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Importance of “physically effective fibre” in ruminant nutrition: A review

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ABSTRACT

Dietary carbohydrates can be divided into two basic fractions: fibre and nonfibre carbohydrates (NFC). Fibre in dairy cow rations is essential for animal health, since it is required to support an appropriate rumen function and physiology. Therefore, ruminants require fibre in coarse physical form for a more effective chewing and ruminal activity. Increasing fibre content and forage particle size in diet effectively increases chewing activity resulting in increased saliva flow, rumen pH, acetate-to-propionate ratio, and milk fat levels. Increasing chewing activity and salivary buffer production are believed to be indicators of improving the dietary effect on rumen health and function. However, the physically effective NDF (peNDF) of a feed is related to the physical properties of its fibre (primarily particle size) that stimulates chewing activity and establishes the biphasic stratification of ruminal contents (floating mat of large particles on a pool of liquid and small particles). Thus, objective of this review discussing several parameters, including chewing, ruminal pH, acetate: propionate ratio, and milk fat percentage, have been used as animal responses to assess the effectiveness of NDF in dairy ruminant rations.

Key words: fibre, physically effective NDF, chewing activity, rumen pH, ruminant.

Abbreviations: NDF, neutral detergent fibre; ADF, acid detergent fibre; eNDF, effective NDF; peNDF, physically effective NDF; pef, physical effectiveness factor; NFC, nonfibre carbohydrate; NSC, nonstructural carbohydrate; TMR, total mixed ration; PSPS, Penn state particle separator; DM, dry matter; VFA, voluntary fatty acids; DMI, dry matter intake; U, unit; DF, dietary fibre; SCFA, short chain fatty acid; NDSF, neutral detergent-soluble fiber;

INTRODUCTION

Dietary carbohydrates can be divided into two basic fractions: fibre and nonfibre carbohydrates (NFC) (Figure 1). Fibre plays a fundamental role in ruminant and dairy cattle nutrition. It has been widely demonstrated that both the amount and physical form of dietary fibre are important in lactating dairy cows ration in order to maintain proper ruminal function, animal health status and milk composition. Some nutritionists define fibre as the any component in a feed that is not digested by mammalian enzymes. Some of these components are soluble under

mild extraction procedures and thus result in “soluble” and “insoluble” fibre. Most constituents of soluble fibre (pectin, fructans, beta-glucans) are readily fermented in the rumen and may even be readily fermented in the large intestine of monogastric animals [1,2,3]. Thus, Mertens [3] preferred a more restrictive definition of fibre as the “indigestible and slowly digesting, or incompletely available, fractions of feeds that occupies space in the gastrointestinal tract”, which defines fibre as insoluble components. Nutritionally, fibre has both physical and chemical attributes that are related to the mechanical processes of digestion (chewing and passage) and to enzymatic degradation associated with fermentation [3].

