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Effects of Physically Effective Fiber on Digestive Processes and Milk Fat Content in Early Lactating Dairy Cows Fed Total Mixed Rations

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ABSTRACT

Data from recent research studies were analyzed quantitatively, and the random effect of experiment was assessed to define the physiological responses of dairy cows in early lactation to intake of physically effective neutral detergent fiber (peNDF). All studies were conducted with lactating Holstein cows (84.8 ± 3.54 days in milk) in Latin square designs, and feeds were offered ad libitum as total mixed rations (TMR). The peNDF was estimated by 2 measurement techniques, the NDF content of TMR multiplied by amount of dry matter (DM) retained on a 1.18-mm screen ($peNDF_{>1.18}$) and NDF content of TMR multiplied by the proportion of DM retained by 19- and 8-mm Penn State Particle Separator screens ($peNDF_{>8}$). Other factors, including concentrations of NDF, forage NDF, nonfiber carbohydrates, the amount of digestible organic matter of forages (FDOM), and the intake of ruminally degradable starch (RDSI) from grain in the diet were also investigated. The studied animal response variables included feed intake, ruminal fermentation, chewing activity, fiber digestibility, and milk production and composition. The ruminal pH (day mean) in this study ranged from 5.30 to 6.59. Using $peNDF_{>1.18}$ approach, the requirements for physically effective fiber in high-yielding dairy cows fed TMR in an ad libitum intake were estimated to be about 19% of ration DM or 4.1 kg/d or 0.6 kg/100 kg of body weight to maintain a ruminal pH of about 6.0. When peNDF was measured as $peNDF_{>8}$, ruminal pH responded in a quadratic fashion but the confidence of estimation was lower (R^2 = 0.27) compared with the $peNDF_{>1.18}$ approach (R^2 = 0.67). Results of these data analyses showed that $peNDF_{>1.18}$ provided a satisfactory estimation of the mean ruminal pH (R^2 = 0.67) and NDF digestibility (R^2 = 0.56). Furthermore, $peNDF_{>1.18}$ was poorly, although positively, correlated to daily chewing (R^2 = 0.17), and rumination (R^2 = 0.24) activity. On the other hand, results from these analyses showed that milk parameters are less sensitive to the effects of dietary peNDF than other variables, such as ruminal pH, chewing activity, and fiber digestibility. Dietary FDOM correlated positively (moderately) to ruminal pH (R^2 = 0.24), daily chewing (R^2 = 0.23), and rumination (R^2 = 0.29) activity, whereas the daily RDSI from grain correlated negatively to ruminal pH (R^2 = 0.55) and positively to total volatile fatty acids (R^2 = 0.27). Inclusion of FDOM and RDSI from grain along with $peNDF_{>1.18}$ in the models that predict rumen pH further improved the accuracy of prediction. This approach appeared to further complement the concept of peNDF that does not account for differences in ruminal fermentability of feeds.

Key words: physically effective fiber, dairy cow, rumen pH, chewing activity

INTRODUCTION

High-concentrate diets for high-yielding dairy cows must contain sufficient physically effective fiber (i.e., fiber that stimulates rumination, saliva production, and rumen buffering) to prevent ruminal dysfermentation and subacute ruminal acidosis (**SARA**). The concept of physically effective fiber was created to amalgamate the chemical characteristics and particle size of forages, and to quantify its value to rumen function (Mertens, 2000). According to Lammers et al. (1996), physically effective NDF (**peNDF**) could be measured as a proportion of DM retained by the 19- and 8-mm Penn State Particle Separator (**PSPS**) screens multiplied by dietary NDF content (**$peNDF_{>8}$**). Mertens (1997) determined peNDF as the proportion of DM retained by a 1.18-mm screen multiplied by dietary NDF (**$peNDF_{>1.18}$**) using a dry-sieving technique. It is, however, unclear which measure of peNDF provides the most accurate estimate of chewing, saliva production, and rumen buffering (Einarson et al., 2004). Although a number of recent studies have been conducted to investigate the effects of peNDF on rumen fermentation, feed intake, milk production, chewing activity, and nutrient digestibility in high-yielding, early lactation dairy cows, the results obtained from these studies are not conclusive. Differences in measurement and definition of dietary peNDF and interactions between levels

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of concentrate inclusion, forage and grain sources, and animal-response variables among studies make peNDF recommendations difficult. The NRC (2001) does not give requirements for peNDF due to lack of a standardized, validated method for measuring effective fiber in feeds and to establish requirements for effective fiber.

Part of the difficulty in assigning fiber requirements for high-yielding dairy cows related to the interpretation of response variables. Despite the fact that milk fat percentage is an easily measured parameter, low fiber in the diet can detrimentally affect animal health without significant milk fat depression (Mertens, 1997). Ruminal pH may be a better indication of ruminal health and optimal function, and a better basis for determining fiber requirements of dairy cows in early lactation than the maintenance of milk fat production (Allen, 1997; Mertens, 1997).

However, Beauchemin and Yang (2005) concluded that the models used to predict rumen pH should include both peNDF and fermentable OM intake. Because the peNDF concept relates only to the physical properties of fiber, inclusion of forage and grain fermentability characteristics in the models to predict animal response and to evaluate physical effectiveness of dairy cow diets would likely increase the estimation accuracy. Results from several studies showed that increasing the amount of digestible fiber of hay or corn silage in dairy cow diets increased digesta stratification, particle breakdown in the rumen as well as digesta turnover, forage intake, and fiber digestibility without compromising the physical effectiveness at stimulating chewing (Oba and Allen, 2000b; Tafaj et al., 2004b, 2005b). Krause et al. (2002b) found that replacing dry cracked corn with high-moisture corn in a TMR fed to dairy cows significantly reduced ruminal pH. Furthermore, Beauchemin and Rode (1997) reported that rapidly digested starch sources such as barley grain increase the need for effective fiber, suggesting an interaction between ruminal fermentability and physical characteristics of the ration.

This quantitative study aimed to define the physiological responses of high-yielding dairy cows in early lactation to peNDF when estimated as $peNDF_{>1.18}$ and $peNDF_{>8}$. Furthermore, based on the most sensitive animal response variable, an optimization of peNDF concentration in TMR fed ad libitum to this category of dairy cows was also intended. Possible interactions between dietary peNDF, NFC, the amount of digestible OM of forages (**FDOM**), and intake of ruminally degradable starch (**RDSI**) from grains composing TMR were also investigated.

MATERIALS AND METHODS

Description of the Database

To conduct this quantitative study, an independent data set with data on animal characteristics, detailed ration components, and an evaluation of physical structure of the ration was generated. The data file containing 131 treatment means was generated from 33 experiments published from 1997 to 2005 (Table 1). Animals were lactating Holstein cows (84.8 ± 3.54 DIM) (mean ± SE) weighing between 570 and 886 kg and producing 23.1 to 49.3 kg of milk/d. Feeds were offered ad libitum as TMR. The level of DMI ranged from 16.9 to 28.3 kg/d, and the percentage of forage in TMR ranged from 27 to 75% of DM (49.2 ± 0.87%). Dietary NDF ranged from 18.2 to 48.1% of DM (30.9 ± 0.51%) and forage NDF (**FNDF**) ranged from 15.5 to 35.8% of DM (21.3 ± 0.36%). The $peNDF_{>1.18}$ content in TMR ranged from 4.2 to 37.4% of DM (21.1 ± 0.64%) and the content of $peNDF_{>8}$ ranged from 2.0 to 29.5% (15.2 ± 0.73%). The main characteristics of the database, including animal characteristics, investigated dietary factors, and animal response variables (hereafter referred to as response variables) are listed in Table 2. The response variables included data on feed intake, ruminal fermentation, chewing activity, fiber digestibility, and milk production and composition. All experiments included in this study were conducted in Latin square design.

Ruminal fermentation was investigated based on the response of total VFA, molar proportion of individual VFA, acetate to propionate ratio, and pH value in the ruminal fluid. For VFA measurement through GLC, ruminal fluid was collected several times after morning feeding via cannula from the ventral sac of the rumen. Some studies measured pH from ruminal fluid in spot samples collected from the ventral sac of the rumen, whereas in others, ruminal pH was continuously measured (during 24 h) using an industrial electrode placed in the ventral rumen sac. However, in all cases, the measurements of ruminal pH covered at least a period from 8 to 10 and, in several cases, up to 12 h postfeeding. In the present study, values of ruminal pH, total and individual molar amounts of VFA, and the acetate to propionate ratio reported from studies were analyzed as treatment means.

Estimation of peNDF of Diets

As a prerequisite for inclusion in this literature study, articles were expected to give complete information on the components and chemical composition of rations, as well as on the physical evaluation of experimental diets (vertical dry-sieving technique). The $peNDF_{>8}$ content of TMR was determined by multiplying the proportion of DM retained by the 19- and 8-mm screens of PSPS by dietary NDF content (DM basis; Lammers et al., 1996).

