Invited review: Role of physically effective fiber and estimation of dietary fiber adequacy in high-producing dairy cattle

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ABSTRACT

Highly fermentable diets require the inclusion of adequate amounts of fiber to reduce the risk of subacute rumen acidosis (SARA). To assess the adequacy of dietary fiber in dairy cattle, the concept of physically effective neutral detergent fiber (peNDF) has received increasing attention because it amalgamates information on both chemical fiber content and particle size (PS) of the feedstuffs. The nutritional effects of dietary PS and peNDF are complex and involve feed intake behavior (absolute intake and sorting behavior), ruminal mat formation, rumination and salivation, and ruminal motility. Other effects include fermentation characteristics, digesta passage, and nutrient intake and absorption. Moreover, peNDF requirements depend on the fermentability of the starch source (i.e., starch type and endosperm structure). To date, the incomplete understanding of these complex interactions has prevented the establishment of peNDF as a routine method to determine dietary fiber adequacy so far. Therefore, this review is intended to analyze the quantitative effects of and interactions among forage PS, peNDF, and diet fermentability with regard to rumen metabolism and prevention of SARA, and aims to give an overview of the latest achievements in the estimation of dietary fiber adequacy in high-producing dairy cattle. Recently developed models that synthesize the effects of both peNDF and fermentable starch on rumen metabolism appear to provide an appropriate basis for estimation of dietary fiber adequacy in high-producing dairy cows. Data suggest that a period lasting more than 5 to 6 h/d during which ruminal pH is <5.8 should be avoided to minimize health disturbances due to SARA. The knowledge generated from these modeling approaches recommends that average amounts of 31.2% peNDF inclusive particles >1.18 mm (i.e., $peNDF_{>1.18}$) or 18.5% peNDF inclusive particles >8 mm (i.e., $peNDF_{>8}$) in the diet (DM basis) are required. However, inclusion of a concentration of $peNDF_{>8}$ in the diet beyond 14.9% of diet DM may lower DM intake level. As such, more research is warranted to develop efficient feeding strategies that encourage inclusion of energy-dense diets without the need to increase their content in peNDF above the threshold that leads to lower DM intake. The latter would require strategies that modulate the fermentability characteristics of the diet and promote absorption and metabolic capacity of ruminal epithelia of dairy cows.

Key words: dairy cattle, modeling, physically effective neutral detergent fiber, rumen acidosis

INTRODUCTION

A major challenge to the current feeding systems of high-producing dairy cattle is how to reconcile feeding of energy-dense diets, which are necessary for supporting milk production, with adequate amounts of dietary physically effective fiber, which is needed to prevent rumen disorders (Zebeli et al., 2011). Indeed, finding an optimal balance between physically effective fiber and readily degradable carbohydrates in the diet is difficult but crucial not only for maintaining proper rumen metabolism (Zebeli et al., 2006a; Plaizier et al., 2008), but also for maintaining a stable metabolic health status and enhancing the productivity of dairy cattle (Ametaj et al., 2010; Zebeli et al., 2011). Failure of these balancing efforts contributes to the occurrence of subacute ruminal acidosis (**SARA**), a prevalent metabolic disorder of early and mid lactating dairy cows (Enemark, 2008). Field studies in the United States have indicated that up to 19% of early lactation dairy cows and 26% of mid lactation cows suffer from SARA (Garret et al., 1997). The SARA is characterized by variable clinical signs; for example, intermittent anorexia or diarrhea, poor body condition, liver abscesses, impaired rumen motility, laminitis, and decreased milk production (Dirksen, 1985; Enemark, 2008; Aschenbach et al., 2011).

Assessment of dietary physical effectiveness and fiber adequacy in dairy cows has proven to be difficult from the current feed tables mainly due to their insufficient consideration of a feedstuff's physical characteristics such as particle size (**PS**; GfE, 2001; NRC, 2001). However, PS has considerable influence on ruminal digestive and metabolic processes (NRC, 2001; Tafaj et al., 2007; Lechartier and Peyraud, 2010). To include information on PS in dietary formulations, the concept of physically effective NDF (**peNDF**) is receiving increasing attention. This concept integrates information on chemical constituents (i.e., NDF) and structural features (i.e., PS) that act jointly and interdependently to stabilize ruminal fermentation and acid-base balance (Allen, 1997; Mertens, 1997; Tafaj et al., 2007). Using peNDF in diet formulation thus provides a potential tool to evaluate dietary fiber adequacy in dairy cows. Dietary fiber adequacy, in turn, is necessary to reduce the risk of SARA when feeding highly fermentable diets (Allen, 1997; Mertens, 1997; Zebeli et al., 2006a).

The peNDF of a feedstuff is the product of its NDF concentration and the physical effectiveness factor (**pef**). By definition, pef varies from 0, when NDF is not physically effective (e.g., fiber from ground concentrates), to 1, when NDF is fully effective (e.g., fiber from coarsely-chopped hay) in promoting digesta stratification in the rumen, chewing activity, and rumen buffering (Allen, 1997; Mertens, 1997). Two methods of determining peNDF have been developed (Lammers et al., 1996; Kononoff et al., 2003a), and major advances have been achieved in terms of characterizing and understanding the physiological roles of peNDF in dairy cattle (Beauchemin et al., 2003; Yang and Beauchemin, 2006a,b). However, establishment of the peNDF concept as a routine method to determine dietary fiber adequacy has not yet been possible in current dairy feed rationing. This is attributable to the fact that PS has multiple effects on feed intake behavior, chewing, rumination, passage rates, ruminal fermentation, and ruminal acid:base balance, leading to complex and nonlinear relationships between PS and characteristics of ruminal function (Tafaj et al., 2005, 2007; Zebeli et al., 2006a).

To develop an understanding for optimum size and amount of fiber particles in the diet, this review focuses on interactions among forage PS, peNDF, and concentrate fermentability, as well as on quantitative evaluations of their effects on rumen metabolic activity, prevention of SARA, and productive performance. The major aim is to give an overview of the latest achievements in the estimation of dietary fiber adequacy in high-producing dairy cattle and to promote the inclusion of the peNDF concept when designing dairy feed rations in the future.

FIBER STRUCTURE AND PHYSICAL EFFECTIVENESS

Forage Particle Size

The definition of an optimal forage PS in dairy cattle has traditionally been difficult because PS has 2 partially antagonistic effects on animal performance. On the one hand, feeding long forage PS increases the content of peNDF in the diet with positive effects on rumination and rumen buffering, thereby decreasing the risk of SARA (Mertens, 1997; Tafaj et al., 2007). On the other hand, increasing PS lowers the passage rate of digesta and may decrease net fiber degradation in the rumen, due to a lower availability of surface area for microbial attack, and thus decreasing feed intake and nutrient uptake (Tafaj et al., 2007; Storm and Kristensen, 2010).

Recent data from our research as well as research of other teams have demonstrated that fine chopping of roughage to a theoretical PS of 4 to 6 mm adversely affected rumination activity and rumen fermentation in diets containing relatively large amounts of concentrate (50 to 60% DM). This was equally true for corn silage (Kononoff et al., 2003b; Yang and Beauchemin, 2006a; Zebeli et al., 2008b), grass silage (Zebeli et al., 2007, 2008c,d), or silages based on alfalfa or barley (Teimouri Yansari et al., 2004; Yang and Beauchemin, 2007; Alamouti et al., 2009). Studies also showed that a decreased ruminal pH largely contributed to the depression of fiber degradation as well as feed efficiency of the cows (Allen and Mertens, 1988; Krajcarski-Hunt et al., 2002; Zebeli et al., 2010). Moreover, microbiological studies have shown that fine-chopping and grinding of forages in the diet modulates the counts of cellulolytic microbiota and their activity in the rumen digesta both in vivo (Ölschläger, 2007) and in vitro (Witzig, 2009).

