crop in the United States (Martin et al., 2017), Mertens focused his research on corn silage. It was well known that the chop length and processing method for corn silage affected starch utilization by the cow. Studies had shown that variable lactational response to silage processing were likely related to the degree of kernel processing and proportion of intact versus broken kernels (Johnson et al., 2003). As interest in silage processing in the dairy industry expanded, Mertens (2005) identified the high priority need to provide forage testing laboratories with methods to assess whether the corn silage had been adequately processed for cows to effectively digest the starch.

Corn Silage Fragmentation Index

Corn silage is a complex feed with variable percentages of stover and grain; in fact, each portion can have differing chemical composition and physical properties. Using a diverse set of 32 corn silage samples, Ferreira and Mertens (2005) used sieves with apertures $\geq$4.75 mm to isolate intact kernels and large kernel fragments. This fraction of whole or minimally fragmented particles retained on $\geq$4.75-mm sieve was collected and analyzed for starch (i.e., starch $>$ 4.75). Dividing starch $>$4.75 by total starch in the sample provided the proportion of minimally fragmented starch which was positively correlated with mean particle size. The inverse number was defined as the corn silage fragmentation index. In the dairy industry, it is commonly referred to as the corn silage or kernel processing score and it has come to be considered a standard in kernel and silage processing evaluation (Rasmussen and Moeslund, 2019). Based on Mertens's research (Mertens, 2005; Ferreira and Mertens, 2005), commonly cited benchmarks for the corn silage fragmentation index are as follows: $>$70% of starch passing through the 4.75-mm sieve is optimal for starch digestibility; 50 to 70% is considered average; and $<$50% reflects inadequate silage processing.

The range in corn silage fragmentation index was 0 to 91% in the sample set of Ferreira and Mertens (2005) and the index was negatively correlated with silage mean particle size ($r = -0.46$). The relatively low correlation between the fragmentation index and mean particle size was related to variable kernel disruption (i.e., fragmentation) within silage samples having the same chop length.

Ferreira and Mertens (2005) also observed that the difference in in vitro digestible neutral detergent solubles between ground and whole samples was related to the fragmentation index. Consequently, they concluded that the corn silage fragmentation index has potential for adjusting starch digestibility in silages because it reflects variation in the physical attributes of the silage grain kernels. In vivo research is needed, but this fragmentation index may provide a much-improved ability to estimate silage energy content when using the standard summative approach (Van Soest, 1994). Combining corn silage fragmentation index and peNDF provide a comprehensive physical characterization of the corn silage (Mertens, 2005) and they have become routine laboratory analyses of corn silage (Fessenden, 2020; Mahanna, 2020).

Effective Mean Particle Size for Corn Grain

It has been well documented that finely ground corn grain is positively related to ruminal starch fermentability (Gallo et al., 2016; Goeser and Shaver, 2020). Working with researchers at the University of Wisconsin and the Agricultural Research Service, Mertens investigated the concept of effective mean particle size (**eMPS**) for dry and high-moisture corn grain (Hoffman et al., 2012). With this approach, a measurement of mean particle size was adjusted for factors that influence the fermentation potential of grain, and the resulting value was termed eMPS. The factors found to have the greatest effect were prolamin content in dry corn and NH_3-N content for high-moisture corn. Indicating how important this measure may be, 84% of the variability in peak absolute rate of in vitro gas production, reflecting starch fermentation, was explained by eMPS for a diverse set of samples. The concept of eMPS may improve prediction of animal responses, but because it is a new metric, in vivo validation is needed before it is widely adopted by dairy nutritionists.

BUILDING ON THE LEGACY: FUTURE FIBER RESEARCH

The 33rd ADSA Discover Conference held in 2017 was titled "Integrated solutions to fiber challenges." Mertens presented a comprehensive paper on the state of fiber analysis and what we know about how ruminants use fiber. Following the conference, attendees were surveyed and asked to prioritize areas for future fiber research. Results were reported at the 2018 ADSA annual meeting (Mertens, 2018). The top priorities were (1) biological (in vitro, in situ, in vivo) evaluation of fiber degradation, (2) physical analysis of fiber, (3) chemical analysis of fiber, and (4) modeling of fiber degradation, passage, and utilization. This list of fiber research priorities undoubtedly recognized the need to build on Mertens's pioneering work. Within these 4 broad priority categories, several topics specific to fiber and its physical form require further research and understanding.

Perhaps most fundamentally, future research needs to consider differences among sources of NDF. Important differences in chemical composition, degradability, and physical form exist between forage and non-forage sources of NDF (Grant, 1997). Differences in chemical composition, degradability, and structural anatomy also exist among forage types, such as between grasses and legumes (Van Soest, 1994; Raffrenato et al., 2019). We cannot necessarily summarize and infer across all sources of NDF as we develop relationships among fiber, starch, and physical characteristics.