Mertens [4] stressed that chemical definition of dietary fibre such as neutral- (NDF) or acid-detergent (ADF) fibre content was an inadequate description of the fibre content of a diet. The ADF fraction of feedstuffs includes cellulose and lignin as the primary components. Concentrations of ADF and lignin are correlated more with digestibility than with intake [$r = -0.75$ and -0.46 for ADF digestibility and intake, respectively]. Many factors influence the relationship between ADF and digestibility, including forage variety, maturity at harvest, and storage conditions [5,6]. NDF is a measure of cellulose, hemicellulose, and lignin fractions of feeds. NDF is more highly correlated with feed volume and chewing activity than ADF or CF [5,7]. The National Research Council [8] recommends NDF to be maintained at 25% of dietary DM with at least 75% from forage for the NDF requirement. Therefore, there is room for up to 25% of the NDF from nonforage fibre sources (NFFS) to meet the NDF requirement [9]. Mertens [4] proposed definitions for both effective NDF (eNDF) and physically effective NDF (peNDF). The peNDF of a feed is related to the physical properties of its fibre (primarily particle size) that stimulates chewing activity and establishes the biphasic stratification of ruminal contents (floating mat of large particles on a pool of liquid and small particles) [4]. The peNDF content of the diet can be determined by multiplying the NDF concentration by the proportion of particles retained on a 1.18 mm sieve or by its physical effectiveness factor (pef) [9]. The eNDF is related to the sum total ability of a feed to replace roughage so that the percentage of fat in milk is effectively maintained. Because peNDF relates only to the physical properties of fibre, it is a more restricted term and concept than eNDF. The peNDF will always be less than NDF, whereas eNDF can be less than or greater than the NDF concentration in a feed (Figure 2) [10]. Effective NDF is required by dairy cows to stimulate chewing, maintain optimal rumen environment and prevent milk fat depression [4]. Several parameters, including chewing, ruminal pH, acetate:propionate ratio, and milk fat percentage, have been used as animal responses to assess the effectiveness of NDF in dairy rations [11]. The peNDF value of nonforage fibre sources is considerably lower than long-stem forages, but may be higher than some forms of concentrates, grains, and ground forages. Increased amounts of fibre in dairy rations stimulate chewing activity and reduce acid production. The cascade of events leading to a decrease in animal performance when too little effective fibre is fed includes decreased chewing activity, leading to less salivary buffer secretion, which leads to lower ruminal pH and results in altered ruminal fermentation patterns and the low ratios of acetate to propionate (A: P) that ultimately result in modified animal metabolism and reduced milk fat synthesis. It can be argued that inadequate fibre in the ration may not be the primary cause of the foregoing scenario. In many situations, readily fermentable nonfibrous carbohydrates (NFC) or nonstructural (NSC) carbohydrates are used to replace fibre in low fibre rations, and these rapidly fermenting carbohydrates may contribute to animal responses to low fibre rations [1,4]. Thus, objective of this review discussing several parameters, including chewing activity, ruminal pH, acetate:propionate ratio, and milk fat percentage, have been used as animal responses to assess the effectiveness of NDF (peNDF) in dairy ruminant rations.

Chewing Activity

Rate of saliva secretion and amount of saliva produced are determined by chewing activity, which in turn is influenced by the source of forage, forage to concentrate ratio, forage intake and physiological status of the cow. In terms of diet-related factors, intake limiting characteristics of diets such as bulk density, digestibility, rate of digestion, rumination time, total mastication time and passage of digesta from the ruminoreticulum are related to fibre content of the diet and forage: concentrate ratio [12].

The peNDF of a feed is related to the physical properties of its fibre (primarily particle size). This concept is based on the hypothesis that the fibre in long feed particles (> 1 cm) promotes chewing and saliva secretion which helps neutralize the acids produced during ruminal digestion of feeds [13]. The fibre that promotes chewing is considered physically effective [9]. Dietary particle size can influence voluntary intake, rate of digesta passage, and rate and extent of ruminal fermentation [1]. However, various methods are available to measure particle size of diets; the Penn State Particle Separator (PSPS) has become widely accepted as a quick and practical method for routine use on-farm to evaluate particle size of forages and TMR [14]. Using the PSPS a particle distribution can be determined from 3 fractions: proportion of particles retained on the 19.0-mm sieve, proportions of particles that pass through the 19.0-mm sieve but are retained on the 8.0-mm sieve, and proportion of particles that pass through the 8.0-mm sieve [14]. The pef (ranging from 0 to 1) is calculated as the sum of the proportion of particles retained on both 19.0 and 8.0 mm sieves [9].

Particle size reduction decreased chewing activity per kilogram of NDF (Table 1). Chopping forages through screens with 40-mm openings reduced total chewing activity to 80% of the unchopped original material. Grinding forages can reduce chewing activity to 20 to 60% of that for long forage, and chopping forages to a theoretical length of cut of about 5 mm resulted in about 70% of the chewing of forages chopped to a theoretical length of cut of 20 mm (Table 1; Figure 3) [4,15]. Mertens [16] assumed an exponential relationship between theoretical length of cut and chewing activity and predicted that the chewing activity of forages with theoretical lengths of cut of 40, 20, 5, and 1 mm would be 80, 70, 50, and 25%, respectively, of that for long forage. A key question then becomes: what is the critical particle size for passage from the rumen, and which fraction of particles remains in the rumen to stimulate chewing?[4] researcher found that feed particles retained on a 1.18-mm sieve (with a wet sieving technique) had a high resistance to passage from the rumen of sheep [4]. Mertens [16] consequently adopted the 1.18-mm sieving approach to fractionate the larger feed particles requiring chewing to pass from the rumen and this “1.18-mm fraction” has become the standard laboratory assessment for measuring pef for feeds using dry sieving techniques. Yansari et al. [17] showed that chewing activity per unit intake of peNDF was consistent across diets varying in particle length when estimated using systems that incorporated a 1.18-mm sieve. A consistent ratio of chewing activity to peNDF is desirable in terms of predicting chewing time based on peNDF intake. The proportion of particles >19mm may be a primary factor affecting chewing activity [17]. However, chewing activity is one of the most readily available indicators of ruminal health and function and of fibre effectiveness. Mertens [4] related chewing activity to both NDF concentration and particle size and proposed the concept of physically effective NDF (peNDF) to combine these properties in a single measurement. A database of chewing activity information was developed to estimate physical effectiveness factors for NDF from a variety of forages and physical forms. Based on the stimulation of chewing per unit of NDF intake, Mertens [4] reported that the physical effectiveness of coarse, medium and finely chopped corn silage ranged from 0.90 to 1.00, 0.85 to 0.95, and 0.80 to 0.90, respectively. The variation in physical effectiveness within and among chopping lengths indicates that a quantitative method for