On the other hand, a moderate decrease of the theoretical PS of forages to approximately 10 to 15 mm was shown to promote ruminal degradation, likely because of an increase of the available surface area for attachment of ruminal fibrolytic bacteria (Ölschläger, 2007; Weber, 2007; Zebeli et al., 2008b) and protozoa (Zebeli et al., 2008c), without negatively affecting cellulolytic activity and other fermentation processes in the rumen (Ölschläger, 2007; Zebeli et al., 2008b).

Meanwhile, it has become clear that the effects of forage PS on animal performance extend beyond physical effectiveness and fiber degradation kinetics in the rumen when feeding dairy rations as TMR (Tafaj et al., 2007). For example, a moderate decrease of forage PS has been shown to improve the uniformity of TMR which, in turn, often results in less sorting before consumption of the feed (Kononoff and Heinrichs, 2003b;

Zebeli et al., 2008b; Alamouti et al., 2009). Reduced sorting before consumption is related to other beneficial effects, particularly in terms of improving the circadian eating behavior of the cows, lowering diurnal variation of nutrient intake (DeVries et al., 2005), and, most importantly, contributing to a reduction of the risk of ruminal disorders despite feeding cows relatively high amounts of grain (Krause and Oetzel, 2006; Dohme et al., 2008; DeVries et al., 2009).

The beneficial effects of moderately reduced PS on sorting behavior are especially obvious with corn silage-based diets because fine-chopping of corn cobs hinders their selective eating by the dairy cows. Accordingly, a moderate decrease of corn silage PS has been shown to favor a better daily distribution and greater absolute intake of dietary peNDF in one of our studies, and these effects were reflected by greater percentages of milk fat and protein (Zebeli et al., 2008b). Greater milk fat percentage indicates maintenance of a better environment for rumen microbiota and more efficient degradation of fiber, one of the crucial factors known to affect milk composition and, in particular, milk fat content in dairy cows (Mertens, 1997; De Brabander et al., 2002). In addition, greater protein percentage in the milk of cows fed the moderate PS suggests a better nutrient availability, in particular that of microbial protein, likely due to a better distribution of nutrient intake over the day.

With regard to the effects of forage PS on feed intake, no clear consensus exists in the published literature. Feeding shorter PS was shown to increase feed intake levels in some studies (Teimouri Yansari et al., 2004; Tafaj et al., 2007; Alamouti et al., 2009), hence increasing the energy and nutrient supply to high-producing dairy cows. However, this effect was not supported by other research data (Yang and Beauchemin, 2006a,b, 2007), thus confirming the findings of Allen (2000), who postulated that physical rumen fill is not a consistently limiting factor of feed intake in high-producing dairy cows fed large amounts of concentrate (>50% in DM).

In contrast to the variable effects of forage PS on feed intake, however, most of the published literature data agree that forage PS has no effect on milk yield (Teimouri Yansari et al., 2004; Yang and Beauchemin, 2006a; Alamouti et al., 2009). In fact, higher milk production levels had been expected in several studies when dietary PS was decreased moderately, at least in cases where DM intake increased concurrently by roughly 1 to 2 kg/d (Kononoff and Heinrichs, 2003a; Teimouri Yansari et al., 2004; Alamouti et al., 2009). The absence of an effect on milk yield in all of the above-mentioned studies may be related to the fact that these studies were conducted as a Latin square design with relatively short experimental periods. Depending also on the stage of lactation, short-term increased energy and nutrient intake, in particular during mid and late lactation phases, can preferentially be used in the intermediary metabolism to improve body reserves rather than to increase milk synthesis in the mammary gland. Recent data by Al-Trad et al. (2009), who demonstrated that a short-term increase in the intravenous glucose supply enlarges body reserves but not milk yield, support this assumption. Whether dietary PS has a quantifiable effect on milk yield when measured over longer feeding periods remains to be determined by future research.

Ruminal Mat Formation

An extensive stratification of the reticuloruminal contents is typical for grazer ruminants (as opposed to browsers; Hofmann and Stewart, 1972; Hofmann, 1989) and serves the optimization of fermentation end-product harvest (Tafaj et al., 2004; Clauss et al., 2011). A fluid phase is located in the ventral part of the reticulorumen of dairy cattle, whereas the gas cap is in the dorsal rumen, and a thick-packed mat extends from the dorsal to the central part of reticulorumen, consisting of solid digesta with mainly large, newly ingested, buoyant feed particles (Poppi et al., 2001; Tafaj et al., 2004). Ruminal mat formation is considered a presupposition, as well as an indicator, of proper rumen function in dairy cows because of its 2 main physiological functions. One is to optimize the ruminal microenvironment, especially ruminal pH, by physical stimulation of rumination, salivation, and ruminal motility (Poppi et al., 2001; Tafaj et al., 2004; Zebeli et al., 2006b). This function determines whether fiber inclusion is adequate when feeding highly fermentable diets and will thus be analyzed in more detail in a later section devoted to fiber adequacy. The second function of the ruminal mat is to promote particle retention, thus allowing for more efficient digestion of fiber in the forestomach (Poppi et al., 2001; Tafaj et al., 2004; Zebeli et al., 2006b).

Sutherland (1988) described the ruminal mat as a very effective first-stage separator that can modulate the retention time of solid digesta through an increased selective retention ("filter bed" effect) for undigested small feed particles. Through filtration and mechanical entanglement, the ruminal mat functions to retain potentially escapable fiber particles, thus increasing the time allowed for digestion (Zebeli et al., 2006b). The formation, maintenance, and consistency of the ruminal mat strongly depend on dietary PS and the specific gravity of particles (Tafaj et al., 2004; Clauss et al., 2011) and, hence, peNDF content (Allen, 1997; Allen et al., 2006; Zebeli et al., 2007).

Role of peNDF in an Integrated Model on Rumen Metabolism

The role that dietary PS fractions and peNDF play in the formation, maintenance, and consistency of the ruminal mat, as well as its resulting physiological functions mentioned in the previous subsection, is summarized in a hypothetical model in Figure 1. An essential aspect in the latter model is the postulate that ruminal mat consistency is a major determinant for the regulation of rumen passage rate of solid digesta. The better the consistency of the ruminal mat, the lower the probability of feed particles to escape undegraded to the omasum. Increasing the escape of potentially degradable feed particles from the rumen negatively affects fiber degradation and feed utilization (Weidner and Grant, 1994). The model further assumes that a low quality, unstable ruminal mat can accelerate the passage rate of solid digesta, in particular of small-sized particles, from the rumen through a reduced "filter-bed" ability of this mat (Figure 1). This assumption is based on extensive research data that have confirmed that consistency and stability of a thick-packed ruminal mat increase the probability of small feed particles for entrapment into this mat by the filter-bed effect, and reduce the probability of these particles flowing to the omasum (Zebeli et al., 2006b; Kennedy, 2006; Clauss et al., 2011), hence regulating the passage kinetics of particles in the forestomachs. Figure 1 also describes the regulating functions of the consistency of ruminal mat for particle kinetics within the reticulorumen, which can be understood and modeled as a "valve" to regulate the portion of particles flowing back to the dorsal mat (λ_d) or flowing out to omasum (k_p). Impairing the consistency of the ruminal mat by feeding peNDF-limited diets increases the likelihood of feed particles leaving the reticulorumen, and lowers their probability of reintegrating into the dorsal mat (Figure 1). In this model, the likelihood of different particle sizes of digesta leaving the reticulorumen or reintegrating into the dorsal mat is indicated using arrow thickness (Figure 1).