Table 1. List of references and their reported experimental parameters[1] included in the analysis

Reference	NDF	FNDF	peNDF$_{>1.18}$	peNDF$_{>8}$	Feed intake	Chewing activity	Ruminal fermentation	Milk parameters	Digestibility
Allen and Grant (2000)	*	*	*		*	*	*	*	
Bal et al. (2000)	*	*	*		*		*	*	*
Beauchemin et al. (1997)	*	*	*		*	*		*	
Boddugari et al. (2001)	*	*		*	*	*	*	*	*
Calberry et al. (2003)	*	*	*	*	*		*	*	
Clark and Armentano (1997)	*	*	*		*	*		*	
Clark and Armentano (1999)	*	*	*		*	*		*	
Clark and Armentano (2002)	*	*	*		*	*		*	
Einarson et al. (2004)	*	*		*	*		*	*	
Eun et al. (2004)	*	*		*	*		*		*
Fernandez et al. (2004)	*	*	*		*	*	*	*	*
Grant et al. (1990a)	*	*	*		*	*	*	*	
Grant et al. (1990b)	*	*	*		*	*	*	*	
Kononoff and Heinrichs (2003a)	*	*	*	*	*	*	*	*	*
Kononoff and Heinrichs (2003b)	*	*	*	*	*	*	*	*	*
Kononoff et al. (2003a)	*	*	*	*	*	*	*	*	
Krause and Combs (2003)	*	*	*		*	*	*	*	*
Krause et al. (2002a,b)	*	*	*		*	*	*	*	*
Le Liboux and Peyrand (1998)	*	*	*		*	*	*	*	*
Le Liboux and Peyrand (1999)	*	*	*		*	*	*	*	*
Leonardi et al. (2005)	*	*	*		*	*	*	*	*
Oba and Allen (2000a,b,c)	*	*		*	*	*	*	*	*
Onetti et al. (2003)	*	*	*		*		*	*	
Plaizier (2004)	*	*	*	*	*		*	*	
San Emeterio et al. (2000)	*	*	*		*		*	*	*
Schwab et al. (2002)	*	*	*		*	*	*	*	*
Soita et al. (2000)	*	*	*		*	*		*	
Tafaj et al. (2004a, 2005a)	*	*		*	*	*	*	*	*
Teimouri Yansari et al. (2004)	*	*	*	*	*	*	*	*	*
Yang and Beauchemin (2005)	*	*		*	*				*
Yang et al. (2001a,b)	*	*	*	*	*	*	*	*	
Yang et al. (2002); Beauchemin et al. (2003)	*	*	*	*	*	*	*	*	*
Zebeli (unpublished results)	*	*	*	*	*		*	*	*

[1]FNDF = Dietary forage NDF; peNDF$_{>1.18}$ = dietary physically effective NDF measured as the NDF content of TMR multiplied by amount of DM$_{>1.18\ mm}$ (Mertens, 1997); peNDF$_{>8}$ = Dietary physically effective NDF measured as a proportion of DM retained by 19- and 8-mm Penn State Particle Separator screens multiplied by dietary NDF content (Lammers et al., 1996).

Assuming that chewing activity is equal for all particles retained on a 1.18-mm sieve, Mertens (1997) proposed a system for estimating peNDF based on NDF concentration of feeds multiplied by the proportion of particles retained on a 1.18-mm sieve (peNDF$_{>1.18}$) using the vertical oscillating dry-sieving technique. To estimate peNDF$_{>1.18}$ content of TMR in the present study, DM proportion retained on a 1.18-mm sieve, obtained either through the vertical oscillating sieving technique or the new version of PSPS (Kononoff et al., 2003b), was multiplied by NDF content (DM basis) of TMR.

Some studies reported only the particle size distribution of their forages but not of the TMR. Grain is also reported to possess effective fiber according to its physical form (ground, pelleted, or rolled; Mertens, 1997) and degradability characteristics (De Brabander et al., 2002). To account for peNDF$_{>1.18}$ content of concentrates in the present study, the data were used from Mertens (1997), who reported particle size distribution (proportion of particles retained on sieve 1.18 mm) for different concentrate feeds using the vertical oscillating sieving technique. In this case, total peNDF$_{>1.18}$ content of TMR was calculated as a sum of peNDF$_{>1.18}$ obtained from forages (NDF content of forages × DM retained on screens >1.18 mm) with the estimate of concentrate peNDF$_{>1.18}$ (NDF content of grain × DM retained on screens >1.18 mm, taken from tables of Mertens, 1997) according to their proportion in the TMR.

Estimation of FDOM

Nutritive value tables and chemical composition of feedstuffs from the United Kingdom (MAFF, 1990) were used to estimate the amount of FDOM for the present experimental diets. The content of FDOM was used to take into account in the analysis forage quality and the amount of fermentable OM of forages composing TMR. The United Kingdom tables express FDOM as in vitro digestible OM determined using rumen fluid-pepsin;

Table 2. Statistical description of animal characteristics, dietary factors, and response parameters included in the current study

Parameter	n_{Treat}[1]	$n_{Ref.}$[2]	Mean	SE	Minimum	Maximum	Median
Animal characteristics							
BW, kg	131	33	656	4.36	570	886	656
DIM	131	33	84.8	3.54	9.00	170	83.0
Forage in TMR, % of DM	131	33	49.2	0.87	26.8	75.0	50.0
Dietary factors, % of DM unless stated							
NDF	131	33	30.9	0.51	18.2	48.1	31.6
FNDF[3]	131	33	21.3	0.46	11.5	35.8	21.0
$peNDF_{>1,18\ mm}$[4]	110	27	21.1	0.64	4.24	37.4	21.0
Intake of $peNDF_{>1.18}$, kg/d	110	27	4.91	0.16	0.98	9.97	4.86
Intake of $peNDF_{>1.18}$, kg/100 kg of BW	110	27	0.75	0.03	0.15	1.48	0.75
$peNDF_{>8}$[5]	52	15	15.2	0.73	1.98	29.5	14.8
Intake of $peNDF_{>8}$, kg/d	52	15	3.30	0.19	0.49	5.67	3.18
NFC[6]	111	28	35.8	0.63	16.5	53.2	35.5
NFC:NDF ratio	111	28	1.21	0.03	0.35	2.89	1.17
CP	131	33	17.5	0.14	12.7	22.1	17.8
FDOM,[7] g/kg of DM	131	33	301	6.32	147	500	301
RDS,[8] g/kg of DM	131	33	143	4.21	55.0	291	145
RDSI,[9] kg/d	131	33	3.30	0.10	1.20	6.60	3.10
Response variables							
DM intake, kg/d	131	33	23.0	0.17	16.9	28.3	22.8
DM intake, kg/ 100 kg of BW per d	131	33	3.50	0.03	2.40	4.50	3.50
Ruminal pH (day mean)	100	26	6.09	0.02	5.30	6.59	6.09
VFA							
Total VFA, m*M*/L mol/100 mol VFA	100	26	114	2.08	75.0	162	111
Acetate (C_2)	100	26	58.6	0.56	44.6	73.6	59.4
Propionate (C_3)	100	26	22.9	0.50	10.7	35.9	22.9
Butyrate (C_4)	100	26	12.7	0.20	8.9	18.1	12.2
Acetate-to-propionate ratio	100	26	2.66	0.06	1.34	5.05	2.60
Total chewing time							
Min/d	99	24	691	11.2	425	969	702
Min/kg of DM	99	24	30.1	0.59	17.9	47.1	29.7
Min/kg of NDF	99	24	103	2.48	54.3	160	101
Min/kg of $peNDF_{>1.18}$	87	21	167	9.67	70.5	644	143
Rumination time, min/d	99	24	434	8.29	151	632	443
Milk yield, kg/d	131	33	34.9	0.51	23.1	49.3	34.8
Milk fat, %	131	33	3.40	0.03	2.39	4.23	3.43
Milk protein, %	121	32	3.11	0.01	2.63	3.76	3.14
Fat:protein ratio in milk	121	32	1.09	0.01	0.75	1.42	1.12
Digestibility, %							
NDF	73	19	46.9	0.96	28.4	64.6	47.2
ADF	56	15	43.8	1.09	22.0	58.9	44.6

[1]Number of treatment means.

[2]Number of experiments included in this study.

[3]FNDF = Dietary forage NDF.

[4]Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>\ 1.18\text{-mm}}$ (Mertens, 1997).

[5]Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>\ 8\text{-mm}}$ (Lammers et al., 1996).

[6]Nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % ether extract + % crude ash).

[7]FDOM = Amount of digestible OM of forages in TMR estimated by MAFF (1990).

[8]RDS = Ruminally degradable starch from grain in TMR calculated according to Offner et al. (2003).

[9]RDSI = Daily intake of RDS.

for forages constituting diets of this study was set as follows (in g/kg of DM): corn silage (667), alfalfa hay (557), alfalfa silage (547), barley silage (684), mixed grass silage (587), oat silage (684), grass hay (sun-cured) (564). Furthermore, the total amount of dietary FDOM content was calculated based on the proportion of forages in the experimental TMR.