measuring the peNDF of corn silage directly would be useful [4]. Beauchemin and Yang [13] showed that increased forage particle length increased intake of peNDF, but did not affect intake of DM and NDF. Number of chews (chews/d) and chewing time (eating + ruminating time) linearly increased with increasing dietary peNDF [9]. Gencoglu and Turkmen [18] concluded that forage source may have an effect on the chewing activity and rumen pH related to the peNDF and fibre structure. However, the proportion of particles > 19.0 mm and peNDF may be used as predictor of chewing activity.

Ruminal pH

Rumen pH is one of the most variable factors which can influence the microbial population and the levels of volatile fatty acids produced (Figure 4). The rumen pH at which certain functions are optimized can differ. There are two basic groups of bacteria which function at various pH's. The fibre digesters are most active at a pH of 6.2 to 6.8. Cellulolytic bacteria and methanogenic bacteria can be reduced when the pH begins to fall below 6.0. The starch digesters prefer a more acidic environment, a pH of 5.2 to 6.0. Certain species of protozoa can be greatly depressed with a pH under 5.5. To accommodate all these needs, normal feeding practices should maintain a pH range between 5.8 to 6.4. Ruminal pH may be a better indication of ruminal health and optimal function than the maintenance of milk fat production [4,19]. Of the proposed fiber systems, the concept of peNDF proposed by Mertens [4] is most closely related to ruminal pH because it is a measure that reflects the physical characteristics of fiber, mainly particle size, and its ability to stimulate chewing and saliva buffering in the rumen. Ruminal pH is influenced by the relative concentrations of acids, bases and buffers present at any given time. Fermentation of NFC found in high concentrations in concentrates and cereal grains results in rapid production of organic acids, while peNDF consumption stimulates saliva flow. Concurrent consumption of NFC and peNDF sources can be facilitated by combining diet components in a TMR rather than offering forage and concentrate separately [1]. Using approach of PSPS, the requirement for peNDF of dairy cows was determined to be 22% of ration DM to maintain an average ruminal pH of 6.0 [9]. Erdman [20] observed no relationship between ruminal pH and milk fat percentage, he also observed that the relationship between ruminal pH and ADF concentration was linear. Pitt *et al.*, [21] used data from sheep, beef cattle, and dairy cattle and observed a better relationship between eNDF and pH than between NDF and pH. They also observed that the relationship between eNDF and ruminal pH reached a plateau at pH 6.4. Low ruminal pH is the result of an accumulation of VFA due to feeding diets containing high proportions of fermentable concentrate and forage with low physically effective fiber (peNDF) [22]. Nocek [23] demonstrated that feeding the same ingredients and forages under different strategies can influence the length of time that the pH remains below a critical minimum. Longer periods of low pH throughout the day may have a greater detrimental impact on ruminal health and DMI than short periods of low pH.

Acetate: Propionate Ratio

The main products of fermentation of DF are SCFA, predominantly acetate, propionate and butyrate, lactate and succinate, as well as water, various gases (carbon dioxide, hydrogen, and methane) and bacterial cell biomass [24]. Changes in dietary physical form alter the ruminal environment, and may result in a shift in VFA profile. Traditionally, high acetate concentration is associated with fibre fermentation, and elevated propionate concentration is associated with NFC fermentation [1]. Acetate to propionate ratios of less than 2.0 is often associated with milk fat depression, and a positive relationship exists between ADF concentration and milk fat percentage [9].