In addition, according to this model, the rumen digesta is divided into 3 integral parts: the dorsal pool (mat), ventral reticulorumen, and free rumen liquid pool (Tafaj et al., 2004). We assume that the pools of particles obtained daily from TMR are divided into 4 groups: particles >19 mm; particles >8 to 19 mm; particles >1.18 to 8 mm, and particles <1.18 mm (Heinrichs et al., 1999). Each pool of particles contains soluble substrates (e.g., sugars, soluble starches, pectins, and soluble proteins); insoluble, potentially degradable substrates (e.g., starches, cellulose, degradable proteins); and potentially undegradable substrate fractions that include completely indigestible lignins and associated products such as undegradable protein as well as fiber that might not be degraded due to unfavorable rumen conditions (Zebeli et al., 2006b). The model assumes that the particle fraction of <1.18 mm contains larger amounts of soluble and easily degradable fractions and less substrate pertaining to the last group. The reduction in size of particles in the reticulorumen is attributed to factors such as chewing activity during eating and rumination (i.e., the larger the particles, the longer the time spent chewing and the more intensive the comminution of these particles; Fernandez et al., 2004), degradability characteristics of the feed (Zebeli et al., 2006b), as well as microbial activity in the mat and ventral reticulorumen (Ölschläger, 2007), all of which are affected by dietary PS and peNDF content. Factors such as feed degradability characteristics, including the increased resistance to microbial attachment and digestion with increasing PS, and ruminal pH are assumed the most important determinants of microbial activity (Figure 1). Ruminal pH is especially critical when feeding large amounts of readily fermentable carbohydrates and is primarily dependent on short-chain fatty acid (**SCFA**) production and absorption, and HCO_3^- flow into the rumen (Allen, 1997; Aschenbach et al., 2011).

The symbol $\otimes$ in Figure 1 indicates the extraction of SCFA from the rumen, which has recently been reviewed in detail by Aschenbach et al. (2011). Apical uptake of SCFA is partly mediated as $SCFA^-/HCO_3^-$ exchange (Gäbel et al., 1991; Kramer et al., 1996; Aschenbach et al., 2009), and estimates in high-yielding dairy cows indicate that HCO_3^- is introduced into the rumen in approximately equal shares via saliva and via secretion across the ruminal epithelium (Aschenbach et al., 2011). Moreover, apical diffusion of undissociated SCFA will directly remove large quantities of protons from the ruminal content (Gäbel et al., 2002; Aschenbach et al., 2011). The pathways of basolateral exit of SCFA are not fully resolved at present but include the monocarboxylate transporter 1 (Müller et al., 2002; Kirat et al., 2006; Graham et al., 2007), which is most likely complemented by lipophilic diffusion (Gäbel et al., 2002; Gäbel and Aschenbach, 2006), an anion channel permeable to large anions (Stumpff et al., 2009), and $SCFA^-/HCO_3^-$ exchange (Bilk et al., 2005). Direct or indirect coupling of basolateral SCFA extrusion to either proton export or HCO_3^- import could contribute to net removal of H^+ from the epithelial cells into the blood (Allen, 1997; Aschenbach et al., 2011). From a practical point of view, this process is important because it could mitigate the risk of development of SARA in high-producing dairy cows. The model assumes that peNDF content in the diet is essential in stimulating contractions of the reticulorumen. The motility of the ruminal wall, in turn, is believed to enhance the rate
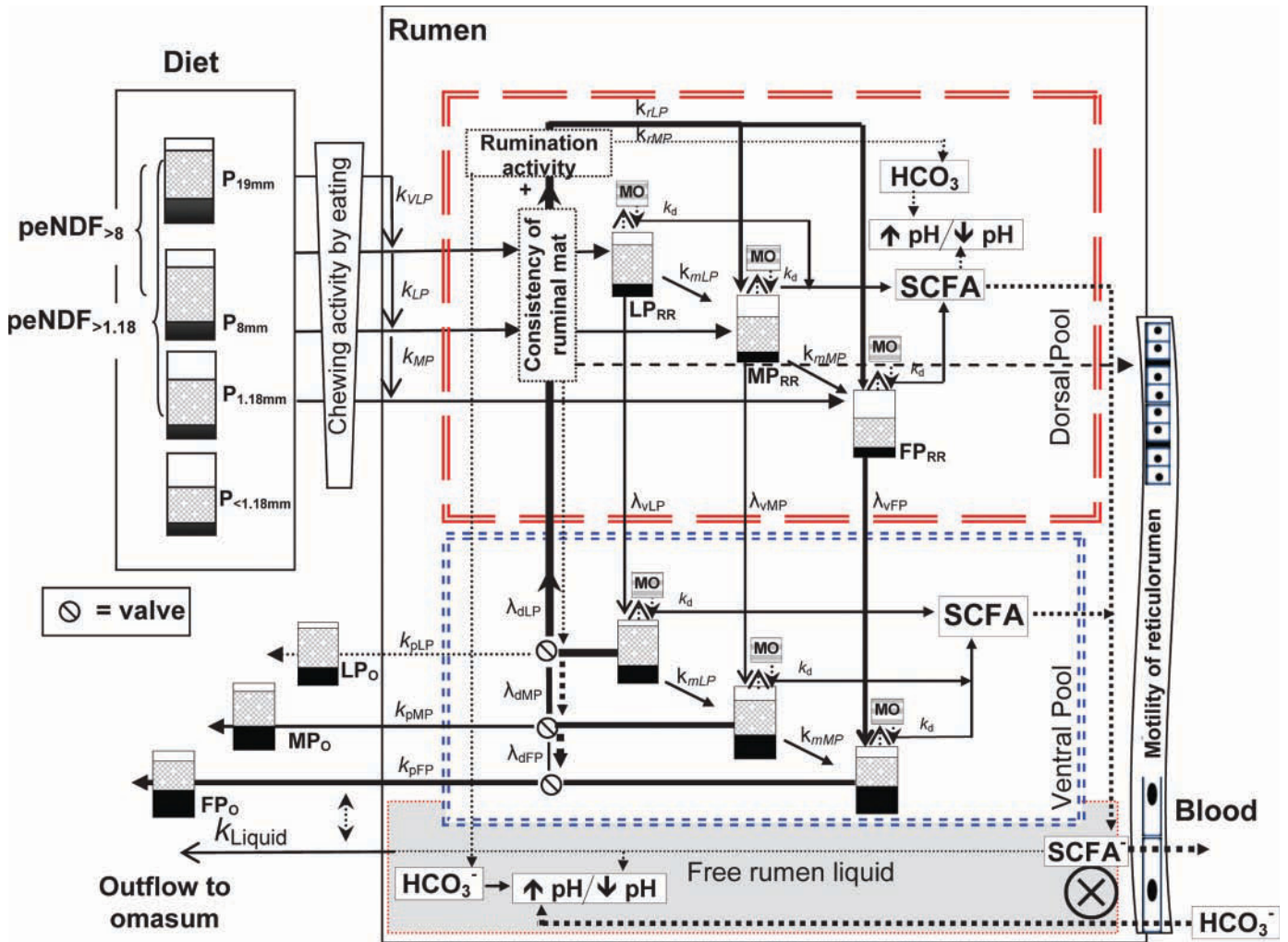
Figure 1. Hypothetical model describing the main physiological effects of dietary particle size (PS) and physically effective NDF (peNDF) on the formation and maintenance of a thick-packed ruminal mat as well as on the regulation of ruminal pH and kinetics of digesta in the rumen of dairy cows (adapted from Zebeli et al., 2006b); proportions of different particle fractions in the TMR (determined by Penn State Particle Separator): P_{19} = fraction of dietary particles >19 mm, P_8 = fraction of dietary particles >8 to 19 mm, $P_{1.18}$ = fraction of dietary particles >1.18 to 8 mm, $P_{<1.18}$ = fraction of dietary particles <1.18 mm, peNDF$_{>1.18}$ = dietary physically effective NDF inclusive of particles >1.18 mm, peNDF$_{>8}$ = dietary physically effective NDF inclusive of particles >8 mm; proportions of different particle fractions of digesta in the reticulorumen (dorsal and ventral pool): LP_{RR} = fraction of large particles (>8 mm) in reticulorumen, MP_{RR} = fraction of medium particles (>1.18–8 mm) in reticulorumen, FP_{RR} = fraction of fine particles (<1.18 mm) in reticulorumen, LP_O = fraction of large particles (>8 mm) flowing to omasum, MP_O = fraction of medium particles (>1.18–8 mm) flowing to omasum, FP_O = fraction of fine particles (<1.18 mm) flowing to omasum; description of the symbols indicating substrates contained in each particle fraction and the microbiota: white bar = soluble substrates, gray bar = insoluble, potentially digestible substrates, dark bar = potentially undigestible substrates, MO = populations of microbiota in the rumen; different rates that show changes in the particle fractions with time after feeding: k_{VLP}, k_{LP}, k_{MP} = comminution of P_{19}, P_8, and $P_{1.18}$ particles of diet during chewing by eating, k_{rLP}, k_{rMP} = comminution of LP_{RR} and MP_{RR} particles in reticulorumen by chewing during rumination, k_{mLP}, k_{mMP} = comminution of LP_{RR}, MP_{RR} particles in reticulorumen through the activity of microbiota, k_d = fractional degradation rate of soluble (e.g., sugars and pectins) and insoluble, potentially degradable (e.g., starches, cellulose) substrates contained in different particle fractions, k_{pLP}, k_{pMP}, k_{pFP} = fractional passage rate of particles (LP_O, MP_O, and FP_O) from reticulorumen to omasum (it is assumed that: $k_{pFP} > k_{pMP} > k_{pLP}$), k_{Liquid} = fractional passage rate of free rumen liquid out of reticulorumen, λ_{dLP}, λ_{dMP}, λ_{dFP} = rate of entrapment/backflow of particles (LP_{RR}, MP_{RR}, and FP_{RR}) from ventral to the dorsal rumen mat (it is assumed that $\lambda_{dLP} > \lambda_{dMP} > \lambda_{dFP}$), λ_{vLP}, λ_{vMP}, λ_{vFP} = rate of sedimentation of particles (LP_{RR}, MP_{RR}, and FP_{RR}) from the dorsal to the ventral rumen pool (it is assumed that: $\lambda_{vFP} > \lambda_{vMP} > \lambda_{vLP}$). Color version available in the online PDF.