Estimation of Ruminally Degradable Starch of Grain

All published studies analyzed provided sufficient information about the components of concentrate mixture of their TMR. To account for differences of ruminal degradability characteristics among grains comprising experimental TMR in the present study, the in situ

effective ruminal degradability of starch from grain was taken into consideration. Starch content of grain in TMR was either taken directly from articles or was taken from tables compiled by Sauvant et al. (2004). The amount of ruminally degradable starch (**RDS**; % of total starch) of grain mixture composing TMR was calculated according to the formula: RDS = $\Sigma p_i \times ERD_i$, where p$_i$ represents the proportion of dietary starch provided from grain i in the mixture, and ERD$_i$ represents starch effective degradability for grain i, which was taken from in situ calculations made from Offner et al. (2003) for a fractional passage rate of 6%/h. To take into account the RDSI from grain in the analysis, RDSI was calculated by multiplying the daily DM intake with RDS of grain comprising TMR. A statistical description of the calculated in situ RDS and RDSI from grain of this study, including mean, range, and median, is given in Table 2.

Statistical Analyses

Data analysis was performed according to St-Pierre (2001) taking into account the random effect of the experiment, using PROC MIXED (version 8.2, SAS Institute, 2001). The variable experiment (hereafter referred as study) does not contain quantitative information and constitutes an additional variation source; it was therefore declared in the CLASS statement. Simple linear regression was performed to test the response of animal variables to dietary factors (refer to Table 2 for information regarding response variables and dietary factors). Therefore, dependent variables in the regression analysis included all response variables and the independent continuous variables included all dietary factors according to the following model:

$$Y_{ij} = \alpha_0 + s_i + \beta_1 X_{ij} + b_i X_{ij} + e_{ij},$$

where Yij = the expected outcome for the dependent variable Y (response variable) observed at level j of the continuous variable X (dietary factor) in the study i, α_0 = the overall intercept across all studies (fixed effect), s$_i$ = the random effect of the study i (i = 1,..., 33), β_1 = the overall regressing coefficient of Y on X across all studies (fixed effect), X$_{ij}$ = the value j of continuous variable X in study i, bi = the random effect of study i on the regression coefficient of Y on X in study i, and eij = the unexplained error.

To take into consideration the unequal variance among studies, all dependent variables were weighted by the reciprocal of their squared standard error. In addition, an unstructured variance-covariance matrix (type = un) was performed at the random part of the model, as suggested by St-Pierre (2001) to avoid the positive correlation between the intercepts and slopes. When dietary factors were $P < 0.05$, their squared term was included in the model to test any likely quadratic relationship (second-order polynomial regression) and a variance components (type = vc) of variance-covariance structure was performed to avoid the positive correlation between the intercepts and slopes (St-Pierre, 2001). To fit the asymptotic relationship of ruminal pH or chewing index to dietary peNDF$_{>1.18}$, a mathematical asymptotic function using PROC NLIN (DUD method; SAS Inst. Inc., version 8.2) according to the following model was used:

$$Y = a + b\, e^{(c\, X)},$$

where Y represents the response variable; a, b, and c are the estimates, and X represents the dietary peNDF$_{>1.18}$.

All significant dietary factors ($P < 0.05$) were further tested using the backward elimination multiple regression similarly to the algorithm reported by Oldick et al. (1999) and Firkins et al. (2001). To limit overparameterization of the model, a variance inflation factor less than 10 for every continuous independent variable tested was assumed, as suggested by Oldick et al. (1999). The best fit was chosen as the one with the lowest root mean square error (**RMSE**), higher determination coefficient (R^2), and the highest Schwarz's Bayesian criterion. For simplicity, only the best-fit equations of multiple regression (backward elimination) that further improved the relationship obtained from linear or polynomial regression are shown.

RESULTS AND DISCUSSION

Intakes of DM and peNDF

A summary of intakes for diets used in this quantitative study is given in Table 2. Intake of DM from 33 studies averaged 23.0 ± 0.17 kg/d or 3.5 ± 0.03 kg/100 kg of BW per d. Intakes of peNDF$_{>1.18}$ from 27 studies and peNDF$_{>8}$ from 15 studies averaged 4.9 ± 0.16 kg/d and 3.3 ± 0.19 kg/d, respectively. Table 3 shows the results of linear regression of DMI response to different dietary factors (for simplicity, only significant relationships are shown, $P < 0.05$). The analysis of backward elimination of multiple regression did not further improve the relationship obtained from linear regression, and therefore, the results are not shown. In general, relationships of dietary factors to DMI were low in this study. The dietary NDF negatively affected DMI (expressed as either kg/d or kg of DM/100 kg of BW per d), although the relationship was moderately higher when peNDF was measured as peNDF$_{>1.18}$ (R^2 = 0.21) and when BW of animals was included in the analysis

Table 3. Equations[1] for linear and polynomial regression of response of DMI (Y, kg/d or kg/100 kg of BW per d) to different dietary factors in dairy cows fed TMR

		Parameter estimates				Model statistics	
DMI (Y)	Dietary factor[2] (X)	Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
kg/d	$peNDF_{>1.18}$, %	24.6	0.87	–0.261	0.084	1.38	0.21
	$peNDF^2_{>1.18}$, %			0.008	0.002		
	NFC:NDF ratio	18.4	1.05	6.319	1.529	1.71	0.16
	NDF, %	26.7	0.73	–0.120	0.023	1.56	0.17
	FNDF, %	25.4	0.60	–0.113	0.027	1.65	0.12
kg/100 kg of BW per d	$peNDF_{>1.18}$, %	4.21	0.10	–0.034	0.005	0.28	0.29
	NDF, %	4.33	0.13	–0.027	0.004	0.29	0.23

[1]Only significant relationships are shown ($P < 0.05$).

[2]$peNDF_{>1.18}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); NFC = Nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % ether extract + % crude ash); FNDF = Forage NDF.

[3]RMSE = Root mean square error.

($R^2 = 0.29$). Dry matter intake also responded positively to NFC:NDF ratio of the diet. These responses are presumably connected with the ruminal physical fill effect of NDF and the high energetic necessity of dairy cows in early lactation. Cows in early lactation are often in negative energy balance because the ingested energy does not meet the energy requirements of lactation (NRC, 2001). The extent to which DMI of lactating dairy cows is regulated by distension in the reticulorumen depends upon the animal's energy requirement and the filling effect of the diet offered (Allen, 2000). However, Allen (2000) stated that physical fill could limit feed intake at the low concentrate inclusion, but a metabolic rather than a physical constraint can be expected to be rate limiting at high concentrate inclusion. Beauchemin et al. (1994) reported an interaction ($P < 0.01$) between forage particle length (alfalfa silage chopped at 5- and 10-mm theoretical length of cut) and percentage of forage in the diet (35 or 65%). In that experiment, DMI was reduced by nearly 3 kg/d when forage percentage was increased from 35 to 65 with diets containing the long-chopped alfalfa silage, but was reduced by less than 0.5 kg/d with diets containing short-chopped silage. Tafaj et al. (2001) reported that reducing dietary hay particle size from 28.7 to 9.2 mm increased DMI by 13% only at a low-concentrate level (13% in DM), but when a high-concentrate diet (~40% in DM) was fed no differences were observed in sheep. Firkins et al. (2001) quantitatively analyzed results from literature in dairy cows with a comparable DMI to the present study (21.3 ± 2.6 kg/d) and reported a negative linear relationship among dietary NDF and FNDF and DMI. Recently, Beauchemin and Yang (2005) reported that reducing dietary $peNDF_{>8}$ from 11.5 to 8.9% ration DM was not a rate-limiting step for particulate passage and hence, for rumen physical fill and feed intake in Holstein cows fed corn silage-based TMR with a high concentrate level (~60% of ration DM).

Ruminal Fermentation

In this study, ruminal pH (day mean) ranged from 5.30 to 6.59 (6.09 ± 0.02) whereas total VFA and acetate to propionate ratio ranged from 75 to 162 m*M*/L and from 1.34 to 5.05, respectively. Acute acidosis is defined as a condition in which ruminal pH is less than approximately 5.0 to 5.2, whereas SARA is defined as a ruminal pH of approximately 5.2 to 5.6 (Owens et al., 1998). Garrett et al. (1999) proposed that a group of cows would be characterized (presence or absence of SARA) correctly 90% of the time if 3 or more of 12 tested cows had readings ≤5.5, whereas Beauchemin et al. (2003) stated that the incidence of subclinical acidosis increases when ruminal pH falls below 5.8. Of 100 treatment means used in the present study, ruminal pH was ≤5.8 in 11 cases (results not shown). Table 2 shows a summary of all parameters of ruminal fermentation analyzed in this study. The regression analysis showed that ruminal pH responded quadratically to $peNDF_{>1.18}$ of the diet (Figure 1). When peNDF was measured as the proportion of particles retained on the 8-mm screen ($peNDF_{>8}$), the relationship was also quadratic but the confidence of estimation was lower (Table 4). The maximal amount of $peNDF_{>8}$ intake associated with the quadratic effect resulted to be about 4.5 kg/d (data not shown).

Table 4 shows the results of linear regression of response of fermentation parameters (pH, total VFA, acetate to propionate ratio, and butyrate molar percentage) to different dietary factors (only significant relationships are shown, $P < 0.05$).

