Modeling the Adequacy of Dietary Fiber in Dairy Cows Based on the Responses of Ruminal pH and Milk Fat Production to Composition of the Diet

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ABSTRACT

The main objective of this study was to develop practical models to assess and predict the adequacy of dietary fiber in high-yielding dairy cows. We used quantitative methods to analyze relevant research data and critically evaluate and determine the responses of ruminal pH and production performance to different variables including physical, chemical, and starch-degrading characteristics of the diet. Further, extensive data were used to model the magnitude of ruminal pH fluctuations and determine the threshold for the development of subacute ruminal acidosis (SARA). Results of this study showed that to minimize the risk of SARA, the following events should be avoided: 1) a daily mean ruminal pH lower than 6.16, and 2) a time period in which ruminal pH is <5.8 for more than 5.24 h/d. As the content of physically effective neutral detergent fiber (peNDF) or the ratio between peNDF and rumen-degradable starch from grains in the diet increased up to $31.2 \pm 1.6\%$ [dry matter (DM) basis] or 1.45 ± 0.22 , respectively, so did the daily mean ruminal pH, for which a asymptotic plateau was reached at a pH of 6.20 to 6.27. This study also showed that digestibility of fiber in the total tract depends on ruminal pH and outflow rate of digesta from reticulorumen; thereby both variables explained 62% of the variation of fiber digestibility. Feeding diets with peNDF content up to $31.9 \pm 1.97\%$ (DM basis) slightly decreased DM intake and actual milk yield; however, 3.5% fat-corrected milk and milk fat yield were increased, resulting in greater milk energy efficiency. In conclusion, a level of about 30 to 33% peNDF in the diet may be considered generally optimal for minimizing the risk of SARA without impairing important production responses in high-yielding dairy cows. In terms of improvement of the accuracy to assessing dietary fiber

adequacy, it is suggested that the content of peNDF required to stabilize ruminal pH and maintain milk fat content without compromising milk energy efficiency can be arranged based on grain or starch sources included in the diet, on feed intake level, and on days in milk of the cows.

Key words: physically effective fiber, dairy cow, ruminal pH, rumen-degradable starch

INTRODUCTION

The challenge primarily met in dairy cow feeding is to provide an energetically high-density ration without compromising ruminal ecosystem, animal welfare, and production performances. Providing high-yielding dairy cows adequate levels of dietary fiber is critical to prevent subacute ruminal acidosis (SARA) and the resulting depressions in fiber digestion, DMI, and milk production as well as alterations in milk composition (NRC, 2001). In contrast, offering diets in excess of fiber may decrease feed intake and lower the efficiency of feed use (Yang and Beauchemin, 2006a). Thus, it is essential to find an optimum of dietary fiber that may decrease the risk of SARA without impairing important production performances in dairy cows.

However, assessment of dietary fiber adequacy in dairy cows from the current feed tables is difficult due to insufficient consideration of physical effectiveness of different feeds. For this reason, the concept of physically effective NDF (**peNDF**) proposed by Mertens (1997) is considered more efficient because it incorporates information on particle length and chemical NDF content of the diet. The latter 2 variables affect digesta stratification in the reticulorumen and rumination activity and, therefore, the ruminal buffering capacity and pH (Mertens, 1997; Zebeli et al., 2006a). The peNDF content of feeds or of TMR can be easily calculated even under on-farm conditions (Plaizier et al., 2004) by using the Penn State Particle Separator (Kononoff et al., 2003a).

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Although different studies conducted over the last decade provide important information into various physiological effects of peNDF in high-yielding dairy cows (e.g., Yang and Beauchemin, 2006a,b; 2007a,b), the optimum concentration of peNDF in dairy cow diets is uncertain. In fact, one of the drawbacks of the peNDF concept is that it does not take into consideration the differences in ruminal fermentability of various feedstuffs. Numerous studies (Allen, 1997; De Brabander et al., 2002; Zebeli et al., 2006b) reported that inclusion of rumen-fermentable OM or starch as a variable in the model together with dietary fiber, particle length index, or peNDF increases the accuracy of prediction of ruminal pH or milk fat content in dairy cows. The content of peNDF may interact with the content of rumen-fermentable carbohydrates and intake level and may modify the response of ruminal fermentation. The level of feed intake may determine important qualitative changes, particularly on passage and digestion kinetics in the reticulorumen (Firkins et al., 2001; Stone, 2004; Seo et al., 2006), which also may confound the response of ruminal pH to dietary peNDF.

Part of the difficulty in assessing adequacy of the dietary fiber and in determining peNDF requirements for dairy cows may also be related to the interpretation of the response of the ruminal pH and its resulting effects on fiber degradation or development of SARA. Ruminal pH in dairy cows is not constant, but fluctuates considerably in a 24-h period. In high-yielding dairy cows fed high concentrate diets at >45% of the ration (DM basis), ruminal pH generally ranges from 6.6 before morning feeding to 5.3 or 5.0 during the intensive rumen fermentation phases, with average pH typically at 6.0 or 6.1. In fact, ruminal pH can drop below these average levels for considerable periods during the feeding cycle. Because the magnitude of diurnal fluctuations of ruminal pH has not been sufficiently characterized, the time of pH measurement may be misleading. Moreover, the rumen pH that defines SARA is still a matter of individual choice, with different researchers using different pH threshold values of 5.6 (Keunen et al., 2002), 5.8 (Beauchemin et al., 2003), or 6.0 (Krehbiel et al., 1995). The length of time per day when ruminal pH is under "suboptimal" levels (Beauchemin et al., 2003; Krause et al., 2003), or the index that weights the time spent under the optimal ruminal pH by the magnitude of the deviation from this pH (Mackie and Gilchrist, 1979), seem a better determinant of fiber degradation and presence of SARA than daily mean ruminal pH, or the lowest (nadir) ruminal pH value. Also, the time duration for which the ruminal pH must remain below this threshold value has not been properly defined.

The complexity of the interactions between feed intake, forage type, concentrate fed, and ruminal degradability of different feedstuffs as well as the uncertainty in defining the response of the ruminal pH make it difficult to quantitatively characterize the effects of peNDF on ruminal fermentation and prevention of SARA. These factors also hamper recommendations on optimal dietary peNDF levels for dairy cows. In this context, quantitative methods are helpful tools to synthesize knowledge and improve predictions of desired animal responses and support an optimal decision-making in formulating healthy diets for dairy cows (St-Pierre, 2001; Dijkstra et al., 2007).

The main objective of this study was to develop practical models to assess and predict the adequacy of dietary fiber in high-yielding dairy cows. Therefore, quantitative methods were used to analyze relevant research data and critically evaluate and determine the responses of ruminal pH and production performance to different variables including physical, chemical, and starch-degrading characteristics of the diet. Furthermore, extensive data were used to model the magnitude of ruminal pH fluctuations and determine the threshold for the development of SARA.