of SCFA absorption from the rumen and, therefore, to improve the acid:base balance of the rumen content (Allen et al., 2006; Figure 1).

On the other hand, the ruminal mat can also improve the buffering of the rumen contents by increasing

the flow of HCO_3^--rich saliva due to the mechanical stimulation of rumination (Poppi et al., 2001; Tafaj et al., 2004; Zebeli et al., 2006b; Figure 1). Thereby, it also counteracts depressions of ruminal pH and helps maintaining a proper environment for multi-species mi-

crobiota and synthesis processes in the rumen (Tajima et al., 2000; Krause and Pell, 2003).

Differences Between Rumen Digesta Phases

Flotation behavior and ruminal mat retention of small particles has mainly been studied for forages to date (Wattiaux et al., 1992; Bhatti and Firkins, 1995), but concentrate particles with large amounts of easily degradable substrate and intensive gas production may also be entrapped in the mat (Tafaj et al., 2004). Thereby, the ruminal mat is not only the site of intensive fiber fermentation but also a site of concentrate fermentation, which has consequences for the chemical and microbial composition of the ruminal mat in concentrate-fed dairy cows (Figure 1). In an attempt to understand the effect of ruminal mat formation on the fermentation processes, Tafaj et al. (2004, 2006a,b) investigated the composition and metabolism of the different phases of digesta in the rumen of dairy cows, including dorsal, medial, and ventral layers, and coined the term particle-associated rumen liquid (**PARL**) for the proportion of fluid attached to digesta particles found in the dorsal sac of the rumen. In contrast, the content of ventral sac consists of extensively digested, small, potentially escapable particles, "swimming" in the free rumen liquid (**FRL**; Tafaj et al., 2004).

Numerous studies have reported differences in microorganism concentration (Martin et al., 1999; Ölschläger, 2007; Witzig, 2009) and metabolism (Tafaj et al., 2004; Storm and Kristensen, 2010), including the concentrations of SCFA and pH values between PARL and FRL. Moreover, our team at the University of Hohenheim was one of the first to conduct research investigating digestive responses to dietary treatments in both PARL and FRL (Tafaj et al., 2001). This research demonstrated that the responses of ruminal fermentation profile and degradation characteristics to dietary changes are different between the 2 phases in dairy cows. As such, dietary responses measured in the FRL do not give full insight into the whole rumen environment (Tafaj et al., 2004; Li et al., 2009; Storm and Kristensen, 2010). Yet, the FRL is the most frequently investigated phase of the rumen, and most rumen physiology research is based on data collected from FRL (Aschenbach et al., 2011). Compared with FRL, however, PARL has been shown to have greater (by up to 50 mmol/L) SCFA and greater amino acid N concentrations, higher fibrolytic bacteria and protozoa counts, but much lower HCO_3^- concentration, lower butyrate proportions, and a pH approximately 0.7 units lower than that of the FRL (Tafaj et al., 2004; Ölschläger, 2007; Zebeli et al., 2008d). Interestingly, the diet-induced changes in the chemical composition of the digesta, in particular the

effects of concentrate level, were more pronounced in PARL than in FRL (Tafaj et al., 2006b; Zebeli et al., 2008c). The latter was explained by greater microbial density and diversity of PARL (Ölschläger, 2007). The mechanisms and consequences behind these adaptations, however, are far from clear at present. It would be of great interest to clarify the mechanisms, particularly in dairy cows fed large amounts of concentrate, because the rumen microbiota inhabiting PARL plays an important role in fiber degradation despite the much lower pH values found in PARL than in FRL.

Potentials and Limitations of the peNDF Concept

Determination of adequate amounts of dietary fiber needed to maintain proper functioning of the rumen ecosystem and to prevent SARA is a key aspect in dairy cattle nutrition (Mertens, 1997; De Brabander et al., 2002). The concept of peNDF is more efficient to indicate physical effectiveness of a diet and determine fiber adequacy in dairy cattle because it incorporates information on PS and chemical fiber content of the diet. Yet, determining physical characteristics of the TMR by simply accounting for theoretical PS of forages has several flaws. This is mainly due to the differences existing in the procedures of measurement and expression of PS of forages. Murphy and Zhu (1997) compared 9 methods for evaluating PS of feedstuffs and observed inconsistency in the estimates of PS measurements. Research conducted by Heinrichs et al. (1999) also demonstrated that PS of forages before preparing the TMR differs strongly from PS of TMR containing the same forages. To overcome this difficulty, Lammers et al. (1996) and Heinrichs et al. (1999) suggested the fractionation of the TMR into various PS fractions using the manually operated Penn State Particle Separator (**PSPS**). Besides measuring peNDF content, data obtained by PSPS containing 3 screens and a pan can also be used to estimate geometric mean PS ($\mathbf{X_{gm}}$) and geometric standard deviation ($\mathbf{S_{gm}}$; ANSI, 2001; Kononoff et al., 2003a). Compared with theoretical PS of forages, the information of PS distribution based on X_{gm} and S_{gm} is more complete and accurate. For example, forages with a similar theoretical PS and demonstrating similar percentages of material retained above the fine screen of PSPS (e.g., 1.18 mm) can have different X_{gm} and S_{gm}. This is because of the presence of differing proportions of very long and intermediate PS in the diet (Kononoff et al., 2003a). The latter authors tested several sieving protocols of PSPS and concluded that shaking frequency (1.1 Hz or greater/min) and stroke length (17 cm) are important parameters to ensure reproducible measurement of peNDF content of the TMR without differences in X_{gm} and S_{gm}. In contrast,

the moisture content of the sample did not play any role in the sieving results of the TMR (Kononoff et al., 2003a). Overall, when determined under these conditions, peNDF appears to be more advantageous than theoretical PS and helps preventing the bias related to differences in the expression and measurement of PS of the forages.