In domestic sheep and cattle, ruminal acetate and propionate profiles have been altered by modification of dietary NFC [1]. When high amounts of citrus pulp (84.4% of dietary DM) were fed to sheep in place of a 20.4% citrus pulp and 76.5% barley diet, propionate decreased numerically from 17.6 to 14.4 molar % and acetate increased from 65.0 to 69.1 molar % [25]. Using continuous culture *in vitro* fermentations with mixed ruminal microbes from cattle inoculum, Ariza *et al.*, [26] observed changes in molar concentrations of propionate and acetate when starch was decreased from 24.0 to 11.0% and neutral detergent-soluble fiber (NDSF) was increased from 8.8 to 14.4% by altering the substrate ratio of hominy feed to citrus pulp. Propionate decreased from 22.7 to 16.7 molar % and acetate increased from 62.6 to 68.9 molar %. The acetate: propionate ratio increased from 2.8 to 4.1. Furthermore, the early lactation period is usually characterized by a higher concentrate intake compared with the mid and late lactation or dry period, which results in a lower ruminal acetate: propionate ratio [27]. Jorgenson and Schultz [28] fed lactating cattle 7.26 kg of ground corn daily, along with long-stem (control) or pelleted alfalfa hay in *ad libitum* amounts. Feeding pelleted hay decreased acetate (as a percentage of totals VFA) from 60.3 to 55.6%, increased propionate from 20.1 to 27.0%, and decreased butyrate numerically from 17.0 to 15.3%.

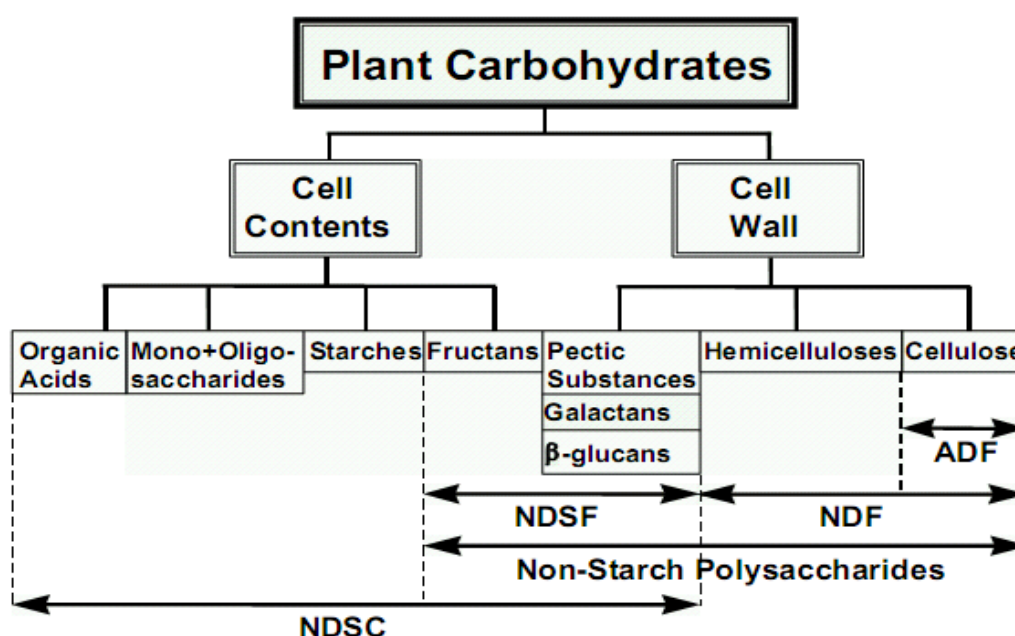


Figure 1: carbohydrate partitioning [1].

Milk Fat Percentage

Effectiveness of the fibre in a specific feed for maintaining milk fat production was estimated relative to fibre in a standard or reference feed. Effective fibre values were based on several standards such as cottonseed hulls, hay, or alfalfa silage, which made it difficult to use these systems over the full range of feeds fed to ruminants. The effects of the amount and source of fibre on milk fat production have been known for a long time [2, 3, 4, 15]. Using approach of PSPS, the requirement for peNDF of dairy cows was determined to be 20% of ration DM to maintain the milk fat percentage of early to mid lactation Holstein cows at 3.4% [9]. Milk fat depression has been linked to inadequate dietary fibre intake in lactating cows. Milk fat depression perhaps can be observed in high producing dairy goats during early lactation [29]. Research indicated that finer particle size of alfalfa hay caused reductions in both rumination time and milk fat in lactating dairy cattle [2]. The mechanism that explains milk fat depression syndrome in high producing lactating ruminants involves dietary fibre intake, chewing activity,

salivation, and ruminal fermentation. A high-fibre diet results in higher chewing activity, which in turn increases salivation and favors the growth of cellulolytic microbes and production of acetic acid. Higher acetate to propionate ratio in the rumen liquor favors the synthesis of milk fat, since acetate is the major precursor of milk fat.