MATERIALS AND METHODS

Responses of Ruminal pH and Production Performance to Diet Characteristics

Description of Database. To define the responses of ruminal pH and production performance to physical and chemical characteristics of the diet, a database with data on animal performance, detailed ration components, and an evaluation of physical structure of the ration was generated. To evaluate the effects of dietary factors on production responses, data of feed intake, actual milk yield, 3.5% FCM, milk fat yield, and milk energy efficiency (MEE) were considered. The MEE was calculated by dividing milk fat yield by DMI, and this was expressed as grams of milk fat produced per kilogram of DMI. This database was compiled from 58 studies containing a total of 238 treatment means, published mainly over the last 10 yr, and conducted with high-yielding dairy cows fed TMR. (A full list of references from studies included in this database is available in Table A1 of the appendix.) A statistical description of main characteristics of the database, including cow data, diet characteristics, and response variables are listed in Table 1. All studies used lactating Holstein cows (95.5 ± 48.4 DIM; mean $\pm$ SD) weighing between 528 and 886 kg and producing 18.1 to 49.3 kg of milk/d (33.6 kg/d of 3.5% FCM; Table 1). Milk fat content ranged from about 2.3 to 4.4%, whereas the MEE averaged 51.8 ± 7.57 g/kg of DMI. The level of DMI averaged

Table 1. Statistical description¹ of cows, diet characteristics, and response variables included in the database used to model the responses of ruminal pH and milk production in dairy cows

Item	Statistics								
	n _{Treat}	n _{Exp}	Mean	SD	Minimum	25 _{Perc}	Median	75 _{Perc}	Maximum
Cow data									
BW, kg	238	58	639	49.6	528	606	648	658	886
DIM	234	57	95.5	48.4	9.00	61.0	95.0	124	230
DMI, kg/d	238	58	22.3	3.28	14.2	20.8	22.8	24.8	28.3
Milk protein, %	202	51	3.11	0.21	2.63	2.98	3.11	3.24	3.76
Diet characteristic, % of DM									
Forage in TMR	238	58	49.4	10.6	26.8	40.3	49.4	55.0	80.8
CP	219	54	17.2	1.56	12.7	16.3	17.5	18.0	22.1
NDF	238	58	32.5	6.38	18.2	26.9	32.2	36.2	49.0
Forage NDF	206	50	21.9	5.98	11.5	17.4	21.1	24.9	44.9
peNDF ²	187	45	24.1	7.10	4.24	20.5	24.1	29.1	40.6
NFC ³	214	55	37.5	6.54	16.5	33.5	38.3	42.5	53.2
Starch from grains	210	54	17.6	6.01	5.40	13.8	17.5	21.6	33.8
RDSG ⁴	210	54	13.7	4.46	4.46	11.0	13.1	17.0	25.8
Starch from forages	210	54	7.50	5.95	0.10	1.30	7.05	11.4	24.8
RDSF ⁵	210	54	6.05	5.36	0.08	0.56	5.14	10.3	22.3
RDS ⁶	210	54	19.6	4.44	9.20	15.7	19.3	22.9	28.6
peNDF:RDSG ratio	179	43	1.92	1.29	0.25	1.19	1.60	2.35	9.67
Response variable									
Ruminal pH (daily mean)	205	54	6.10	0.26	5.30	5.95	6.07	6.28	6.73
SE of daily mean ruminal pH ⁷	205	54	0.07	0.03	0.01	0.05	0.07	0.10	0.15
VFA, mM	196	50	116	19.2	74.9	101	117	129	162
Actual milk yield, kg/d	212	53	34.9	5.78	18.1	30.6	35.0	39.1	49.3
3.5% FCM, kg/d	212	53	33.6	5.94	22.2	29.0	33.0	37.8	49.0
Milk fat, %	212	53	3.46	0.39	2.39	3.23	3.50	3.77	4.43
Milk fat yield, kg/d	212	53	1.17	0.21	0.78	1.02	1.16	1.32	1.71
MEE, ⁸ g of milk fat/kg of DMI	212	53	51.8	7.57	34.5	46.5	52.3	56.1	81.7
Total-tract NDF digestibility, %	142	35	48.2	7.35	28.4	44.7	47.9	50.3	64.6
k _p , ⁹ %/h	140	34	4.06	1.40	1.90	2.99	3.78	4.59	8.40

¹n_{Treat} = number of treatment means; n_{Exp} = number of experiments; 25_{Perc} = 25th percentile; 75_{Perc} = 75th percentile; a full list of references for studies included in this database is available in the appendix (Table A1).

²peNDF = physically effective NDF, measured as the NDF content of TMR multiplied by amount of DM particles retained on a 1.18-mm sieve (Mertens, 1997).

³NFC calculated by 100 – (% CP + % NDF + % ether extract + % crude ash).

⁴RDSG = ruminally degradable starch from grain in TMR.

⁵RDSF = ruminally degradable starch from forages in TMR.

⁶RDS = ruminally degradable starch from both grains and forages in TMR.

⁷Standard error of the treatment mean reported from studies.

⁸MEE = milk energy efficiency (expressed as g of milk fat produced per kg of DMI/d).

⁹Outflow rate of particulate digesta from reticulorumen, measured using external markers.

22.3 ± 3.28 kg/d and the percentage of forage in TMR ranged from 26.8 to 80.8% of DM (49.4 ± 10.6%). Dietary NDF was from 18.2 to 49.0% of DM (32.5 ± 7.09%) and forage NDF (**FNDF**) between 11.5 and 44.9% of DM (21.9 ± 5.98%). Data on total-tract NDF digestibility and outflow rate of digesta from the reticulorumen (**k_p**) were also included. Most of the studies included in this database recorded ruminal pH during 24 h either by using an indwelling electrode placed in the ventral rumen sac or by measuring pH from ruminal fluid in spot samples collected from the ventral sac of the rumen via rumen cannula. In some studies, ruminal pH was measured from spot fluid samples covering a time from shortly before to 12 h after morning feeding. In such cases, an average pH was calculated and considered as

daily mean ruminal pH in this database. The **k_p** was measured using external markers (e.g., ytterbium, chromium). Overall, daily mean ruminal pH ranged from 5.30 to 6.73 (6.10 ± 0.26), NDF digestibility varied from 28.4 to 64.6%, and **k_p** ranged from 1.9 to 8.4 %/h. All studies were conducted in Latin square or double reversal designs and the sample size varied between 4 and 8 ruminally cannulated cows per study.