However, the use of the peNDF concept as a routine method to determine dietary fiber adequacy in dairy cows has not yet been established despite some advantages compared with other methods and the large volume of gathered research data on the physiological effects of dietary peNDF. The hesitance to use the peNDF concept in dairy nutrition appears to be based on 3 main limitations.

One limitation is the different methods of measuring peNDF, which refers to both sieve architecture (i.e., spacing between the holes, thickness of the material, and shape of the instrument) and sieve hole size. Most published literature data were collected using the PSPS. Lammers et al. (1996) introduced PSPS as a simple method for the calculation of peNDF based on the sum of DM proportion retained on sieves of 19 mm and 8 mm of PSPS multiplied by the NDF content of the diet ($peNDF_{>8}$). More recently, the same team at the Pennsylvania State University (Kononoff et al., 2003a) introduced an additional sieve of 1.18 mm screen size and calculated the peNDF content as the sum of particles retained on sieves of 19, 8, and 1.18 mm multiplied by the NDF content of the diet ($peNDF_{>1.18}$). In both cases, however, a uniform distribution of NDF was assumed throughout the fractions retained on the different sieves. To overcome the latter limitation, NDF fractions were measured separately as retained on the sieve 8 mm ($peNDF_{>8-NDF}$), or 1.18 mm ($peNDF_{>1.18-NDF}$) of PSPS. Although this increased the precision of expressing the peNDF content of TMR, different studies have shown that both these methods gave similar rankings of the dietary peNDF contents (Rustomo et al., 2006a; Zebeli et al., 2008b; Alamouti et al., 2009). Because measurement of $peNDF_{>8}$ and $peNDF_{>1.18}$ is a more practical and less costly procedure than the measurement of $peNDF_{>8-NDF}$ and $peNDF_{>1.18-NDF}$, the first method would be more applicable on the farm. However, it is not yet clear whether the different measurements can be used interchangeably or which measure of peNDF provides the most accurate estimate of physiological responses such as rumination, saliva production, rumen buffering, and SARA prevention (Einarson et al., 2004; Yang and Beauchemin, 2006a,b).

Another limitation is related to the variation due to different mixing procedures used to prepare TMR, which poses a challenge for implementing peNDF in ration balancing software. In this regard, Heinrichs et al. (1999) demonstrated that the actual PS and the content of peNDF of the fed TMR is strongly dependent on factors including PS of grains and factors related to processing, mixing, or delivery of the TMR to the cows. These factors may serve as an important source of variation and hamper production of a TMR with desired peNDF content. Additional research efforts are required to standardize the methods of mixing the TMR.

Another reason that the scientific community has been reluctant in accepting the peNDF concept was the lack of strong evidence for a relationship between the feeds' physical effectiveness and the cow's important digestive responses such as the maintenance of ruminal pH, risk of SARA, and nutrient (fiber) digestion. Research results relating to this issue were not conclusive in many cases (Allen, 1997; Mertens, 1997; Tafaj et al., 2007). For example, feeding different PS or amounts of peNDF in the diet affected ruminal pH and fiber digestibility in some experiments (Mertens, 1997) but not in others (for review, see Zebeli et al., 2006a). This discrepancy in results hampers the drawing of conclusions regarding the effects of peNDF in dairy cattle nutrition. Different concentrate compositions with grain of various degrees of fermentability may explain the major discrepancies in the results reported by different research articles (Zebeli et al., 2006a; Tafaj et al., 2007). In fact, the peNDF concept does not take into consideration the differences in ruminal fermentability of feedstuffs, and this limits our ability to provide recommendations of peNDF. For example, the dietary responses might be completely different when barley instead of corn grain is fed to the cows even if the diet contains the same amount of peNDF (Khorasani et al., 2001; Zebeli et al., 2006b; Weber, 2007).

Last, the interpretation of the response of the ruminal pH and its resulting effects on fiber degradation or development of SARA is a controversial issue. The threshold of ruminal pH below which SARA develops has not yet been properly defined (Aschenbach et al., 2011), and different researchers use different threshold values such as 5.6 (Keunen et al., 2002), 5.8 (Beauchemin et al., 2003), or 6.0 (Plaizier, 2004). In addition, the complexity of the interactions between feed intake, grain type, concentrate amount fed, and ruminal degradability of different feedstuffs, as well as the uncertainty in defining the response of the ruminal pH, makes it difficult to quantitatively characterize the effects of peNDF on ruminal fermentation and prevention of SARA.

Taken together, the limitations in assessing fiber adequacy from peNDF content result in part from the different methods used to determine peNDF content, and from the use of different SARA thresholds to define

the effect of peNDF. These issues can be resolved in future by further efforts toward standardization. More importantly, however, the application of the peNDF concept to assess fiber adequacy in dairy diet formulation is greatly dependent on the incorporation of grain fermentability into the peNDF concept. This will be analyzed in more detail in the next sections.

DIET FERMENTABILITY

Grain Fermentability in the Diet

The increase of the genetic merit of dairy cows for milk production during the last decades has led to the use of high-starch diets to compensate the deficit of energy intake needed to meet the requirements for milk production (NRC, 2001; Plaizier et al., 2008). Feeding of the latter diets, in particular during early lactation phases, often occurs at the expense of the proportion of peNDF in the diet, which is needed for proper and healthy ruminal functioning. Figure 1 shows the distribution of particle fractions for a typical dairy diet in terms of the distribution of particle size pools; pools of particles obtained daily from TMR are divided into 4 groups; that is, particles >19 mm; particles >8 to 19 mm; particles >1.18 to 8 mm, and particles <1.18 mm. However, increasing the amount of grain in TMR to increase its energy content is associated with greater particle fraction of <1.18 mm, and this pool of particles contains larger amounts of soluble and easily degradable substrates and less structural carbohydrates (Figure 1).

Several research articles have shown that the requirement for physical effective fiber is strongly dependent on factors related to dietary grain, such as forage to grain ratio (Tafaj et al., 2004), grain processing (Yang and Beauchemin, 2004), and grain source (Beauchemin and Rode, 1997; Khorasani et al., 2001), as well as the amount and fermentability of starch contained therein (De Brabander et al., 2002; Silveira et al., 2007a; Iqbal et al., 2009). For example, starches of several cereals such as corn and oat grains are less degradable in the rumen (Firkins et al., 2001; Offner et al., 2003). In addition, Rustomo et al. (2006b) estimated a lower acidogenic potential of oat than other cereal grains such as barley or wheat using a promising in vitro method to estimate the acidogenic values of the feeds. These data indicated that the latter grains in the diet of dairy cows have greater acidic load potentials in the rumen, hence requiring greater amounts of peNDF to balance these high acidogenic values (Rustomo et al., 2006a,b).