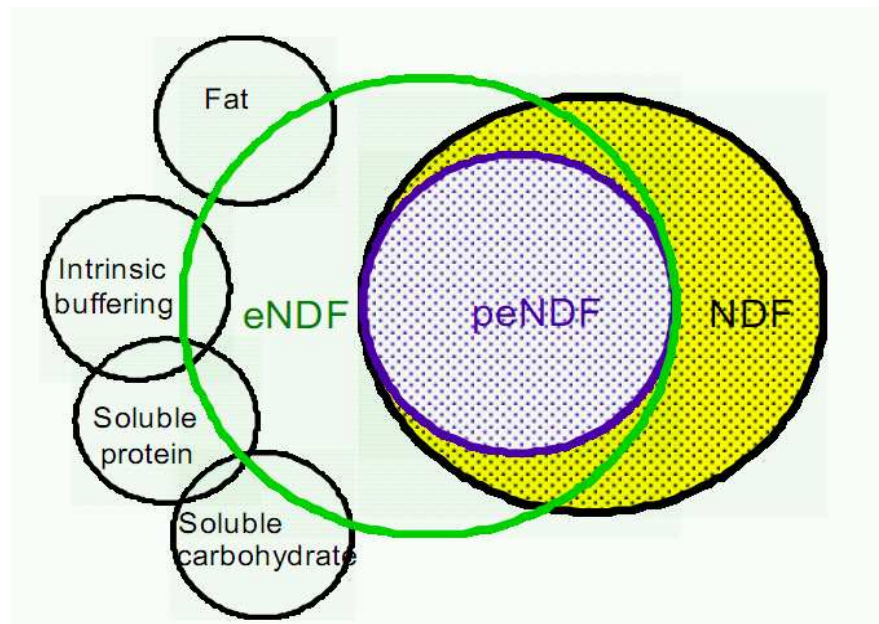


Figure 2: Illustration the relationships among NDF, physically effective NDF, and effective NDF [10]

Table 1: The effect of particle size of forages on the chewing activity of cows.

Feed and physical form	NDF		Total chewing activity	
	% of DM	min/kg of DM	min/kg of NDF	% reduction
Alfalfa hay				
Long	54	72	134	100
Chopped (3.8 cm) ¹	54	59	109	82
Bermudagrass hay				
Long	72	108	149	100
Chopped (3.8 cm)	72	85	118	79
Alfalfa hay				
Long	53	62	117	100
Chopped (3.8 cm)	53	44	84	72
Oat straw				
Long	84 ²	163	194	100
Ground	75 ²	84	113	58
Ryegrass				
Long	65 ²	90	139	100
Finely ground (1.2 cm)	64 ²	19	29	21
Corn silage				
1.9 cm TLC ³	68	66	97	100
1.3 cm TLC	62	60	96	99
0.6 cm TLC	60	40	66	68
Alfalfa hay				
2.5 cm TLC	55	52	95	100
0.5 cm TLC	45	30	66	69

¹Screen aperture diameter.

²NDF calculated from crude fibre concentration.

³Theoretical length of cut.

Adapted from [4].

Feeding of corn silage from brown midrib mutants depressed milk fat concentration in cows when fed in a low NDF diet [29]. Lower lignin content compounded with low dietary NDF contributed to the milk fat depression. One must recognize that diets with lower fibre do not always result in low milk fat even though the chewing activities were depressed [30]. In that study sufficient amount of effective fibre was presented in the low fibre diet. In primiparous lactating goats milk fat was 0.4% higher when longer forage particle length was fed [31]. This was associated in an increase in chewing activities, slightly higher acetate to propionate ratio, and only 0.1U increase in pH value in the rumen liquor. In another study when primiparous goats were studied, milk fat decreased from 3.62 to 2.92% when the concentrate was increased from 25 to 55% of the diet [32]. There was a clear association among dietary fibre intake, chewing activities and milk fat content [29]. Shaver *et al.*, [33] found a significant reduction in both milk fat (3.11% vs. 3.62%) and chewing activity (3.2 vs. 9.5 h/day) of dairy cows when alfalfa hay was provided in ground and pellet form compared to the unchopped form.