According to Figure 1, $peNDF_{>1.18}$ estimates ruminal pH with $R^2 = 0.67$ and an RMSE of 0.137 pH units. Increasing the dietary peNDF increased the ruminal pH quadratically. The same relationship was found when $peNDF_{>1.18}$ was expressed as intake (kg/d) or intake per kg of BW (kg/100 kg of BW). It means that

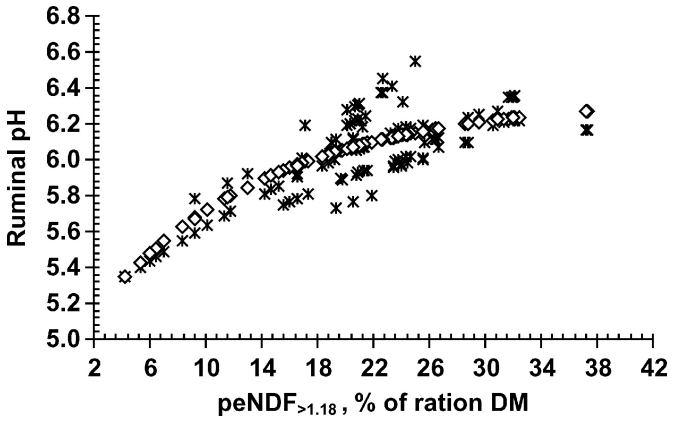

Figure 1. Relationship of physically effective NDF ($peNDF_{>1.18}$) to observed ruminal pH value adjusted for the random study effect and unequal variance. The best-fit, quadratic regression pH = 5.06 (±0.09) + 0.069 (±0.008) $peNDF_{>1.18}$ − 0.001 (±0.0002) $peNDF^2_{>1.18}$, root mean square error = 0.137, R^2 = 0.67; Asymptotic function (◇) pH = 6.34 − $1.39e^{(-0.08\ peNDF>1.18)}$ using Proc NLIN (SAS Institute, 2001).

with increasing dietary $peNDF_{>1.18}$, ruminal pH does not increase indefinitely, but rather attains an asymptotic plateau in response to dietary $peNDF_{>1.18}$. Allen (1997) stated that roughages have a critical particle length and any increase thereafter does not further improve their physical effectiveness. However, in this study, the relationship between ruminal pH and dietary $peNDF_{>1.18}$ appeared to follow a quasi-linear course up to a pH value of approximately 6.0. Subsequently, the mathematical asymptotic function revealed an asymptotic relationship of ruminal pH with dietary $peNDF_{>1.18}$, showing an approximated plateau at a ruminal pH of 6.2 and in response to about 30% dietary $peNDF_{>1.18}$ (Figure 1). Pitt et al. (1996) calculated ruminal pH from the equilibrium between ruminal acidity and buffering. In fact, they postulated that the crossover point representing acid-base equilibrium and the predicted steady state ruminal pH resulted at a ruminal pH of about 6.1. Mertens (1997) also reported a quadratic relationship between dietary $peNDF_{>1.18}$ and ruminal pH (R^2 = 0.71). Pitt et al. (1996) used data from sheep, beef cattle, and dairy cattle and observed a quadratic relationship between effective NDF and ruminal pH (R^2 = 0.52). In the study of Pitt et al. (1996), the sheep consumed a high-forage diet, which probably accounted for a higher plateau of ruminal pH in that study (~6.4).

Furthermore, our analysis also shows that dietary NDF, FNDF, and FDOM positively influenced ruminal pH, whereas both the NFC:NDF ratio and RDSI from grain indicated a linear negative effect (Table 4). This result is partly in accordance with Allen (1997), who found a positive correlation only between FNDF and

Table 4. Equations[1] for linear and polynomial regression of response of rumen fermentation parameters to different dietary factors in dairy cows fed TMR

Rumen parameters (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
Rumen pH	$peNDFI_{>8}$, kg/d	5.79	0.05	0.180	0.039	0.14	0.27
	$peNDFI^2_{>8}$, kg/d			–0.021	0.006		
	NDF, %	5.46	0.07	0.019	0.002	0.13	0.44
	FNDF, %	5.70	0.05	0.017	0.002	0.13	0.32
	NFC:NDF	6.34	0.05	–0.208	0.038	0.16	0.23
	FDOM, g/kg DM	5.76	0.06	0.001	0.0001	0.14	0.24
	RDSI, kg/d	6.47	0.03	–0.114	0.009	0.11	0.55
VFA, m*M*/L	$peNDF_{>1.18}$, %	137	5.47	–0.915	0.247	16.7	0.12
	$peNDFI_{>8}$, %	131	2.99	–1.491	0.233	15.5	0.25
	NDF, %	161	7.24	–1.506	0.230	15.4	0.25
	FNDF, %	145	5.68	–1.497	0.258	15.6	0.22
	NFC:NDF	91.3	5.11	4.015	6.497	16.8	0.19
	RDSI, kg/d	86.1	4.16	0.19	0.027	14.9	0.27
C_2:C_3 ratio	NDF, %	1.54	0.24	0.034	0.007	0.51	0.13
	NFC:NDF	3.16	0.17	–0.481	0.134	0.56	0.11
C_4, mol/100 mol of VFA	FNDF, %	9.72	0.60	0.135	0.027	1.49	0.19
	NFC, %	16.7	0.92	–0.119	0.024	1.40	0.22

[1]Only significant relationships are shown ($P < 0.05$).

[2]$peNDFI_{>8}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>8\text{-mm}}$ (Lammers et al., 1996); FNDF = forage NDF; FDOM = amount of digestible OM of forages in TMR estimated by MAFF (1990); $peNDF_{>1.18}$ = physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); NFC = nonfiber carbohydrate calculated by difference 100 − (% CP + % NDF + % ether extract + % crude ash); RDSI = intake of ruminally degradable starch from grain.

[2]RMSE = Root mean square error.

Table 5. Estimating the physically effective NDF ($peNDF_{>1.18}$[1]) required to maintain a specified ruminal pH of cows in early lactation fed TMR

	Rumen pH regressed on $peNDF_{>1.18}$		
	kg/100 kg of BW	kg/d	% of ration DM
Polynomial regression			
Rumen pH intercept of all experiments	5.40 (0.08)[2]	5.18 (0.07)	5.07 (0.09)
Linear regression coefficient	1.31 (0.21)	0.27 (0.03)	0.069 (0.008)
Quadratic regression coefficient	–0.54 (0.13)	–0.017 (0.002)	–0.001 (0.0002)
Root mean square error (RMSE)	0.144	0.127	0.137
R^2	0.60	0.66	0.67
$peNDF_{>1.18}$ required for ruminal pH of:			
5.8	0.35 (0.01)	2.8 (0.07)	13 (0.15)
5.9	0.47 (0.01)	3.4 (0.08)	16 (0.15)
6.0	0.58 (0.01)	4.1 (0.08)	19 (0.17)
6.1	0.80 (0.02)	5.1 (0.10)	23 (0.20)

[1]$peNDF_{>1.18}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997).

[2]Numbers in parentheses are standard errors of the estimates.

ruminal pH (R^2 = 0.63) and not between total dietary NDF and pH. Firkins et al. (2001) also reported that ruminal pH in dairy cows correlated positively to FNDF and negatively to nonstructural carbohydrates in the ration. The estimated RDSI from grain in this study represents both the amount of ruminally degradable starch from grain and DMI. Firkins et al. (2001) found that an increase in DMI would still result in an increase in ruminally degradable starch, despite a reduction in the percentage of ruminally degraded starch caused by the increase of passage rate. In this context, Stone (2004) stated that high-producing cows might have an increased risk of SARA simply due to higher DMI. As expected in the present study, RDSI from grain correlated negatively to daily ruminal pH, explaining 55% of its variation (Table 4). This study shows that the intake of rapidly fermentable carbohydrates is more important than total NFC percentage of the diet to be taken into account in terms of avoiding SARA in high-yielding dairy cows.

Using the inverse regression, Mertens (1997) reported that a peNDF intake of 4.4 kg/d or a concentration of 22.3% of ration DM is needed to maintain a mean pH of 6.0. According to the results of our analysis, an intake of $peNDF_{>1.18}$ of either 4.1 kg/d, or of 0.58 kg/100 kg of BW, or a concentration of ~19% of ration DM is needed to maintain a pH of 6.0 (Table 5).

Although in the present study, the required concentration of $peNDF_{>1.18}$ to maintain a ruminal pH of 6.0 is lower (19 vs. 22.3% of ration DM), the absolute intake of $peNDF_{>1.18}$ (4.1 kg of $peNDF_{>1.18}$/d) is much closer to the estimation of Mertens (1997; 4.4 kg of peNDF/d). It is noteworthy that in the study of Mertens (1997), dietary peNDF ranged between 12 and 57% of DM, whereas in this study, $peNDF_{>1.18}$ ranged from 4.2 to 37.4% of ration DM. Moreover, the benchmark of ruminal pH was ~5.65 in the study of Mertens (1997), whereas in the present study, it was 5.30. This suggests the presence of different dietary conditions in these 2 studies, particularly with respect to TMR feeding and high-yielding dairy cows. This was also reflected by a higher asymptotic plateau of ruminal pH (about 6.5) found by Mertens (1997). The methodology reported by Mertens (1997) for measuring ruminal pH does not vary substantially (pH was measured during at least an 8-h period after feeding) from that used in the present study. Therefore, dietary differences could be attributed to discrepancies between estimations in the absolute peNDF intake and peNDF concentration to maintain a specified ruminal pH in the study of Mertens (1997) and this study. Allen (1995) suggested that NDF requirements could vary by ±5 units around a mean of 30% of ration DM, whereas Mertens (1997) suggested that the peNDF amount needed to maintain a ruminal pH of 6.0 should be arranged ±1.0 to 2.0 units. A similar approach may be needed for the estimation of $peNDF_{>1.18}$, in the present study (see Table 5).