Mounting evidence indicates that the differences observed in the physiological responses of cows fed diets based on corn versus barley grain can be attributed to diverse compositional structure and degradation characteristics of their starch. The major part of corn starch consists of amylose, whereas barley starch typically contains the more easily degradable amylopectin (Theurer, 1986). Corn starch is encased in a poorly rumen-degradable endosperm compared with barley starch (Theurer, 1986; Walker et al., 2009) and, as a consequence, corn contains greater amounts of bypass starch than barley (Huntington, 1997). Thus, degradation kinetics and the effective ruminal degradability of starch are lower for corn grain than for barley grain (Offner et al., 2003).

The fact that cows fed on corn-based diets have a lower risk of developing SARA than cows fed diets based only on barley grain has been documented by several workers (DePeters and Taylor, 1985; Overton et al., 1995; Khorasani et al., 2001). In a dose-response trial by Tafaj et al. (2006a), dairy cows tolerated up to 60% corn-based concentrate in the diet without experiencing rumen disorders, despite declining levels of peNDF. With barley grain as concentrate source, Ametaj et al. (2010) demonstrated in another dose-response study that already 45% concentrate in TMR impaired rumen fermentation profile, generating harmful metabolites for the host's health. These findings indicate that low peNDF levels would be better tolerated with diets based on corn grain as opposed to barley grain. However, also within cereal grains, fermentability may vary based on the composition of the endosperm, with fermentability being lower for corn grain with vitreous versus floury endosperm (Taylor and Allen, 2005a; Allen et al., 2008; Lopes et al., 2009). Vitreous endosperm has a lower potential to lower ruminal pH values than floury endosperm (Taylor and Allen, 2005b), which equally implies a lesser requirement for peNDF in the ration.

Similar effects in the variability of starch within a grain source were documented for barley (Silveira et al., 2007a; Walker et al., 2009). For example, Silveira et al. (2007a) compared 2 barley grain cultivars at 2 levels of starch differing in expected ruminal starch degradation of these barley cultivars. They found completely different responses such as a significant reduction of NDF degradation when barley grain of faster ruminal starch degradation was fed. An explanation could be the time during which ruminal pH was <5.8, which was significantly longer for the rapidly degradable barley starch diets, and this effect likely impaired fiber degradation in the rumen. Additional variation sources of starch degradability have been suggested. For example, conservation method can also have an effect on starch degradation rate. Data summarized by Offner et al. (2003) indicated that high-moisture maize grain has a higher effective degradation rate in the rumen

compared with dry maize grain, indicating that diets based on preserved grain sources might have a greater degradability in the rumen.

Chemical processing of rapidly degradable grains, such as barley grain, in the rumen to slow down their ruminal degradation has received increasing interest recently. Lowering the ruminal degradation characteristics of the starch of barley grain (and hence the potential of this cereal to causing rumen metabolic perturbations when fed in large amounts) without impairing the overall digestion of starch in the gastrointestinal tract is an interesting strategy to improve the feeding and health value as well as utilization of barley grain in ruminant animals. Martínez et al. (2005) used tannic acid to lower ruminal degradation of barley and suggested this method as an effective strategy for slowing down the ruminal disappearance of barley to improve starch utilization by ruminants. A recent study by Iqbal et al. (2009) demonstrated that steeping barley grain in low concentrations of lactic acid for 48 h before feeding to the cows lowered degradation rate in situ and prevented ruminal pH decreases after the morning feeding. Although all diets in the study by Iqbal et al. (2009) contained similar amounts of forages (55% in DM), forage PS, and hence peNDF, the feeding of steeped barley grain enhanced rumen pH, hence lowering the requirements for peNDF compared with cows that consumed untreated barley grain. Feeding of cereal grains with lowered rumen starch degradation might be particularly important in the feeding of early lactation high-producing dairy cows, in which the requirements for energy and, in particular for peNDF, are more difficult to meet.

Forage Digestibility in the Diet

Besides considering grain fermentability, the digestibility of forages in the diet is also believed to play a role in the cow's responses to dietary peNDF. The rationale behind this relationship is that forages with greater fermentability, such as brown midrib corn silage with enhanced NDF digestibility, may be physically more fragile, and thus less effective in stimulating chewing (Taylor and Allen, 2005c). However, although forages with greater fermentability might be more fragile, their degradation rate in the rumen is much lower than that of grains and by-products; hence their rapid degradation does not create a problem for rapid VFA accumulation in the rumen. Inclusion of greater amounts of forages having high NDF digestibility often occurs at the expense of grain proportion in the diet, thus resulting in lower intake of grain and greater NDF intake per day (Zebeli et al., 2006a).

On the other hand, effects of enhanced NDF digestibility of forages on chewing activities and rumen pH are not consistent in literature; greater NDF digestibility of forages was shown to affect positively (Zebeli et al., 2006a), negatively (Taylor and Allen, 2005c), or not (Oba and Allen, 2000) the chewing activities in dairy cattle. For example, Zebeli et al. (2006a) observed in a meta-analysis that the amount of peNDF in the diet and digestible organic matter of forages in the diet correlated positively to chewing ($R^2 = 0.23$) and rumination activity ($R^2 = 0.29$). In contrast, research conducted by Oba and Allen (2000) indicated that feeding brown midrib corn silage (high NDF digestibility) had no effect on ruminating time per day or per kilogram of NDF intake, whereas those by Taylor and Allen (2005a,c) showed that cows fed brown midrib corn silage decreased ruminating time and total chewing time (Taylor and Allen, 2005c), and rumen pH (Taylor and Allen, 2005b); however, total NDF digestibility was increased and no negative effects were observed on the performance of the cows (Taylor and Allen, 2005a). The effect of forage degradation characteristics on chewing activities, and hence on the interactions among forage fermentability and the content of peNDF is another area of interest that warrants further research before quantitative relationships can be derived or definite conclusions drawn.

DETERMINING REQUIREMENTS FOR PHYSICALLY EFFECTIVE NDF AND ADEQUACY OF DIETARY FIBER

Including adequate amounts of dietary peNDF are important for the optimization of ruminal pH when feeding highly fermentable diets to dairy cows. When defining the requirement for peNDF, it is important to account for the peNDF fraction(s) included. The measurements of peNDF are different when measured as $peNDF_{>1.18}$ (Kononoff et al., 2003a) and $peNDF_{>8}$ (Lammers et al., 1996), because the $peNDF_{>1.18}$ concept additionally includes the particle fraction between 1.18- and 8-mm screens. We have used a meta-analytical modeling approach comprising experiments conducted over the last 2 decades to compare the predictive value of the different peNDF pool sizes for different response variables (Zebeli et al., 2008a, 2010). Interestingly, the modeling data summarized in Table 1 indicate that the prediction capabilities of $peNDF_{>1.18}$ and $peNDF_{>8}$ are similar for some variables such as ruminal pH, and this finding suggests that they can be used interchangeably to predict the risk of SARA. However, their effects differed for the prediction of some other physiological variables such as chewing and rumination activity and DM

Table 1. Best-fit equations to predict various physiological responses to dietary physically effective NDF (peNDF) in TMR in high-yielding dairy cows (adapted from Zebeli et al., 2008a, 2010)

Response parameter (Y)	Dietary factor[1] (X)	Parameter estimates[2]				Model statistics	
		Intercept	Slope	π	Plateau	RMSE[3]	R^2
Feed intake (kg of DM/d)	$peNDF_{>8}$ (% of DM)	27.6	−0.28	14.9	23.4	0.67	0.48
Rumen pH	$peNDF_{>8}$ (% of DM)	5.57	0.034	18.5	6.22	0.12	0.62
Time pH <5.8 (h/d)	$peNDF_{>8}$ (% of DM)	13.4	−0.58	17.0	3.67	2.02	0.61
ADF digestibility (%)	Time pH <5.8 (h/d)	49.3	−0.93	3.55	46.0	4.23	0.31
Rumen pH	$peNDF_{>1.18}$ (% of DM)	5.59	0.022	31.2	6.27	0.14	0.50
Rumination (min/d)	$peNDF_{>8}$ (% of DM)	512.7	$- 243 \times \exp^{-0.0768}$	—	—	39.8	0.42
Chewing activity (min/d)	$peNDF_{>8}$ (% of DM)	574.4	9.072	—	—	86.2	0.25

[1]$peNDF_{>8}$ = peNDF inclusive of particles >8 mm; $peNDF_{>1.18}$ = peNDF inclusive of particles >1.18 mm.