Measurement of peNDF of Diets. As a prerequisite for inclusion in this study, publications were expected to give complete information on the components and chemical composition of rations, as well as on the physical evaluation of experimental diets, using dry sieving techniques. The aim was to account for fiber and physical characteristics of the diet by including a measure-

ment that included both NDF content and particle size (i.e., peNDF content) of the diet. The system proposed by Mertens (1997) for estimating peNDF based on NDF concentration of the diet multiplied by the proportion of particles retained on a 1.18-mm sieve (**peNDF**_{>1.18}) using dry sieving techniques was used in the present study, because this measurement was previously shown to be a good indicator of physical characteristics of TMR in dairy cows (Mertens, 1997; Zebeli et al., 2006b). Thus, to measure peNDF_{>1.18} content of TMR in the present study, the DM proportion retained on a 1.18-mm sieve, obtained either through the vertical oscillating sieving technique or the new version of the Penn State Particle Separator (Kononoff et al., 2003a), was multiplied by NDF content (DM basis) of TMR. The differences in the content of peNDF_{>1.18} of the TMR between these 2 methods have been shown to be negligible, particularly when diets are based on forages other than corn silage (Yansari et al., 2004; Yang and Beauchemin, 2006b). For simplicity, hereafter in the text peNDF_{>1.18} will be simply presented as peNDF. As shown in Table 1, the peNDF content of TMR in this database was measured in 45 published studies with 187 treatment means, ranging from 4.2 to 40.6% of DM (on average 24.1 ± 7.1%).

Estimation of Ruminally Degradable Starch from Grains and Forages in TMR. Because the concept of peNDF does not account for ruminal OM fermentability of TMR, rumen degradability of starch from different grains and forages composing the TMR was estimated and included in the analysis. This study focused on the effects of starch degradation rather than OM degradation, assuming that kinetics of starch degradation in the rumen is a more sensible variable for ruminal pH than OM degradation. The latter may be confounded by degradation characteristics of soluble and particularly insoluble cell wall components, which are shown to be very variable in the feedstuffs (Sauvant et al., 2004). In addition, OM degradation was shown not to be a proper indication of starch degradation, especially in barley grains (Ramsey et al., 2001).

Rumen degradability of starch from grains was estimated separately from that of forages to investigate the weight of each source of dietary starch on rumen fermentation and milk parameters. Rumen degradability of starch from different grains, including various by-products, was considered to take into account both the different starch amounts and differences in rumen degradability of starch among grain sources (e.g., barley vs. corn) in TMR, and physical or chemical treatments of grains (e.g., ground, dry rolled, steam-rolled, cracked, flaked, dry or high-moisture corn), which may modify their ruminal degradability. However, because of insignificant content in starch, the degradability character-

istics of starch from soy products or other protein-rich concentrates was ignored in this analysis. Starch from forages was included in the analysis particularly to take into account those forage sources of TMR rich in starch, such as corn, oat, or barley silage.

All studies included in this database provided detailed information about the components of concentrate mixture and forage sources of TMR. Starch content of grains and forages either was taken direct from publications or was obtained from tables compiled by Sauvant et al. (2004). The effective ruminal degradability (**ERD**) of the starch from grains and forages was calculated from in situ degradation parameters (a, b, and k_d) of starch for different feedstuffs compiled by Offner et al. (2003), as follows:

$$ERD = a + b \, k_d / (k_d + k_p) \quad [1]$$

where a = soluble starch fractions (%); b = slowly disappearing starch fractions (%); k_d = fractional rate of disappearance of starch (%/h), and k_p = fractional passage rate of starch (%/h) from reticulorumen. The k_p was estimated using the equations of Seo et al. (2006) as shown below:

$$k_p \text{ for concentrates (\%/h)} = 1.169 + 0.1375 \times FpBW + 0.1721 \times CpBW \quad [2]$$

$$k_p \text{ for forages (\%/h)} = 2.365 + 0.0214 \times FpBW + 0.0734 \times CpBW + 0.069 \times FDMI \quad [3]$$

where FpBW = forage DMI as the proportion of BW (g/kg BW), CpBW = concentrate DMI as the proportion of BW (g/kg of BW), and FDMI = forage DMI (kg).

Subsequently, the content of ruminally degradable starch of concentrate mixture (**RDSG**) was calculated according to the formula:

$$RDSG = \sum_{i=1}^n p_i \times ERD_i \quad [4]$$

where p_i represents the proportion of dietary starch provided from grain i in the concentrate mixture, and ERD_i represents starch effective degradability for grain i , and n is the number of grains in the concentrate mixture of TMR. The formula [4] was also used to calculate the content of ruminally degradable starch from forages (**RDSF**) in TMR. The total content of degradable starch in the diet was calculated as the sum of RDSG and RDSF and was also included as a variable in the analysis.

Table 2. Statistical description¹ of the database used to characterize the relationship between daily mean and fluctuation of ruminal pH

Item	Statistics								
	n _{Treat}	n _{Exp}	Mean	SD	Minimum	25 _{Perc}	Median	75 _{Perc}	Maximum
Ruminal pH (daily mean)	326	80	6.09	0.27	5.49	5.93	6.09	6.25	6.72
SE of daily mean ruminal pH ²	326	80	0.08	0.06	0.01	0.05	0.07	0.10	0.40
Time pH <5.8, h	326	80	5.74	1.94	0.00	3.72	5.90	9.13	19.6
Lowest ruminal pH	191	49	5.50	0.29	4.80	5.27	5.47	5.71	6.44
SE of lowest ruminal pH ²	191	49	0.11	0.13	0.01	0.07	0.09	0.12	1.07

¹n_{Treat} = number of treatment means; n_{Exp} = number of experiments; 25_{Perc} = 25th percentile; 75_{Perc} = 75th percentile; a full list of references for the studies included in this database is available in the appendix (Table A2).

²Standard error of the treatment mean reported from studies.

Characterization of Ruminal pH Fluctuation and SARA Challenge

To characterize the magnitude of ruminal pH fluctuation (i.e., relationships between daily mean and time length of pH below 5.8, or the lowest ruminal pH) throughout the day, another database containing a total of 326 treatment means was generated from 80 studies conducted with dairy cows and steers and published from 1991 to 2007. (A full list of references included in this database is shown in Table A2 of the appendix.) This database was focused only on studies reporting ruminal pH both as daily mean and duration of time with pH <5.8. Daily mean ruminal pH of this database ranged from 5.49 to 6.72 (6.09 ± 0.27), time length of pH <5.8 ranged from 0.0 to 19 h/d (average 5.74 ± 1.94 h/d), and the lowest ruminal pH varied between 4.80 and 6.44 (Table 2).