The results of analysis of multiple regression using the backward elimination procedure, where all significant dietary factors were included, are shown in Table 6. To avoid overparameterization of the model, FDOM and RDSI were separately analyzed. This analysis showed that dietary $peNDF_{>1.18}$ (quadratically) and FDOM (linearly) significantly affected ($P < 0.05$) ruminal pH. The same effect on ruminal pH was observed when RDSI along with $peNDF_{>1.18}$ was tested in the multiple backward elimination regression, only that RDSI negatively correlated to ruminal pH. In fact, the concept of peNDF does not account for differences in fermentability of feeds. The FDOM (expressed as g/

Table 6. Best-fit equations for multiple regression[1] of responses of rumen fermentation parameters to different dietary factors in dairy cows fed TMR

Rumen parameters (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
Rumen pH[4]							
Model 1	$peNDF_{>1.18}$, %	4.87	0.10	0.065	0.009	0.12	0.72
	$peNDF^2_{>1.18}$, %			–0.001	0.0002		
	FDOM, g/kg of DM			0.001	0.0001		
Model 2	$peNDF_{>1.18}$, %	5.43	0.08	0.076	0.007	0.12	0.75
	$peNDF^2_{>1.18}$, %			–0.001	0.0001		
	RDSI, kg/d			–0.092	0.011		
VFA, m*M*/L	$peNDF_{>8}$ %	127	9.30	–1.995	0.312	15.3	0.47
	NFC:NDF			12.133	5.876		
C_4, mol/100 mol of VFA	FNDF, %	11.5	1.05	0.139	0.025	1.34	0.33
	NFC, %			–0.055	0.020		

[1]For simplicity, only the best-fit equations of multiple regression (backward elimination) that improved further the relationship obtained from linear or polynomial regressions are shown.

[2]$peNDF_{>1.18}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); FDOM = amount of digestible OM of forages in TMR estimated by MAFF (1990); FNDF = forage NDF; NFC = nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % fat + % ash); $peNDF_{>8}$ = physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>8\text{-mm}}$ (Lammers et al., 1996); RDSI = intake of ruminally degradable starch from grain.

[3]Root mean square error.

[4]Two models are shown because including FDOM and RDSI in the same model to predict ruminal pH induced model overparameterization.

kg of DM) is an indicator particularly of the quality (ruminal degradability) of forage in TMR, whereas RDSI (kg/d) accounts for daily intake of ruminally degradable starch from grain. The positive relationship of FDOM to pH ($R^2 = 0.24$) showed that FDOM affects the rumen conditions and should be considered when formulating TMR for dairy cows. Similarly, Allen (1997) reported a linear positive relationship ($R^2 = 0.18$) between ruminal pH and the amount of OM truly degraded in the rumen. Inclusion of FDOM along with $peNDF_{>1.18}$ in the model slightly increased the accuracy of estimation of ruminal pH from $R^2 = 0.67$ to $R^2 = 0.72$. The positive effect of FDOM on ruminal pH was probably a result of the positive effect of good-quality forage in promoting digesta stratification and turnover in the rumen and consequently stimulating forage intake and chewing activity (Tafaj et al., 2004b, 2005b). On the other hand, inclusion of RDSI in the model with $peNDF_{>1.18}$ increased the accuracy of estimation of ruminal pH up to 75%. Krause et al. (2002b) found that diets containing finer haylage particles and high-moisture corn reduced mean ruminal pH more than diets containing coarser haylage and dry ground corn. Furthermore, Beauchemin and Rode (1997) reported that rapidly digested starch sources, such as barley grain, increase the need for effective fiber. The results of the present study indicate that ruminal pH is influenced both by dietary components affecting chewing and salivary secretion, and by those affecting ruminal carbohydrate fermentation. Nevertheless, even though FDOM and RDSI serve as an indication of forage quality and of the intake in ruminally degradable starch, respectively, we are aware that in vitro- and in situ-estimated FDOM and RDSI cannot completely represent the in vivo ruminal degradation of OM of the experimental TMR used in this study. More research with known in vivo FDOM and RDSI is needed to validate this assumption.

Kohn (2000) reported that ruminal pH is a function of digestion and absorption, changes in strong ion concentration, and changes in the partial pressure of CO_2 in the rumen fluid. This study supports the theory that ruminal pH is an important parameter for determining physical effectiveness of dairy rations. However, the estimation proposed here should be adjusted for further details, such as rumen site and time of pH measurement, which in turn influences the pH readings. As described in Materials and Methods, there were differences among studies in measuring ruminal pH over time. Some studies measured pH from ruminal fluid from spot samples, whereas in others, ruminal pH was continuously measured. Although the measurements of ruminal pH covered at least a period until 8 to 10 h postfeeding and the analysis accounted for unequal variances among studies and for random effect of reporting results from studies with different laboratorial and experimental conditions, the methodological variability cannot be completely excluded. The pH values analyzed in this study tended more to characterize a daily mean pH measured in the ruminal fluid, and

hence represents neither pH readings in the peak of fermentation nor ruminal solid-phase pH. Nordlund and Garrett (1994) proposed sampling within 4 to 8 h postfeeding in TMR-fed herds to measure ruminal pH near the nadir. Furthermore, several researchers (Yang and Varga, 1989; Martin et al., 1999) recorded pH that was 0.2 to 0.4 units higher in the ventral rumen sac than in the dorsal rumen sac. In addition, Tafaj et al. (2005a) reported pH values 0.3 and 0.6 units higher in free rumen liquid than in the squeezed rumen liquid of solid digesta phase collected from the top and bottom of the rumen sac, respectively.

However, results of this study indicate that accounting for dietary physically effective fiber is a more efficient procedure to assess effective fiber adequacy of dairy cow ration than simply taking into account dietary NDF or FNDF. In this context, the PSPS constitutes a useful on-farm choice for frequent on-site examination of ration particle size and ration physical effectiveness, thus increasing the efficacy for controlling SARA on dairy farms. But, as this study demonstrates, not only physically effective fiber, but also the amount of digestible OM of forages and grain fermentability affects ruminal pH, which are not accounted for when using PSPS to calculate peNDF.

Effects of dietary factors on ruminal pH were not completely consistent with the effects on ruminal VFA content or molar percentage of acetate, propionate, or butyrate, which were not affected to the same extent or were not affected at all compared with ruminal pH (Tables 4 and 6). The effects of dietary particle size on the production and absorption of VFA are often contradictory. Reducing dietary particle size might increase the ruminal degradation rate of fiber, but this does not inevitably lead to an increase of rumen OM degradability or the production of VFA, as particulate passage rate can also be increased (Soita et al., 2003). However, Allen (2000) stated that decreasing forage particle size might increase DMI, which could also increase the availability of ruminally digested OM and hence the production of VFA.

Total VFA was negatively affected by peNDF, whether expressed as $peNDF_{>8}$ (R^2 = 0.25) or $peNDF_{>1.18}$, (R^2 = 0.12). This decrease of VFA in the rumen fluid with increasing dietary peNDF might be attributed to the positive effect of peNDF on rumen motility. Taylor and Allen (2005) stated that as ruminal motility increases, VFA molecules are expected to be replenished at the rumen wall more rapidly, increasing the concentration gradient across the ruminal epithelium and rate of VFA absorption. Increasing the dietary NFC:NDF ratio, NFC content, or RDSI from grain increased the ruminal VFA linearly, whereas acetate to propionate ratio and butyrate percentage decreased (Tables 4 and 6). This is in accordance with the results found by Firkins et al. (2001), who reported that acetate to propionate ratio correlated positively to FNDF and negatively to nonstructural carbohydrates in the diet of dairy cows.