[2]π = breakpoint of X; plateau = asymptotic plateau value of Y.

[3]RMSE = root mean square error.

intake level, which were better predicted by $peNDF_{>8}$ (Zebeli et al., 2010) than by $peNDF_{>1.18}$ (Zebeli et al., 2008a). The latter finding is in line with the already stated fact that longer particles contribute better to ruminal mat formation; that is, $peNDF_{>8}$ is a better predictor of physical fill in the reticulorumen.

A main outcome of our modeling approaches was that the effect of peNDF on different response variables showed breakpoints where a plateau was reached; that is, inclusion of peNDF above the breakpoint did not affect the response variable any further (Table 1). For example, the discovery of similar asymptotic associations between ruminal pH and rumination time with dietary $peNDF_{>8}$ up to 16.4 to 20.6% in the diet (Table 1; Zebeli et al., 2010) indicated the presence of physiological limits beyond which $peNDF_{>8}$ cannot further improve rumination and rumen buffering in lactating dairy cattle.

Another main innovation of the modeling approaches was the mathematical description of the interaction between peNDF and fermentable starch in the diet. The determination of dietary fiber adequacy essentially needs to take into account the amount of degradable starch from grains when predicting the depression of ruminal pH. Based on the multiple regression equation developed by Zebeli et al. (2008a), the model was used to estimate the required concentrations of peNDF in the diet needed to maintain normal rumen function in dependency of theoretical values of DM intake and rumen-degradable starch from grains. As shown in Table 2, dairy cows can tolerate diets where $peNDF_{>1.18}$ is lower than the recommended 31.2% $peNDF_{>1.18}$ within certain limits, when the amount of rumen-degradable starch contained in the concentrate mixture and the DM intake level of the cows are lowered. A low quantity of rumen degradable starch in the diet can be obtained by feeding cereal grains containing low amounts of degradable starch such as corn grain (Overton et al.,

1995; Khorasani et al., 2001; Tafaj et al., 2006a), barley grain varieties that are bred to contain low amounts of fermentable starch (Silveira et al., 2007a,b), or most recently by treating barley grain chemically with low concentrations of lactic acid (Iqbal et al., 2009), or in situ with tannic acid (Martínez et al., 2005). To better quantify the response of ruminal pH to the amount of $peNDF_{>1.18}$ and degradable starch coming from grains, our data recommend to aim for inclusion of a ratio between $peNDF_{>1.18}$ and degradable starch coming from grains of 1.45 or higher (Zebeli et al., 2008a). The amount of rumen degradable starch was estimated using data of in situ studies by Offner et al. (2003) and Sauvant et al. (2004; for details, see Zebeli et al., 2008a)

The threshold of the ratio between $peNDF_{>1.18}$ and rumen-degradable starch of grains in the TMR mentioned above can be viewed as optimal in terms of balancing diets for peNDF and degradable carbohydrates. In practical terms, however, it should be mentioned that a ratio of 1.45 may be difficult to reach in cases when high-grain diets are based on cereals rich in rumen-degradable starch, such as barley or wheat. It is sensible to assume that such diets should benefit from the inclusion of greater amounts of dietary peNDF to help the neutralization of the released SCFA either by increasing their absorption through ruminal epithelia or through neutralization by salivary bicarbonate and phosphates (Allen, 1997; Aschenbach et al., 2011). However, feeding diets with an excess of $peNDF_{>8}$ was shown to decrease feed intake (Figure 2). Other studies have shown that feeding excessive amounts of peNDF can lower both feed intake and the efficiency of feed use (Yang and Beauchemin, 2007; Zebeli et al., 2008a). Consequently, the determination of a breakpoint in dietary peNDF is important beyond which no further advantages on ruminal pH response can be expected, particularly in terms of maximization of production responses in high-producing dairy cows.

Table 2. Requirements in peNDF$_{>1.18}$ (% of diet DM) in dependency of varying DMI amounts and the content of ruminally degradable starch from grains (RDSG) of the diet of dairy cows[1]

RDSG (% of DM)	DMI (kg/d)				
	18	20	22	24	26
10	28.5	29.2	29.9	30.7	31.4
14	30.0	30.8	31.5	32.2	32.9
18	31.6	32.3	33.0	33.8	34.5
22	33.1	33.8	34.6	35.3	36.0

[1]peNDF$_{>1.18}$ = physically effective NDF inclusive of particles >1.18 mm. Analysis performed according to the equation of Table 5 in Zebeli et al. (2008a).

The findings obtained with respect to thresholds for ruminal pH and DM intake in response to dietary peNDF$_{>8}$ are relevant from the perspective of the optimization of peNDF$_{>8}$ requirements in high-producing dairy cows. As shown in Figure 2 (area A), feeding less than 14.9% peNDF$_{>8}$ results in an imminent risk of SARA, and these diets can be seen as peNDF-limited diets. However, the inclusion of a concentration of peNDF$_{>8}$ in the diet beyond 14.9% of diet DM may lower DMI level (Figure 2) and potentially the produc-

tion of lactating dairy cows. Feeding cows between 14.8 and 18% peNDF$_{>8}$ may be viewed as safer in terms of the occurrence of SARA, although these diets may still result in lower DMI level (area B of Figure 2). It is clear, on the one hand, that peNDF$_{>8}$ is required to maintain normal ruminal pH, whereas, on the other hand, large amounts of peNDF$_{>8}$ are associated with decreased feed intake. Although these contradicting associations among peNDF$_{>8}$ and ruminal pH versus DMI are not a challenge when feeding cows with average milk produc-
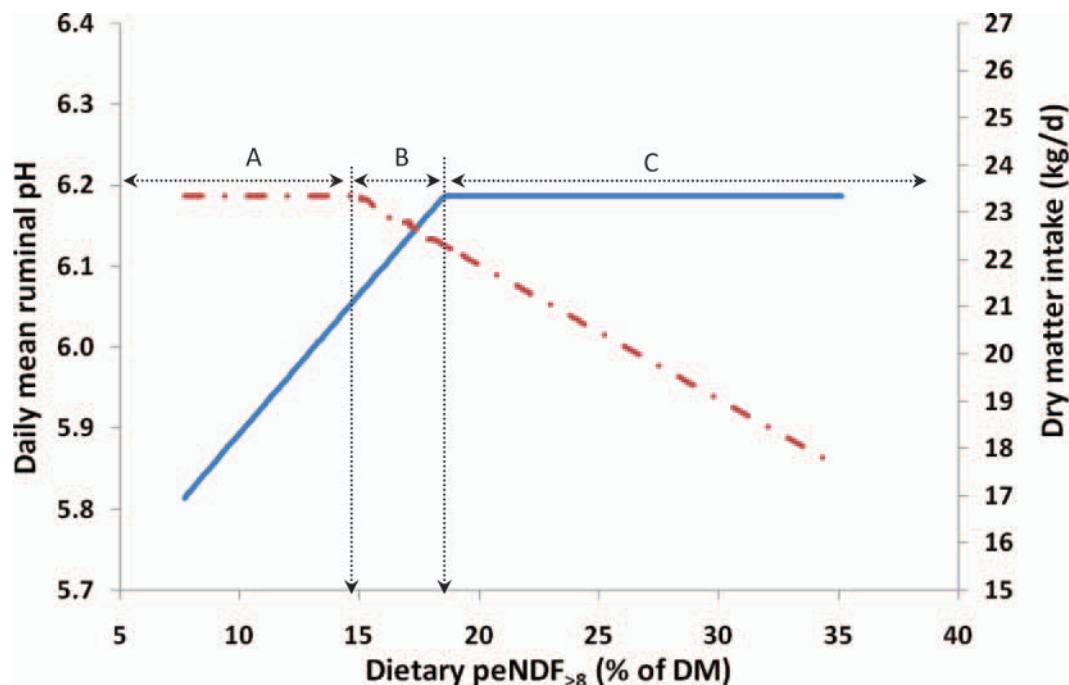