Ruminal pH of 5.8 was considered detrimental for rumen function, below which fiber digestion by the rumen microorganisms is suboptimal, and as a threshold for the development of SARA in dairy cows (Beauchemin et al., 2003; Yang and Beauchemin, 2007a). However, it was assumed that the effects of ruminal pH on rumen function or SARA development depend on the duration of time in which pH remains below 5.8. To define ruminal pH (both in terms of daily mean and duration of time of pH <5.8) in dairy cows with challenging SARA or not, results of 20 experiments from 17 recent published studies were summarized in a database. (A full list of references included in this database is shown in Table A3 in the appendix.) In these studies, SARA was experimentally induced and monitored in dairy cows (17 experiments) and steers (3 experiments). These studies recorded ruminal pH over 24 h for several days and reported both daily mean ruminal pH and time length of pH below 5.6 and 6.0 or below 5.8. If not directly reported from studies, the duration of time of ruminal pH below 5.8

was calculated as an average from time length of pH below 5.6 and 6.0.

Analysis of Data

Ruminal pH Response to Dietary Factors. To evaluate and model the response of ruminal pH and milk parameters to dietary factors, the data generated from 58 studies with high-yielding dairy cows with a total of 238 dietary treatment means were subjected to mixed model analysis using PROC MIXED (SAS Institute, 2003), considering the random effect of the study (St-Pierre, 2001), as shown below:

$$Y_{ij} = \alpha_0 + \beta_1 X_{ij} + s_i + b_i X_{ij} + e_{ij} \quad [5]$$

where Y_{ij} = the expected outcome for the dependent variable Y (i.e., response of ruminal pH or milk parameters being modeled) observed at level j ($j = 2, \dots, n$) of the predictor variable X (dietary factor) in the study i ; n is the number of treatment means in study i ; α_0 = the overall intercept across all studies (fixed effect); β_1 = the overall regression coefficient of Y on X across all studies (fixed effect); X_{ij} = the value j of continuous variable X in study i ; s_i = the random effect of the study i ($i = 1, \dots, 58$); b_i = the random effect of study i on the regression coefficient of Y on X in study i , and e_{ij} = the unexplained error. Thus, the random effect components of the model include $s_i + b_i X_{ij} + e_{ij}$, and the distributions are shown below:

$$e_{ij} \sim iid N(0, \sigma_e^2) \text{ and } \begin{bmatrix} s_i \\ b_i \end{bmatrix} \sim iid N \left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \Sigma \right],$$

which assumes that e_{ij} is normally distributed with a mean of 0 and constant variance, and that s_i and b_i are normally distributed, have means of 0, and Σ is their variance-covariance matrix:

$$\Sigma = \begin{bmatrix} \sigma_s^2 & \sigma_{sb} \\ \sigma_{sb} & \sigma_b^2 \end{bmatrix}.$$

An unstructured variance-covariance structure matrix (TYPE = UN) was adopted to avoid the positive correlation between the intercepts and slopes, as suggested by St-Pierre (2001). To take the unequal variance among studies into consideration, the dependent variable was weighted by the reciprocal of its squared SE (SE of treatment means were taken directly from studies). When a dietary factor was significant ($P < 0.05$), its squared term was included in the model to test any quadratic relationship. In this case, the variance-covariance matrix was modeled as variance components (TYPE = VC) to assure the convergence. After a visual inspection of the data using PROC GPLOT (SAS Institute, 2003), daily mean ruminal pH response to dietary peNDF was modeled as a linear-plateau using PROC NLIN (SAS, 2003; method = Marquardt), as shown below:

$$Y = \begin{cases} a + b \times x & \text{if } x < x_0 \\ a + b \times x_0 & \text{if } x \geq x_0 \end{cases} \quad [6]$$

where Y is daily mean ruminal pH, a is the intercept, b is the slope (of the linear portion of the model), x is dietary peNDF, and x_0 is the break-point (the point beyond which there is no significant change of Y). Because of a better fitting, the response of DMI and milk parameters to dietary peNDF was modeled using the broken-line regression technique (i.e., single- or double-breakpoint models; Robbins et al., 2006) with PROC NLIN (SAS Institute, 2003; method = Marquardt), as shown below:

$$Y = \begin{cases} a + b_1 \times x & \text{if } x \leq R_1 \\ a + b_1 \times R_1 + b_2 \times (x - R_1) & \text{if } R_2 \geq x > R_1 \\ a + b_1 \times R_1 + b_2 \times (R_2 - R_1) + b_3 \times (x - R_2) & \text{if } x > R_2 \end{cases} \quad [7]$$

where Y is the response variable, a is the general intercept, b_1 , b_2 , and b_3 are the slopes for the first, second, and third straight-line segment, respectively, x is dietary peNDF, and R_1 and R_2 are the first and second breakpoints, respectively. Root mean square error (RMSE) and determination coefficient (R^2) were subsequently computed and used to evaluate the goodness of fit.

Further, all significant dietary factors ($P < 0.05$) were also tested together using the backward elimination technique, similar to the algorithm reported by Firkins et al. (2001). In this case, to limit model over-

parameterization, a variance inflation factor less than 10 (which assumes no significant multicollinearity among predictor variables tested) for every continuous independent variable tested was assumed (Neter et al., 1996).

Ruminal pH Fluctuation and Threshold of SARA. To characterize the relationship between time length of ruminal pH <5.8 and daily mean ruminal pH, data obtained from observations as summarized in Table 2 were used. The statistical rationale used was the same as model [5], only that the response variable was the time length of pH <5.8, and daily mean ruminal pH was used as a predictor variable. Random effect of study was also considered, and to take into consideration the unequal variance among studies, the dependent variable was weighted by the reciprocal of its squared SE, which can improve the overall precision and ensure homogeneity of variance for the model (St-Pierre, 2001). Relationship between the lowest pH and the daily mean ruminal pH was tested using PROC CORR (SAS Institute, 2003). After a visual inspection of the data using PROC GPLOT (SAS Institute, 2003), time length of pH <5.8 response to daily mean ruminal pH was modeled as a linear-plateau using PROC NLIN (SAS Institute, 2003; method = Marquardt), as indicated by model [6].

As previously mentioned, data summarized from 20 experiments, which were conducted to experimentally induce and characterize SARA, were used to determine cut-off points of ruminal pH (i.e., daily mean and diurnal time of pH remaining below 5.8 per day) for cows with challenged SARA conditions. The least-squares means and confidence intervals (CI; 95 and 99%) were calculated using PROC GLIMMIX (SAS Institute, 2003) with a lognormal distribution function (DIST=LOGNORMAL), which is reported as appropriate to analyze data from small samples under moderate non-normality (Douglas, 2006). Confidence intervals give a range of plausible values for the true ruminal pH characterizing SARA or normal ruminal fermentation. For estimation of parameters, the pseudo-likelihood method was used, whereas degrees of freedom were approximated using Satterthwaite's method. To account for differences among studies, the random effect of the experiment was considered in the analysis.