Chewing Activity

Total chewing time ranged from 425 to 969 min/d (691 ± 11.2 min/d; mean ± SE), and rumination time ranged between 151 and 632 min/d (434 ± 8.29 min/d; mean ± SE). The mean value of rumination found here is consistent with that found by Beauchemin et al. (1994), who reported that high-producing dairy cows consuming large quantities of DM tended to ruminate more than 360 min/d unless digestive upset occurs. This was equivalent to a ruminative minimum of 16 min/kg of DM for 22 kg/d of DMI. About 14% of 99 treatment means used for rumination in this study did not achieve a rumination time of 360 min/d; and 25% of the reports gave values lower than 16 min/kg of DM (data not shown). Although the mean DMI in this study was about 1.03 kg/d higher than in that of Beauchemin et al. (1994), if we consider these criteria, it could be stated that these results do not represent a sufficient rumination activity. Table 2 gives an overview of the chewing indices. The range of time spent chewing and ruminating was high in this study; cows spent 17.9 to 47.1 min of chewing per kg of DM (30.1 ± 0.59 min/kg of DM) and 54.3 to 160 min/kg of NDF (103 ± 2.48 min/kg of NDF), whereas chewing time spent per kilogram of $peNDF_{>1.18}$ was 167 ± 9.67 min. Sudweeks et al. (1981) proposed that chewing corrected for DMI as a criterion for physical effectiveness of forages. They further proposed values equal to or greater than 30 min/kg of DM as suitable for limiting the risk of digestive disorders. Based on the recommendation of Sudweeks et al. (1981), 51% of 99 treatment means analyzed here were below this criterion, ranging from 17.9 to 29.9 min/kg of DM (data not shown). De Brabander et al. (2002) suggested that dairy cows should achieve between 59 and 72.8 min of chewing time per kg of DM from forages to prevent ruminal disorders and milk fat depression. Only 2 treatment means out of 99 were below this criterion in this study (result not shown). Tafaj et al. (2005c) estimated that for dairy cows to achieve a chewing time of 74 min/kg of DM from a long-chopped hay, diets should contain at least 10.7% long-chopped hay-crude fiber, which in turn corresponded to 28% NDF or 19% peNDF and 60% slowly degradable concentrate in the diet. Furthermore, Tafaj et al. (2005c) reported that rations should contain at least 10.0% long-chopped hay-crude fiber to maintain 3.4% milk fat, which is close to 10.7% long-chopped hay-

Table 7. Equations[1] for linear regression of response of chewing parameters to different dietary factors in dairy cows fed TMR

Chewing parameters (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
Total chewing time, min/d	$peNDF_{>1.18}$, %	563	27.9	5.86	1.26	85.1	0.17
	$peNDFI_{>8}$, %	627	19.6	6.46	1.71	92.3	0.13
	FNDF, %	521	27.0	7.75	1.23	74.1	0.23
	FDOM, g/kg of DM	521	27.2	0.54	0.09	72.6	0.23
	NFC, %	495	62.9	4.94	1.67	95.3	0.10
Rumination time, min/d	$peNDF_{>1.18}$, %	317	20.9	5.38	0.94	63.7	0.24
	$peNDF_{>8}$, %	365	11.8	6.25	0.92	61.1	0.27
	FNDF, %	312	20.1	5.39	0.91	54.9	0.21
	FDOM, g/kg of DM	288	19.2	0.45	0.06	51.3	0.29

[1]Only significant relationships are shown ($P < 0.05$).

[2]$peNDFI_{>8}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>8\text{-mm}}$ (Lammers et al., 1996); $peNDF_{>1.18}$ = physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); FNDF = forage NDF; FDOM = amount of digestible OM of forages in TMR estimated by MAFF (1990); NFC = nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % ether extract + % crude ash).

[3]RMSE = Root mean square error.

crude fiber needed to achieve a chewing time of 74 min/kg DM from long-chopped hay.

In Table 7, the significant linear relationships between dietary factors and chewing parameters are given, and in Table 8, the results of the analysis of multiple regression using backward elimination procedure are summarized. Total chewing and rumination time are positively affected by peNDF, FNDF, and FDOM contents of the ration, albeit to a lower extent than on ruminal pH. Total chewing activity was positively affected by dietary NFC, presumably because of the positive effect of dietary NFC on DMI. These results agree with those of Firkins et al. (2001), who reported that increasing dietary FNDF and nonstructural carbohydrate concentrations linearly increased chewing activity (min/kg of NDF). Similarly, Beauchemin and Yang (2005) reported a linearly increased chewing time from 702 to 783 min/d, and rumination time from 441 to 494 min/d with increasing $peNDF_{>8}$ in the diet from 8.9 to 11.5%. Based on this finding, Beauchemin and Yang (2005) postulated that a level of $peNDF_{>8}$ above 10% in the dairy cow diet is required to avoid reduction of chewing activity.

Figure 2 shows the relationship between time spent chewing per kilogram of $peNDF_{>1.18}$ intake and the concentration of $peNDF_{>1.18}$ in TMR. Cows spent less time chewing per unit of $peNDF_{>1.18}$ when the percentage of dietary $peNDF_{>1.18}$ was increased. The chewing index (min/kg of $peNDF_{>1.18}$) was quadratically reduced when the percentage of $peNDF_{>1.18}$ in TMR was increased. This finding is in agreement with Beauchemin and Yang (2005), who reported a linearly increased chewing index from 326 to 378 min/kg of $peNDF_{>8}$ with decreasing dietary $peNDF_{>8}$ from 11.5 to 8.9% of ration DM. Similarly, Tafaj et al. (2005c) reported a linearly increased time spent chewing from 99.4 to 134.8 min/kg

Table 8. Best-fit equations for multiple regression[1] of chewing parameters to different dietary factors in dairy cows

Chewing parameters (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
Total chewing time, min/d	$peNDF_{>1.18}$, %	165	68.0	6.51	1.40	76.4	0.44
	FDOM, g/kg of DM			6.69	1.36		
	NFC, %			0.39	0.11		
Rumination time, min/d	$peNDF_{>1.18}$, %	231	28.4	5.14	1.08	59.7	0.36
	FDOM, g/kg of DM			0.33	0.08		

[1]For simplicity, only the best-fit equations of multiple regression (backward elimination) that improved further the relationship obtained from linear regressions are shown.

[2]$peNDF_{>1.18}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); FDOM = amount of digestible OM of forages in TMR estimated by MAFF (1990); NFC = nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % ether extract + % crude ash).

[3]RMSE = Root mean square error.

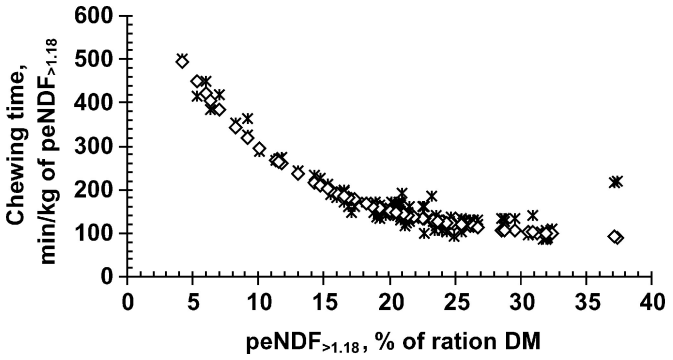

Figure 2. Relationship of physically effective NDF ($peNDF_{>1.18}$) to observed chewing index adjusted for the random experiment effect and unequal variance. The best-fit, quadratic regression chewing time = 628.8 (±13.8) – 38.8 (±1.35) $peNDF_{>1.18}$ + 0.73 (±0.03) $peNDF^2_{>1.18}$; root mean square error = 24.82; R^2 = 0.91; Asymptotic function (◇) chewing time = $80.4 + 664e^{(-0.94\ peNDF>1.18)}$ using Proc NLIN (SAS Institute, 2001). To achieve 150 min/kg of $peNDF_{>1.18}$ the ration should contain about 20% $peNDF_{>1.18}$.

of peNDF as dietary peNDF reduced from 39 to 19% of ration DM. These results suggest that dietary peNDF may affect chewing activity either through prolonging chewing time or decreasing chewing index. Mertens (1997) suggested that dairy cow diets should contain 22.3% peNDF to assure a chewing activity of 150 min/kg of peNDF to maintain optimal ruminal function. As shown in Figure 2, TMR should contain ~20% $peNDF_{>1.18}$ to achieve 150 min/kg of $peNDF_{>1.18}$, which is again somewhat lower than the peNDF percentage recommended by Mertens (1997).

Among the systems proposed to estimate the minimum amount of fiber necessary in rations for lactating dairy cows, most have attempted to guide ration formulation by predicting the amount of chewing that various feedstuffs would generate, or their relative effectiveness at maintaining milk fat percentage (Mertens, 2000). Mertens (1997) suggested that for cows to maintain 3.6% milk fat, they should achieve a chewing time of 744 min/d or 36.1 min/kg of DM. The chewing time needed to maintain a specified milk fat percentage from cows in early lactation fed TMR is shown in Table 9. Cows needed a chewing time of 797 min/d or 36.5 min/kg of DM to maintain 3.6% milk fat. Chewing index (min/kg of DM) corresponded better than total chewing time to the estimation of Mertens (1997).

Fiber Digestibility

Digestibilities of NDF and ADF were linearly increased as dietary peNDF and NDF were increased, whereas NDF digestibility decreased linearly with increasing NFC concentration and NFC:NDF ratio in the diet (Table 10). Increasing $peNDF_{>1.18}$ in TMR by 1% increased NDF digestibility about 0.41% (R^2 = 0.56). Increasing peNDF in TMR positively affected chewing activity and especially ruminal pH, thus probably increasing saliva secretion that prevents ruminal pH from declining especially during meal consumption, as concluded by Beauchemin (2000) and Beauchemin and Yang (2005). Increased salivation during eating could enable the cow to buffer the large quantity of fermentation acids produced soon after the feed is consumed, whereas an increase in saliva output during rumination allows rumen buffering for a longer period after ingestion (Allen, 1997).