Future research should also focus on the relationship between NDF degradability and particle size reduction. Limited research suggests that, for at least some fiber sources, greater NDF degradability enhances rate of particle breakdown (Grant, 2010). What combination of chemical and physical characteristics of feeds most influence particle fragility, density, buoyancy, and rumen turnover remains unanswered. Future ration evaluation or formulation systems that include measures of NDF degradability plus particle size may improve the peNDF system. Likewise, systems that consider NDF degradability, starch, and its fermentability, together with various measures of particle size, may better predict ruminal responses such as the proposed paNDF system previously discussed (White et al., 2017a,b; NASEM, 2021).

There is a need to explore other potentially useful measures of physical form in addition to sieving and particle size measures based on particle distributions. For instance, the 3-dimensional shape of the particle may be as important as the length or width. At the least, we need to standardize how particle size is measured for pef. It is well known that physical measures of particle size may differ greatly as a function of dry versus wet or moist samples, dry versus wet sieving techniques, and horizontal versus vertical shaking systems (Van Soest, 1994). Currently, several different particle sizing systems are being used, and the data are sometimes used interchangeably, although the results may not be comparable (Maulfair and Heinrichs, 2012). In the context of the peNDF system, the inherent biology is currently being obscured by too many differing particle sizing methods that yield quite different pef for the same feed. Research on how best to define the physical attributes of a feed will be critical for future refinement of the peNDF system, or any future system, designed to meet the ruminant's fiber requirements based on physical as well as chemical characteristics. In addition to NDF, there may be value in the concept of multiplying a measure of physical form, such as pef, by other chemically and nutritionally relevant fractions comprising the potentially degradable and the undegradable fiber of forage and non-forage sources of fiber. The underlying question is the relative importance of physical form and fiber undegradability at affecting chewing and rumen dynamics. In any case, the fraction of interest may not be uniformly distributed across all sieves, which is an inherent assumption of peNDF or similarly designed systems.

The same issue of how best to assess physical form applies also to the future development of ruminal NDF degradation and passage models. For progress to be made in these ruminal models of fiber turnover, we will need measures of particle size or other physical attributes that relate meaningfully to ruminal digesta characteristics, size reduction, and kinetics of particle passage. For example, a ruminal digestion and sequential passage model such as the one proposed by Mertens and Ely (1979) would allow incorporation of new data on digestion and particle size reduction to improve modeling of ruminal fiber turnover. Large, buoyant particles are selectively retained in the rumen, and these particles in turn help to sequester small particles. The ability to accurately predict ruminal fiber dynamics rests on the ability to appropriately characterize the physical as well as the chemical attributes of forages and other feeds.

There are a multitude of questions that must be answered to continue moving forward in our understanding of physical characterization of feeds and how the chemical and physical properties of fiber (and other fractions) affect behavior, ruminal function, performance, and ultimately the well-being of the animal. Well-being that reflects an optimally managed rumen environment, where delivery of salivary buffer and rumen pH are accurately predicted, and the relationships between eating, ruminating, and rumen particle dynamics are understood and optimized. In an era of limited resources for forage research, prioritizing these and other research questions looms large for future researchers in fiber nutrition.

PERSPECTIVES ON A MASTER BUILDER

This review has covered only one aspect of Mertens's manifold contributions to our understanding of fiber requirements. It is clear that he built up a tremendously useful edifice in the peNDF system and related measures of physical form for silages and grain, notably the corn silage fragmentation index. Mertens laid out a comprehensive system for integrating NDF and particle size of feeds into 1 measure, peNDF. Based on total chewing time, peNDF has enabled ration formulation to meet the minimum fiber requirements of ruminants and is widely used in the dairy industry. When combined with his NDF-Energy Intake System, peNDF has provided the industry with a powerful means of formulating rations that ensure that minimum fiber requirements are met, and that fiber does not constrain DMI. In short, Mertens created a feeding system that better described the forage biology affecting ruminal digestion and passage than any previous attempt with an analytical focus on fiber characteristics that allow formulation of maximal, optimal, or minimal NDF rations.

It is fortuitous that Mertens arrived at the University of Georgia in the midst of the research on roughage value with his desire to make NDF a cornerstone of ration formulation. Equally fortunate for the dairy industry have been Mertens's teaching and mentoring skills, his insistence on publishing in industry-focused proceedings as well as peer-reviewed journals, and his willingness to actively participate in numerous fiber-focused research groups over the years. Mertens's undeniable research impact and his scientific leadership will ensure his enduring legacy. Ralph Waldo Emerson wrote "He builded better than he knew; the conscious stone to beauty grew." The comprehensive system that David Mertens built for meeting the fiber requirements of ruminants transformed ration formulation and ranks him as a master scientific, systematic builder.

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