Evaluation of Dietary Fiber Adequacy. An Excel (Microsoft Office, version 2003) spreadsheet version was built from the previously mentioned model, which predicts the ruminal pH response to multiple dietary factors, to allow changes in the running parameters of this model. Subsequently, this spreadsheet was linked to RiskAMP version 2.65 (Structured Data LLC, New York, NY), a software program that works by a Monte Carlo simulation engine, to run stochastic

simulations, as described by Zebeli and Drochner (2007). Monte Carlo stochastic simulations were performed to evaluate the risk of occurrence of the time length of pH < 5.8 when apparently adequate levels of peNDF were offered (i.e., adequate peNDF level was previously estimated), but differing in RDSG content and DMI level. The PERT distribution was used to generate the stochastic variables characterizing the variation of ruminal pH response to dietary scenarios tested, where minimum and maximum values were included based on empirical observations reported from published studies and summarized in the database, and the most likely estimates were obtained as a product of the predictions from the model. The PERT distribution is a special case of the beta distribution that uses the parameters (i.e., minimum, maximum, and most likely) to create a smooth curve that fits well to the normal or lognormal distributions (Vose, 2000). The description of probability density function of PERT distribution is given below:

$$f(x) = \frac{1}{B(\alpha_1, -\alpha_2)} \frac{(x-a)^{\alpha_1-1}(b-x)^{\alpha_2-1}}{(b-a)^{\alpha_1+\alpha_2-1}} \quad [8]$$

where a and b are the boundary parameters of the stochastic variable x ($a < b$), m is the most likely value of x ($a \leq m \leq b$), and α_1 and α_2 are parameters describing the shape of the curve.

$$\alpha_1 = \frac{4m + b - 5a}{b - a} \text{ and } \alpha_2 = \frac{5b - a - 4m}{b - a}. \quad [9]$$

Outputs of the analysis (i.e., the probabilities of occurrence of any duration time of pH below 5.8) are shown in the form of cumulative distribution functions (CDF). Cumulative distribution functions of the stochastic variable $\times [F_X(x)]$ is the probability that this variable, having a probability density function of $f_X(x)$, takes on a value less than or equal to x (Vose, 2000), and is expressed as follows:

$$F_X(x) = P(X \leq x) = \int_{-\infty}^x f_X(X) dx. \quad [10]$$

A sufficiently large number of simulation iterations were run (10,000), so that the CDF were adequately described (Isukapalli et al., 1998).

RESULTS

Diurnal Fluctuations of Ruminal pH and SARA

The model characterizing the relationship between duration of time for ruminal pH < 5.8 and daily mean

Figure 1. Model showing the relationship between time of ruminal pH remaining below 5.8 per day (Y) and daily mean ruminal pH (X): $Y = 5.59 (\pm 0.031) + 0.0218 (\pm 0.002) \times X$, when $X < 6.25 \pm 0.02$, (estimate $\pm$ SE), asymptotic plateau of $Y = 0.97$ h/d; root mean square error = 1.7 h/d, $R^2 = 0.88$, number of experiments = 80, number of treatment means = 326.

ruminal pH is shown in Figure 1. The duration of time for ruminal pH < 5.8 was negatively correlated to daily mean ruminal pH ($R^2 = 0.88$). The linear-plateau model revealed that the break-point of daily mean ruminal pH is reached at 6.25 ± 0.02 , which corresponded to an asymptotic plateau of about 1 h/d for the time length of pH < 5.8. The lowest (nadir) pH correlated positively to daily mean ruminal pH according to the following equation:

$$\begin{aligned} \text{Daily mean ruminal pH} &= 1.92 (\pm 0.163) \\ &+ 0.745 (\pm 0.029) \times \text{nadir pH}, \quad [11] \\ \text{RMSE} &= 0.12, r = 0.89; P < 0.001. \end{aligned}$$

The least squares means and CI for daily mean and time length of ruminal pH < 5.8 in cows with challenged SARA or that experienced normal fermentation are given in Table 3. This analysis showed that, with 99% likelihood, the true values of daily mean pH and time length of ruminal pH < 5.8 for cows with challenged SARA lie between 5.82 and 6.14, or within the range from 5.47 to 15.54 h/d, respectively (i.e., lower and upper bound of 99% CI). In contrast, with 99% likelihood, this data analysis revealed that cows may not experience SARA if daily mean ruminal pH is higher than 6.16 or the time in which ruminal pH is below 5.8 does not exceed 5.24 h/d (i.e., lower bound of 99% CI for daily mean pH and upper bound of 99% CI for time of pH < 5.8 showing no SARA conditions, respectively).

Response of Ruminal pH to Dietary Factors and Fiber Digestibility

Results showing the response of daily mean ruminal pH to some individual dietary factors (only factors sig-

Table 3. Least squares means (LSmeans) and confidence intervals (CI; lower and upper bound of 95 and 99% CI) of ruminal pH (i.e., daily mean and time of pH below 5.8) from cows challenging subacute ruminal acidosis (SARA) or experiencing normal fermentation (control)¹

Measurement of ruminal pH	Treatment	LSmeans	95% CI		99% CI	
			Lower	Upper	Lower	Upper
Daily mean pH	SARA	5.98	5.87	6.09	5.82	6.14
	Control	6.32	6.21	6.44	6.16	6.49
Time of pH <5.8, h/d	SARA	9.02	6.29	13.2	5.47	15.5
	Control	2.98	1.98	4.49	1.62	5.24

¹For calculations data were used stemming from experiments in which SARA was induced and monitored experimentally; a full list of references for the studies used is available in Table A3 of the appendix.

nificantly affecting ruminal pH) are shown in Table 4. Ruminal pH was positively affected by NDF and FNDF, and negatively by NFC, NFC:NDF ratio, and RDSG in the diet. The model showing the relationship between daily mean ruminal pH and dietary peNDF is shown in Figure 2. Increasing dietary peNDF up to $31.2 \pm 1.6\%$ (DM basis) significantly increased ruminal pH, of which the asymptotic plateau was achieved at a pH of 6.27. Also the peNDF:RDSG ratio significantly affected ruminal pH. As shown in Table 4, increasing peNDF:RDSG ratio in the diet increased ruminal pH in a curvilinear fashion. Hence, ruminal pH was found to plateau at 6.20 in response to a ratio of 1.45 ± 0.22 of peNDF to RDSG in the diet.

The analysis of backward elimination showed that inclusion of more dietary factors in the same model increased the accuracy of prediction of ruminal pH response compared with the models when only individual factors were separately tested (Table 5). Thus, this analysis indicated that ruminal pH may increase ($R^2 = 0.65$; $P < 0.001$) when dietary peNDF (quadratically)

increases, and both RDSG and DMI (linearly) decrease.