It is also believed that peNDF is the portion of a diet that stimulates chewing activity and ruminal digesta stratification (Mertens, 1997) and enhances mat consistency in the reticulorumen (Zebeli et al., 2005). On the other hand, increasing the consistency of ruminal mat improved fiber digestibility (Bal et al., 2000; Harvatine et al., 2002), through an increased selective retention ("filter bed" effect) of ruminal mat for undigested small feed particles (Sutherland, 1988). Furthermore, Tafaj et al. (1999, 2001) found that feeding dairy cows a ground- (2.9 mm) vs. a long- (28.7 mm) or a chopped- (9.2 mm) hay impaired rumen conditions and reduced total mean retention time of digesta by 10 h, which in turn led to a significant reduction of fiber digestibility of about 14% in dairy cows. Results of the present study show that depression of rumen pH due to reduction of peNDF in the diets likely contributes to the reduction of fiber digestibility, supporting the hypothesis that ruminal pH promotes cellulolytic activity. Ruminal cellulolytic activity is compromised when ruminal pH drops below 6.0 based on in vitro studies (Mouriño et al., 2001). Dietary peNDF, expressed as $peNDF_{>1.18}$, appears to be a reliable predictor of fiber digestion. Because the amount of fiber that can be digested in the large intestine is limited, Yang and Beauchemin (2005) concluded that influence of dietary peNDF on digestibility is more pronounced for fiber than for starch, in which low ruminal digestion can be compensated for by high intestinal digestion. According to the equation given in Table 10, an NDF digestibility of 46.2% would be observed for a percentage of ~19 of dietary $peNDF_{>1.18}$ (to maintain a rumen pH of 6.0), which corresponds with the mean NDF digestibility reported in this study (46.9 ± 0.96%; Table 2).

Milk Production and Composition

In this study, cows produced between 23.1 and 49.3 kg of milk/d and were between 9 and 170 d in milk (84.8 ± 3.54 DIM; Table 2). All articles included in this study gave information about milk production and its composition. This is probably because milk parameters

Table 9. Estimating the chewing time (min/d) and (min/kg of DM) required to maintain milk fat percentages of cows in early lactation

	Milk fat percentage regressed on chewing time	
	min/24 h	min/kg of DM
Linear regression		
Mean milk fat intercept of all experiments	2.16 (0.13)[1]	2.50 (0.11)
Linear regression coefficient	0.0018 (0.0002)	0.030 (0.0037)
Root mean square error (RMSE)	0.188	0.202
R^2	0.50	0.41
Requirement for specified milk fat percentage		
3.6% milk fat	797	36.5
3.4% milk fat	687	30.0
3.2% milk fat	577	23.3

[1]Numbers in parentheses are standard error of estimates.

are easy to record, but as observed in this study, they did not satisfactorily respond to dietary factors considered.

Table 11 shows the results of linear regression of response of milk parameters to different dietary factors (only significant relationships are shown). The analysis of backward elimination of multiple regression did not further improve the relationship obtained from linear regression, and therefore no results are shown here. Milk yield was negatively affected by dietary NDF and FNDF and positively by NFC:NDF ratio, presumably because of their effect on DMI and energy concentration of the diet. Firkins et al. (2001) reported a negative correlation between milk yield and FNDF. Milk protein was not significantly affected by dietary factors studied here. However, the milk fat:protein ratio increased linearly with increasing $peNDF_{>1.18}$, FNDF, and FDOM in the diet. Milk fat percentage increased linearly with increasing dietary FNDF and FDOM. Firkins et al. (2001) reported that milk fat content responded in a quadratic fashion to dietary FNDF.

Beauchemin et al. (1994) and Mertens (1997) concluded that effects of particle size on milk fat content were likely to be observed when NDF levels were lower than the minimum recommended requirement. The NRC (2001) recommends a minimum of 25% dietary NDF and 19% FNDF for dairy cows. However, in 16 cases (12% of treatment means), both NDF and FNDF content in TMR were below the NRC (2001) recommendations (data not shown) in this study.

Failure to observe effects of dietary peNDF on milk yield and fat percentage contrasts with the effect of increasing dietary $peNDF_{>1.18}$ on increasing ruminal pH and fiber digestibility. It is apparent that milk parameters are less sensitive to the effects of dietary peNDF than are other variables, such as ruminal pH, chewing activity, and fiber digestibility. It is well recognized, however, that cows are in negative energy balance in early lactation; thus, animals must mobilize fat (NRC, 2001) and consequently, milk fat content artificially increases. On the other hand, milk fat is a variable that is closely related to dietary fat and the genetic

Table 10. Equations[1] for linear regression of response of fiber digestibility to different dietary factors in dairy cows fed TMR

Parameter (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
NDF digestibility, %	$peNDF_{>1.18}$, %	38.6	0.82	0.41	0.04	2.15	0.56
	$peNDF_{>8}$, %	43.3	0.63	0.36	0.05	2.96	0.30
	NDF, %	31.4	1.83	0.51	0.06	2.88	0.42
	NFC, %	54.1	1.96	–0.19	0.05	2.97	0.14
	NFC:NDF	58.8	1.64	–10.2	1.29	5.38	0.37
ADF digestibility, %	$peNDF_{>1.18}$, %	34.2	1.08	0.51	0.05	3.30	0.51
	$peNDF_{>8}$, %	38.8	1.00	0.47	0.08	5.20	0.23
	NDF, %	30.3	2.07	0.42	0.07	4.40	0.24

[1]Only significant relationships are shown ($P < 0.05$).

[2]$peNDF_{>1.18}$ = Physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); $peNDFI_{>8}$ = physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>8\text{-mm}}$ (Lammers et al., 1996); NFC = nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % ether extract + % crude ash).

[3]RMSE = Root mean square error.

Table 11. Equations[1] for linear regression of response of milk parameters to different dietary factors in dairy cows fed TMR

Milk parameter (Y)	Dietary factor[2] (X)	Parameter estimates				Model statistics	
		Intercept	$SE_{Intercept}$	Slope	SE_{Slope}	RMSE[3]	R^2
Milk yield, kg	NDF, %	46.9	2.44	–0.389	0.077	5.19	0.16
	FNDF, %	42.9	1.95	–0.375	0.088	5.34	0.12
	NFC:NDF	19.7	3.23	21.851	4.715	5.27	0.18
	$NFC:NDF^2$			–6.652	1.660		
Milk fat, %	$peNDF_{>1.18}$, kg	2.76	0.19	0.212	0.072	0.34	0.11
	$peNDF^2_{>1.18}$, kg			–0.014	0.006		
	FNDF, %	2.77	0.11	0.029	0.005	0.31	0.20
	FDOM, g/kg of DM	2.66	0.11	0.002	0.0003	0.29	0.27
Fat-to-protein ratio in milk	$peNDF_{>1.18}$, %	0.91	0.04	0.008	0.001	0.11	0.17
	FNDF, %	0.90	0.04	0.008	0.001	0.11	0.14
	FDOM, g/kg of DM	0.80	0.04	0.0009	0.0001	0.10	0.32

[1]Only significant relationships are shown ($P < 0.05$).

[2]FNDF = Forage NDF; NFC = nonfiber carbohydrate calculated by difference 100 – (% CP + % NDF + % fat + % ash); $peNDF_{>1.18}$ = physically effective NDF measured as the NDF content of TMR multiplied by amount of $DM_{>1.18\text{-mm}}$ (Mertens, 1997); FDOM = amount of digestible OM of forages in TMR estimated by MAFF (1990).

[3]RMSE = Root mean square error.

merit of the animal. Mertens (1997) concluded that ruminal pH may be a better indication of ruminal health and optimal function than the maintenance of milk fat production in this stage of lactation for dairy cows.

Systems for Estimation of Physically Effective Fiber and Response Variables

For physical evaluation of forages or TMR, different wet and dry sieving techniques have been proposed. Murphy and Zhu (1997) compared 9 methods (3 dry and 6 wet) for evaluating particle size distribution of feedstuffs. Based on median particle size estimates (central tendency), they concluded that 6 of those (including all dry sieving techniques tested) had relatively consistent estimates of particle size distribution. Lammers et al. (1996) developed the simplified method for evaluating particle size distribution of forages and TMR using PSPS. The PSPS is based on the properties of Standard S424 of the American Society of Agricultural Engineers (ASAE, 1998) and has been proven to generate similar results to the vertical oscillating sieving method (Lammers et al., 1996; Buckmaster, 2000; Teimouri Yansari et al., 2004). The PSPS device contains 2 sieves and a bottom pan. Using the PSPS, particle distribution is determined by separating particles according to size; >19 mm, between 19 and 8 mm, and <8 mm (Lammers et al., 1996).