Figure 2. Best-fit broken line models describing the conflicting associations among dietary physically effective fiber (measured inclusive particles >8 mm; peNDF$_{>8}$) with daily mean ruminal pH (solid line) and DMI (dashed dotted line) in dairy cows (adapted from Zebeli et al., 2010; both equations to predict ruminal pH and DMI from dietary peNDF$_{>8}$ are in Table 1). (A) This area is typical for high-producing cows in early lactation with very high energy and nutrient demands (>23.5 kg of DMI/d) at an imminent risk of subacute ruminal acidosis (SARA); the same area also pertains to peNDF-limited diets, and grain fermentability becomes highly important in these diets to mitigate low levels of peNDF. (B) Diets falling in this area are potentially limited in peNDF but, due to lower feed intake (<23.5 kg of DM/d), these cows are at a lower risk of SARA than cows in the (A) area of the graph; however, grain fermentability is still important in these potentially peNDF-limited diets. (C) This area is typical for average-producing dairy cows in mid and late lactation consuming <22 kg of DM/d, which are at no risk of SARA, because these diets are not limited in peNDF; hence, grain fermentability in the diet does not play a role in modulating the risk of SARA. Color version available in the online PDF.

tion potential or during mid to late lactation (area C in Figure 2), they set clear limits when aiming to supply adequate amounts of peNDF$_{>8}$ to high-producing cows having high intake and production levels (areas A and B of Figure 2).

The contradicting associations found among peNDF$_{>8}$ and ruminal pH versus DMI (Figure 2) emphasize the difficulty and limitations in supplying adequate amounts of peNDF to high-producing cows having, at the same time, high demands for energy and nutrients. Dairy nutritionists are challenged to formulate diets that guarantee maximal feed and energy intake for high-producing dairy cows while providing adequate amounts of peNDF to maintain proper rumen function. Nutritional strategies for high-yielding dairy cows aim to maximize energy and nutrient intakes to support the high demand and prevent disorders related to energy deficiency such as ketosis. This challenge becomes particularly relevant during early lactation. For high-producing cows during early lactation, a rewarding feeding strategy is to decrease the amount of ruminally degradable starch in the diet, thereby reducing the requirement of peNDF, which, in turn, can increase the DMI by roughly 2 kg/d (Silveira et al., 2007b; Weber, 2007; Lechartier and Peyraud, 2010). This strategy might be a useful alternative for cows with high feed intake and milk production potential to meet their fiber requirements without impairing performance.

The modeling data recommended in this review derive from studies that tested physiological effects of peNDF in diets based on traditional cereal grains such as corn or barley. However, diets based on by-products contain lower amounts of degradable starch but are rich in other nutrients, such as cell wall soluble components, rumen undegradable protein, total sugars, and potentially digestible fiber (Sauvant et al., 2004). Indeed, by-products are increasingly replacing traditional grains as energy or protein sources in the diets of dairy cattle due to relatively low cost, growing availability (e.g., milling industry or bio-ethanol production), and relatively high organic matter digestibility (Eastridge, 2006). Although by-product research has received greater interest during the last decade, studies investigating rumen physiological effects of peNDF in diets substituting large amounts of cereal grains are still scarce.

In a recent study in which pelleted beet pulp partially substituted barley and corn grains, ruminal pH was not affected in Holstein cows, whereas apparent digestibility of all nutrients (including fiber) was increased independent of the peNDF content in the diet (Alamouti et al., 2009). We anticipate that diets based on such by-products may better tolerate marginal peNDF contents compared with grain-based diets. The reason for this is that high contents of dietary starch in grain based-

diets having rapid degradation rates typically stimulate acid accumulation in the rumen, resulting in reduction of ruminal pH to acidotic values. Conversely, although by-products rich in pectins, β-glucans, and fructans are also readily degradable in the rumen, they do not mimic the pH-lowering effect of starch because they generally are not fermented to lactate and their fermentation is ceased at low pH (Hall and Herejk, 2001).

Finally, extensive research conducted from many teams worldwide has shown that the inclusion of by-products in the diets of dairy cows to substitute traditional grains does not adversely affect cow performance and nutrient digestibility (Batajoo and Shaver, 1994; Depies and Armentano, 1995; Pereira and Armentano, 2000). For example, results of the study by Pereira and Armentano (2000) showed that adding alfalfa NDF to the low-forage/high-starch diet increased in situ degradation of forage NDF more than adding byproduct NDF, and the replacement of dietary starch with NDF from byproducts decreased OM digestibility; however, energy intake was similar across diets due to increased intake with the byproduct diets. An earlier study by Weidner and Grant (1994) suggested that inclusion of soybean hulls in coarsely chopped alfalfa hay-based diets improved digestion and feed utilization in dairy cows. In addition, Boddugari et al. (2001) reported greater ruminal mat consistency associated with a lowered outflow rate of solid digesta and a greater ruminal fiber digestibility and milk fat yield in early lactating dairy cows by partial replacement of concentrates with corn milling feed by-product. Milk production did not differ even when corn hominy was replaced with citrus pulp (Leiva et al., 2000) or when pelleted beet pulp substituted high-moisture corn (Voelker and Allen, 2003).

CONCLUSIONS

Feeding dairy cows a short forage PS has consistently been related to a high risk of SARA. However, research results summarized in this review indicate that a moderate reduction of PS can be helpful in promoting fiber degradation in the rumen, and improving the uniformity of ration. The latter is important because it results in less sorting of the feeds and improved circadian eating behavior of the cows, and even lowers the risk of rumen disorders due mainly to a better distribution of the peNDF intake during the day. As a plausible consequence of the aforementioned positive effects, the same diets can also increase feed intake and, hence, the nutrient supply for milk production of high-producing dairy cows. The models developed recently, which synthesize the latest knowledge, are an appropriate basis for estimation of dietary fiber adequacy in high-producing

dairy cows. The majority of the summarized scientific data suggest that a period lasting more than 5 to 6 h/d during which ruminal pH is <5.8 should be avoided to minimize health disturbances due to SARA. This modeling approach suggested that 31.2% $peNDF_{>1.18}$ or 18.5% $peNDF_{>8}$ in the diet (DM basis) is needed to ensure prevention of SARA. Because feeding of more than 14.9% $peNDF_{>8}$ in the diet DM may lower DMI and most likely the production of high-producing dairy cows, new feeding strategies are needed that allow the inclusion of more energy-dense diets without the need to increase their content in peNDF. In the light of increasing pressure for high milk production and, at the same time, more stable health in high-producing cows, future research areas should focus on strategies to modulate the fermentability characteristics of the diet, and to promote the absorption and metabolic capacity of ruminal epithelia. Because overall effects of peNDF in the diet depend on many other dietary (e.g., grain amount and fermentability, starch characteristics, forage PS, forage fermentability) and nondietary factors (e.g., sorting behavior and dynamic processes in the rumen), the development and use of dynamic models that take into account several dietary and nondietary factors, as outlined in the Figure 1, would be very helpful to formulate more customized diet-specific recommendations.

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