Figure 3 shows the CDF for the occurrence of any duration time of ruminal pH <5.8 resulting from variation of ruminal pH response when diets were simulated with constant, though apparently adequate peNDF levels (i.e., 31.2% in DM), but differing in the content of RDSG (i.e., 14 and 22% in DM) and amount of DM consumed (i.e., 20 and 25 kg DM/d). A low CDF indicates a lower risk of occurrence of any certain time length of ruminal pH <5.8, and conversely, a higher CDF indicates a high risk of occurrence. Overall, data showed that increasing RDSG in the diet from 14 to 22% and DMI from 20 to 25 kg/d increased the risk of occurrence of any length of time of ruminal pH <5.8, despite the similar peNDF content.

This study also showed that digestibility of NDF in the total digestive tract depends on ruminal pH and k_p ; therefore, both variables explained 62% of the variation of NDF digestibility. Hence, NDF digestibility increased linearly with increasing ruminal pH, decreasing k_p (%/h), or both, according to the following equation:

$$\begin{aligned} \text{NDF digestibility (\%)} &= -32.24 (\pm 15.25) \\ &+ 14.91 (\pm 2.38) \text{ ruminal pH} - 2.54 (\pm 0.42) k_p; \\ \text{RMSE} &= 0.68, R^2 = 0.62 \end{aligned} \quad [12]$$

Response of Feed Intake and Milk Parameters

Relationship between DMI and dietary peNDF was low in this study (RSME = 3.03 kg DM/d; $R^2 = 0.18$; Figure 4). The broken-line model revealed that DMI tended to increase with increasing peNDF content up to $21.6 \pm 2.92\%$ in TMR. Further, when feeding a diet with a peNDF content ranging from 21.6 to $31.9 \pm 1.97\%$, the model showed that DMI slightly declined (slope: -0.245 ± 0.122 ; Figure 4). However, when diets exceeded the latter content of peNDF, a higher depres-

Figure 2. Model showing the relationship between daily mean ruminal pH and dietary physically effective NDF (peNDF) in high-yielding dairy cows: ruminal pH = $5.59 (\pm 0.031) + 0.0218 (\pm 0.002) \times \text{peNDF}$, when peNDF $< 31.2 \pm 1.60\%$ (estimate $\pm$ SE), asymptotic plateau of pH 6.27; root mean square error = 0.14, $R^2 = 0.50$, number of experiments = 45, number of treatment means = 187.

Table 4. Equations showing the response of ruminal pH to different dietary factors in dairy cows¹

Dietary factor ²	Parameter estimates				Model statistics ³	
	Intercept	SE _{Intercept}	Slope	SE _{Slope}	RMSE	R ²
NDF, % of DM	5.45	0.07	0.019	0.001	0.16	0.37
Forage NDF, % of DM	5.61	0.05	0.020	0.002	0.15	0.41
NFC, % of DM	6.35	0.08	-0.008	0.002	0.15	0.12
NFC:NDF	6.36	0.04	-0.256	0.029	0.17	0.28
RDSG, % of DM	6.37	0.03	-0.020	0.001	0.13	0.34
peNDF:RDSG ⁴	5.53	0.03	0.449	0.016	0.15	0.41

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

²NFC calculated by $100 - (\% \text{ CP} + \% \text{ NDF} + \% \text{ ether extract} + \% \text{ crude ash})$; RDSG = ruminally degradable starch from grains of TMR; peNDF = physically effective NDF, measured as the NDF content of TMR multiplied by amount of DM particles retained on a 1.18-mm sieve (Mertens, 1997).

³RMSE = root mean square error.

⁴Relationship was nonlinear: breakpoint for peNDF:RDSG ratio = 1.45 ± 0.22 , asymptotic plateau of ruminal pH = 6.20.

sion of DMI was estimated (slope: -0.897 ± 0.349 ; Figure 4).

Effects of peNDF and other dietary factors on milk parameters are shown in Figure 5 and Table 6. Milk yield was increased with increasing DMI and RDSF content in the diet (Table 6). In contrast, the model showed that dietary peNDF had a poor, though negative effect (slope: -0.174 ± 0.237) on actual milk yield in this study (RSME = 6.1 kg milk/d; $R^2 = 0.09$, result not shown), particularly when peNDF content in the diet was lower than an average of $32.0 \pm 1.85\%$. When

exceeding the latter average content of peNDF, the decline in milk yield was higher (slope: -1.486 ± 0.677 , result not shown).

As shown in Figure 5A, peNDF content in the diet positively affected milk fat content, particularly beginning with a dietary peNDF content of about $20 \pm 3.2\%$. This was reflected in a higher MEE, particularly by increasing peNDF content in the diet from 17.1 to 32.4% (Figure 5B). After this, the MEE was reduced (slope: -1.14 ± 0.847), although milk fat content linearly increased (Figure 5A,B). In general, the backward elimi-

Figure 3. Cumulative probability distribution showing the risk of occurrence of any duration time of ruminal pH below 5.8 when simulations were performed for cows fed diets containing constant physically effective NDF (31.2% in DM), but differing in ruminally degradable starch from grains in TMR (14 and 22% in DM) and levels of DMI (20 and 25 kg of DM/d).

Table 5. Best-fit equation showing the response of ruminal pH to different dietary factors using backward elimination technique

Dietary factor ¹	Parameter estimates				Model statistics ²			
	Intercept	SE _{Intercept}	Slope	SE _{Slope}	RMSE	R ²	VIF	P =
peNDF, % of DM	6.05	0.115	0.044	0.0069	0.11	0.66	5.99	<0.001
peNDF ² , % of DM	—	—	-0.0006	0.0001	—	—	8.97	<0.001
RDSG, % of DM	—	—	-0.017	0.0026	—	—	2.41	<0.001
DMI, kg/d	—	—	-0.016	0.0034	—	—	1.24	<0.001

¹peNDF = physically effective NDF, measured as the NDF content of TMR multiplied by amount of DM particles retained on a 1.18-mm sieve (Mertens, 1997); RDSG = ruminally degradable starch from grains of TMR.

²RMSE = root mean square error; VIF = variance inflation factor (VIF <10 is assumed to show no significant multicollinearity among predictor variables).

nation procedure revealed that milk fat yield and FCM were positively affected by peNDF content and DMI and negatively by RDSG and DIM (Table 6).

DISCUSSION

Diurnal Fluctuations of Ruminal pH and SARA

Data analyzed to characterize the diurnal fluctuations of ruminal pH showed that cows spent several hours per day in which ruminal pH remained <5.8. One finding of this study was that this time length could be characterized with reasonable accuracy from the daily mean ruminal pH, whereby the latter can be estimated from nadir value of the ruminal pH. In fact, the precise time when the nadir of ruminal pH occurs could not be

evaluated in this study. However, assuming that this nadir is reached at 10 to 14 h after the morning feeding in dairy cows fed high concentrate diets ad libitum (Krause and Oetzel, 2005; Tafaj et al., 2005; Yang and Beauchemin, 2007a), it is possible that by using this measurement, both daily mean ruminal pH and the time length of pH <5.8 can be assessed through the relationships established for these variables in this study.