The new version of PSPS (Kononoff et al., 2003b) is constructed from 3 sieves with pores measuring 19, 8, and 1.18 mm and a solid bottom pan, permitting the estimation of $peNDF_{>1.18}$ according to Mertens (1997). Teimouri Yansari et al. (2004) estimated $peNDF_{>1.18}$ of forages (alfalfa and corn silage) and TMR using both a vertical oscillating sieve and the new PSPS and reported very similar results. The PSPS is a quick, cost-effective method, and produces consistent results in measuring particle size distribution of forages and TMR. These properties made the PSPS method a valuable on-farm choice to estimate forage and TMR particle size distribution around the world.

As shown in Table 2, the amount of physically effective NDF in TMR was higher when estimated as $peNDF_{>1.18}$ than when estimated as $peNDF_{>8}$. This is because $peNDF_{>1.18}$ contains a large pool of particles retained on the lower screens (i.e., particles greater than 1.18 mm and smaller than 8 mm). Research results (Kononoff and Heinrichs, 2003a; Kononoff et al., 2003a; Plaizier, 2004) showed that the proportion of this pool could range from 30 to 50% in the TMR. Beauchemin et al. (2003) reported a 50% higher peNDF of TMR when it was estimated as $peNDF_{>1.18}$ compared with $peNDF_{>8}$, because $peNDF_{>8}$ does not consider particles <8 mm or steam-rolled concentrate, whereas $peNDF_{>1.18}$, does.

Results of this study showed that differences in the quantity of $peNDF_{>8}$ and $peNDF_{>1.18}$ were reflected by their effects on the response variables studied. Thus, regarding the chewing activity, the $peNDF_{>8}$ affected rumination time to a slightly higher extent than did $peNDF_{>1.18}$ ($R^2 = 0.27$ vs. $R^2 = 0.24$), whereas total chewing time was more accurately estimated when peNDF was expressed as $peNDF_{>1.18}$ ($R^2 = 0.17$ vs. $R^2 = 0.13$). On the other hand, the accuracy of estimation for ruminal pH and NDF digestibility was higher when peNDF was expressed as $peNDF_{>1.18}$. Although the content of $peNDF_{>8}$ is lower than $peNDF_{>1.18}$ in the TMR, the effectiveness of $peNDF_{>8}$ to stimulate rumination is higher. Buckmaster (2000) proposed an effective fiber index that weights NDF content by particle size. To calculate

the effective fiber index of a ration, NDF content of each fraction of particles retained on each sieve is multiplied by a relative effectiveness coefficient, which is different for every particle fraction retained on the screens of PSPS. Based on these relative effectiveness coefficients, Buckmaster (2000) stated that particles >19 mm are twice as effective for stimulating rumination and contributing to a rumen mat as those between 8 and 19 mm, whereas particles <8 mm have one-fifth of the effectiveness of particles between 8 and 19 mm. This contrasts with the $peNDF_{>1.18}$ method of Mertens (1997), which equally weights particle mass >1.18 mm in stimulating chewing activity and neglects the rest. Krause et al. (2002b) corrected the particle size distribution of TMR by that of orts and found a good relationship only between chewing and rumination activity with DMI from particles retained on the 19-mm screen of PSPS (r = 0.61 each), but not with DMI from particles retained on the 8-mm screen or the pan. Furthermore, Krause et al. (2002b) found no relationship between ruminal pH and DMI from particles retained on the 19- and 8-mm screens of PSPS.

Results of ruminal pH and NDF digestibility in the present study did not support dietary peNDF measured as the proportion of particles retained on 8 mm sieve as the best indicator to express the physical effectiveness of TMR, even though $peNDF_{>8}$ slightly better estimated rumination time. Indeed, the relationship between chewing and rumination time and ruminal pH was low in this study (r = 0.25 and r = 0.33, respectively; results not shown). Cassida and Stokes (1986) estimated saliva flow rates of 150, 177, and 300 mL/min during resting, eating, and ruminating, respectively. Using these estimated flow rates, the contribution in saliva production in the present study would be 112, 46, and 130 L/d for resting, eating, and ruminating time, respectively (data calculated based on chewing times given in Table 2). It could be stated that decreased saliva flow associated with a decreased rumination time could be partly balanced by saliva secretion during resting time. Krause et al. (2002b) reported that salivary buffering is only one of many factors determining ruminal pH.

Discrepancies between $peNDF_{>8}$ and $peNDF_{>1.18}$ to estimate rumination time, ruminal pH, and fiber digestibility observed in this study indicate that these concepts cannot be used interchangeably. Although the $peNDF_{>8}$ concept represents particles retained on the 8-mm sieve, which are expected to provoke an intensive saliva output, $peNDF_{>8}$ was not the best parameter to estimate ruminal pH and fiber digestibility.

It is believed that diets with less than 7% long particles (particles retained on the top screen of the separator) put cows at increased risk of SARA, particularly if these diets are also borderline or low in chemical fiber content (Grant et al., 1990a). However, increasing chemical fiber content may compensate for short particle length (Beauchemin et al., 1994). On the other hand, diets having excessive long forage particles can paradoxically increase the risk of SARA, especially when long particles are unpalatable and sortable (K. M. Krause and G. R. Oetzel, unpublished data). Several researchers (Calberry et al., 2003; Leonardi and Armentano, 2003; Beauchemin and Yang, 2005) reported different particle size distributions for TMR and orts for cows fed TMR ad libitum, indicating selective consumption. By feeding Holstein cows a corn silage-based TMR, we found (Junck et al., 2004) that across treatments (4 different theoretical particle lengths, 5.5, 8.1, 11, and 14 mm), difference between the offered TMR and orts were 26% for particles retained on the 8-mm screen (i.e., sum of particles retained on 19- and 8-mm sieves of PSPS). This difference was only 9% for particles retained on the 1.18-mm screen (i.e., sum of particles retained on 19-, 8-, and 1.18-mm sieves of PSPS) (in both cases were more long particles in orts than in the offered TMR). This indicates that if we evaluate our TMR only based on particles retained on the 8-mm screen (i.e., $peNDF_{>8}$), our estimation to evaluate effective fiber content of the truly consumed TMR was biased 26% compared with only 9% bias if we estimated the peNDF of TMR based on particles retained on the 1.18-mm screen (i.e., $peNDF_{>1.18}$). This was because cows sorted against coarse particles of TMR and preferred to consume short particles and crushed corn kernels, which are more palatable and digestible. However, this sorting against the coarse particles was more evident for TMR containing the longest levels of corn silage (11 and 14 mm) compared with TMR containing the shortest levels (8.1 and 5.5 mm), which showed a lower sorting rate. It seems, therefore, that an advantage of estimating peNDF of the ration based on particles retained on 1.18-mm screen consists in this, that this system, better reflects the TMR really consumed by dairy cows and can reduce the estimation bias related to sorting consumption. Under practical conditions on dairy farms, the evaluation of particle size distribution is mainly carried out in TMR and not in orts. For this reason, the evaluation of the ration based only on the pool of long particles of the original TMR does not appear to be an adequate approach for estimation of physical effectiveness in dairy cows fed TMR ad libitum.

CONCLUSIONS

This study showed that the concentration and intake of $peNDF_{>1.18}$ should be considered in formulation of TMR for high-yielding dairy cows. Results of this data

analysis showed that $peNDF_{>1.18}$ provided a satisfactory estimation of mean ruminal pH and fiber digestibility. Indeed, the $peNDF_{>1.18}$ approach explained 67% of the variation in ruminal pH. On the other hand, $peNDF_{>1.18}$, was poorly, although positively, correlated to daily chewing ($R^2 = 0.17$) and rumination ($R^2 = 0.24$) activity. Results from this analysis showed that milk parameters are less sensitive to the effects of dietary peNDF than are other variables, such as ruminal pH, fiber digestibility, and chewing activity.

Using the $peNDF_{>1.18}$ approach, the requirements for physically effective fiber in high-yielding dairy cows fed TMR in an ad libitum intake were estimated to be about 19% of ration DM (4.1 kg/d or 0.6 kg/100 kg of BW) to maintain a ruminal pH of about 6.0. Inclusion of FDOM and RDSI from grain in the model together with $peNDF_{>1.18}$ appeared to be advantageous in improving the accuracy of estimation. This approach appeared to complement the concept of peNDF that does not account for differences in ruminal fermentability of feeds. Moreover, this study showed that the intake of rapidly fermentable carbohydrates is more important than total NFC percentage of the diet to be taken into account in terms of avoiding SARA in high-yielding dairy cows.

When peNDF was measured as the proportion of particles retained on an 8-mm PSPS screen ($peNDF_{>8}$), ruminal pH responded in a quadratic fashion but the confidence of estimation was lower ($R^2 = 0.27$) compared with $peNDF_{>1.18}$. Furthermore, measuring physically effective NDF as $peNDF_{>1.18}$ might be more realistic in terms of expression of effective fiber in the TMR truly consumed by dairy cows.

Results of this study indicated that accounting for dietary physically effective fiber is a more efficient procedure to assess effective fiber adequacy of dairy cow rations than simply taking into account dietary NDF or FNDF. In this context, the PSPS constitutes a useful on-farm choice for frequent on-site examination of ration particle size and ration physical effectiveness.

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