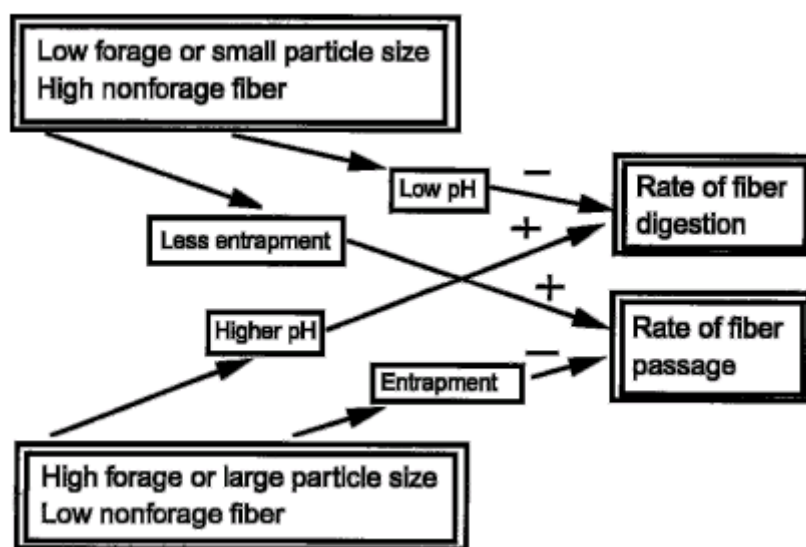


Figure 3: Potential interactions among forage level and particle size and amount of nonforage fibre on rate on ruminal fibre digestion and passage. The model implies that, when high levels of nonforage fibre are fed instead of forage, the amount of dietary forage is necessarily low; therefore, forage particle size must be adequate to stimulate rumination and entrap small feed particles [15].

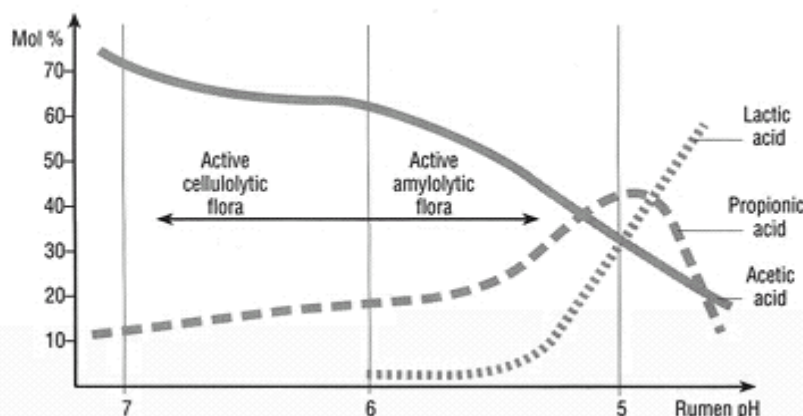


Figure 4: Ruminal fermentation as a consequence of adaptation due to pH regulation [19].

CONCLUSION

Physical characteristics of dairy rations are very critical for obtaining proper ruminal fermentation as well as for animal production. In this regard, physical forms of both forages and concentrates should be in an appropriate particle size to avoid milk composition changes. One of the most important factors related to fibre physical form is dry matter intake (DMI): when ration is equilibrated and the energy requirement is high, DMI mainly depends upon physical issues. The high energy requirement reduces rumen wall sensibility to distension potentially increasing feed consumption. In these conditions, DMI became limited mainly by passage rate, the latter being closely related to dietary particle size and fibre physical form. Fibre physical form has been in fact demonstrated to affect ruminal stratification, ruminal filling and retention such as ruminal feed degradation and fermentation [2]. Lactating dairy cows have obligate requirements for fibre in order to maintain normal rumination, chewing and saliva production, and normal ruminal function. In diets for high producing cows, the amount of fibre in the diet tends to decline as energy density increases. Recently the terms, physical effectiveness factor (pef) and physically effective NDF (peNDF), have been used to clarify either forage or total mixed ration (TMR) particle size, causing chewing activity along with obtaining proper milk fat concentration.

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