The present study showed that a break-point for the time length of the ruminal pH <5.8 was reached when the daily mean pH value was 6.25 ± 0.02 . The latter corresponded to an asymptotic plateau of 1 h for the time length of pH <5.8 (Figure 1). This time length was less than the lower bound of 99% CI (i.e., 1.62 h/d) for

Figure 4. Model showing the relationship between DMI and dietary physically effective NDF (peNDF) in dairy cows: $DMI = a + b_1 \times x$, if $x \leq R_1$; $DMI = a + b_1 \times R_1 + b_2 \times (x - R_1)$, if $R_2 \geq x > R_1$; $DMI = a + b_1 \times R_1 + b_2 \times (R_2 - R_1) + b_3 \times (x - R_2)$, if $x > R_2$ ($a = 22.57 \pm 1.19$, $b_1 = 0.023 \pm 0.067$; $b_2 = -0.245 \pm 0.122$; $b_3 = -0.897 \pm 0.349$; $R_1 = 21.6 \pm 2.92\%$ peNDF; $R_2 = 31.9 \pm 1.97\%$ peNDF; x = dietary peNDF); root mean square error = 3.03; $R^2 = 0.18$.

Figure 5. Models showing the relationship between milk fat content (A) or milk energy efficiency (MEE; g milk fat/kg DMI; B) and dietary physically effective NDF (peNDF) in dairy cows: A, Milk fat = $a + b_1 \times x$, if $x \leq R_1$; milk fat = $a + b_1 \times R_1 + b_2 \times (x - R_1)$, if $x > R_1$ ($a = 3.13 \pm 0.162$, $b_1 = 0.006 \pm 0.011$; $b_2 = 0.0373 \pm 0.011$; $R_1 = 20.0 \pm 3.21\%$ peNDF; x = dietary peNDF); root mean square error = 0.29; $R^2 = 0.37$; B, MEE = $a + b_1 \times x$, if $x \leq R_1$; MEE = $a + b_1 \times R_1 + b_2 \times (x - R_1)$, if $R_2 \geq x > R_1$; MEE = $a + b_1 \times R_1 + b_2 \times (R_2 - R_1) + b_3 \times (x - R_2)$, if $x > R_2$ ($a = 47.32 \pm 3.82$, $b_1 = 0.052 \pm 0.316$; $b_2 = 0.498 \pm 0.153$; $b_3 = -1.410 \pm 0.847$; $R_1 = 17.1 \pm 5.59\%$ peNDF; $R_2 = 32.4 \pm 1.78\%$ peNDF; x = dietary peNDF); root mean square error = 5.53; $R^2 = 0.48$.

the duration that the pH value was <5.8 , indicating minimal risk of SARA. This means that a minimal time length of 1 h/d exists when ruminal pH is <5.8 , and this event is inevitable under feeding conditions in dairy cattle, as summarized in the current database. In fact, the CI for the time length that ruminal pH remains <5.8 , indicating the cut-off point for SARA, was relatively wide (i.e., 5.47 to 15.54 h/d or 6.29 to 13.2 h/d for 99 and 95% CI, respectively). On the other hand, the width of 99 and 95% CI, indicating normal fermentation in the rumen, was narrower (i.e., 1.62 to 5.24 h/d and 1.98 to 4.49 h/d, respectively). This means that

the certainty to define the pH values characterizing normal fermentation in the rumen is higher than the certainty to define the cut-off point of ruminal pH reflecting SARA conditions. Therefore, our data suggest, with 99% certainty, that to maintain a lower SARA occurrence (i.e., 1%), the time length in which the ruminal pH remains <5.8 for longer than 5.24 h/d must be avoided.

Indeed, when the time length of ruminal pH <5.8 was increased from 5.4 to 8.8 h/d in dairy cows (Gozho et al., 2007) or from 0 to 6.8 h/d in steers (Gozho et al., 2006), an acute phase response was activated. Interest-

Table 6. Best-fit equation showing the response of milk parameters (Y) to different dietary and nondietary factors (X) using backward elimination technique

Predictor ¹ (X)	Parameter estimates				Model statistics ²			
	Intercept	SE _{Intercept}	Slope	SE _{Slope}	RMSE	R ²	VIF	P =
Actual milk yield, kg/d								
DMI, kg/d	16.29	2.805	1.071	0.0974	4.01	0.58	1.11	<0.001
DIM	—	—	-0.035	0.0068	—	—	1.15	<0.001
RDSF, % of DM	—	—	0.157	0.0632	—	—	1.05	0.014
Milk fat content, %								
peNDF, % of DM	3.60	0.159	0.013	0.0035	0.29	0.39	1.27	<0.001
RDSG, % of DM	—	—	-0.022	0.0053	—	—	1.09	<0.001
DIM	—	—	-0.006	0.0017	—	—	9.17	<0.001
DIM ²	—	—	0.0004	0.00001	—	—	9.59	<0.001
Milk fat yield, kg/d								
peNDF, % of DM	0.589	0.109	0.006	0.0016	0.13	0.61	1.24	<0.001
DMI, kg/d	—	—	0.037	0.0036	—	—	1.28	<0.001
RDSG, % of DM	—	—	-0.015	0.0023	—	—	1.09	<0.001
DIM	—	—	-0.011	0.0022	—	—	1.16	<0.001
3.5% FCM, kg/d								
peNDF, % of DM	15.28	2.718	0.138	0.0390	3.21	0.61	1.31	<0.001
DMI, kg/d	—	—	0.848	0.0809	—	—	1.65	<0.001
RDSG, % of DM	—	—	-0.371	0.0579	—	—	1.09	<0.001
DIM	—	—	-0.027	0.0054	—	—	1.16	<0.001

¹peNDF = physically effective NDF, measured as the NDF content of TMR multiplied by amount of DM particles retained on a 1.18-mm sieve (Mertens, 1997); RDSF = ruminally degradable starch from forages of TMR; RDSG = ruminally degradable starch from grains of TMR.

²RMSE = root mean square error; VIF = variance inflation factor (VIF < 10 is assumed to show no significant multicollinearity among predictor variables).

ingly, presence of the inflammatory response was not associated with disturbances in DMI or in milk production or its composition in dairy cows. Furthermore, in dairy cows fed to experimentally induce SARA, the DMI and milk composition were not affected even when the time length of ruminal pH <5.8 was increased from 0 to 13 h/d (Krause and Oetzel, 2005) or from 1.4 to 12.8 h/d (Krajcarski-Hunt et al., 2002), although in situ NDF digestibility significantly declined (Krajcarski-Hunt et al., 2002).

Recent research indicates alterations in ruminal microbial ecology in steers experimentally challenged to induce SARA (Goad et al., 1998; Purvis et al., 2006). In contrast, research conducted in dairy cows fed high-concentrate diets (>50% of DM) has shown that when ruminal pH remains <5.8 for 3 to 5 h/d it has no effect on the number and activity of fibrolytic bacteria attached to solid or fluid ruminal digesta (Ölschläger et al., 2006; Zebeli et al. 2007a).

Response of Ruminal pH to Dietary Factors

The greater accuracy of dietary peNDF and FNDF in predicting the response of ruminal pH compared with total dietary NDF agrees with results of previous studies. For example, Allen (1997) found a positive correlation only between FNDF and ruminal pH, but not between total dietary NDF and pH. In addition, Mertens (1997) also reported a positive curvilinear relationship

between dietary peNDF and ruminal pH in dairy cows. Pitt et al. (1996), using data from sheep, beef cattle, and dairy cattle, also observed a quadratic relationship between effective NDF and ruminal pH. 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 (approximately 6.4) compared with 6.27 observed in the present study. Because feeding diets in excess of peNDF may decrease feed intake and lower the efficiency of feed use, the determination of a break-point in dietary peNDF, beyond which no further advantages on ruminal pH response can be expected, is important particularly in terms of maximization of production responses in high-producing dairy cows.

The content of peNDF in the diet is important in maintaining a stable ruminal environment. Mertens (1997) suggested that feed particles larger than 1.18 mm (i.e., particles considered in peNDF system) are more effective in stimulating chewing activity and therefore increasing the secretion of saliva and ruminal buffering capacity compared with smaller particles, because the latter readily flow out of the rumen and provide fewer stimuli for chewing activities. However, the increase of ruminal pH due to increasing dietary peNDF is not necessarily related only to positive effects of peNDF on chewing activity (Zebeli et al., 2007b; Yang and Beauchemin, 2007a). The reason for this could be that the flow of saliva alone is unable to neutralize the

increasing quantities of VFA and lactate produced after ingesting high amounts of ruminally degradable OM (Allen, 1997).

In addition, dietary peNDF also contributes to formation and maintenance of a stable, thick-packed ruminal raft in dairy cows (Zebeli et al., 2006a). The latter is important in stimulating contractions of the reticulorumen (Yang and Beauchemin, 2007a), which in turn increase the rate of passage and of absorption of VFA molecules across the rumen epithelium (Taylor and Allen, 2005). Increased VFA absorption increases buffering capacity of the rumen because absorption of VFA has been shown to be linked to secretion of HCO_3^- into the rumen fluid in the ratio of 2:1 (Ash and Dobson, 1963; Gäbel et al., 1991).

The positive effects of peNDF on ruminal fermentation, and hence on attenuating the decline of ruminal pH, may also be related to effects of peNDF on meal patterns. For example, Yang and Beauchemin (2007a) reported that increasing dietary peNDF from 29 to 33% of the diet DM increased the number of meals per day from 8 to 10. In that study cows consumed less DM per meal, but increased meal frequency. The latter meal pattern was associated with decreased large diurnal fluctuations in ruminal pH, which was reflected in shorter time length of pH <5.8 and higher daily mean ruminal pH (from 10 to 1 h/d and from 6.0 to 6.5, respectively). Using a modeling approach, Pitt and Pell (1997) estimated that increased meal frequency could decrease the requirements for effective NDF to maintain a certain pH in the rumen.

Research conducted by Yang and Beauchemin (2006b) also has shown that feeding longer fiber particles shifts the site of starch digestion from rumen into the intestine, lowering the odds for development of ruminal acidosis. Indeed, our results showed positive correlation ($r = 0.50$; $n = 51$; $P < 0.001$) between peNDF content of the diet and the passage rate of fluid digesta out of reticulorumen (results not shown). This indicates acceleration of passage rate of ruminally degradable starch from reticulorumen with increasing peNDF content of the diet. However, in terms of animal health, milk production, and feed efficiency, the relationship between peNDF and RDSG in the diet for high-yielding dairy cows is more complicated than often assumed. Attempts to shift starch digestion from rumen to intestine to improve the efficiency of glucose metabolism have not been very effective. For example, Reynolds (2006) reviewed that although the increased starch digestion in the small intestine increases glucose supply for lactating dairy cow, this occurs at the expense of microbial protein synthesis in the rumen and with an increase in hindgut fermentation and subsequent losses of microbial protein in the feces. Thus, the best way to

increase glucose supply is to have an optimal amount of ruminally degradable starch for enough propionate to be converted into glucose in the liver (Huntington, 1997), though without adversely affecting fiber digestibility and other rumen functions (Firkins et al., 2001).

The backward elimination technique showed that of the dietary factors considered, not only peNDF but also dietary RDSG and DMI level improved the prediction of ruminal pH. Allen (1997) also found that including the content or intake of rumen-degradable OM of the diet in the model together with NDF content and particle length index of forages improved predictions of ruminal pH. The present study showed that increasing dietary RDSG increased requirements for peNDF to stabilize ruminal pH. For example, in simulations for diets containing apparently adequate peNDF levels (i.e., 31.2% of DM), but differing in RDSG and DMI, the response of ruminal pH was different. Thus, the probability to maintain a time length not exceeding 5.24 h/d in which ruminal pH remains <5.8 (a time assessed as being within the normal fermentation patterns) was 0% by feeding a diet with 31.2% peNDF and 14% RDSG, independently from DMI tested. In contrast, this probability increased by 5 and 45% when RDSG in the diet increased to 22% for a theoretical DMI of 20 and 25 kg/d, respectively (Figure 3). It can therefore be concluded that to assess fiber requirements for high-yielding dairy cows, next to peNDF, both RDSG and DMI must be considered. In a previous study, Zebeli and Drochner (2007) assessed that to maintain the ruminal pH within the normal patterns, the requirements for peNDF in the diet may be lowered to 26 or 22%, when RDSG content in the diet is reduced to 10% with a 25 or 20 kg DMI, respectively. Similarly, Yang and Beauchemin (2006b) reported a time length of ruminal pH <5.8 shorter than 5 h/d by feeding a corn grain-based diet (54% concentrate in diet DM) with <15% RDSG (estimated according to Offner et al., 2003), with a dietary peNDF content of 26.5% and DMI of 25 kg/d. In another study, Yang and Beauchemin (2007a) reported an increased time length of ruminal pH <5.8 from 1.2 to 10.3 h/d when RDSG and DMI in the TMR diet increased from 12 to 20% (estimated according to Offner et al., 2003) and 22 to 24 kg/d, respectively, whereas peNDF content of TMR decreased from 33 to 29%. Similarly, Silveira et al. (2007) fed barley grain-based diets (60% concentrate in diet DM) differing in starch level and ruminal degradability and reported an increased time length of ruminal pH <5.8 from 3.4 to 8.2 h/d when RDSG increased from 14 to 24% (estimated according to Offner et al., 2003) and peNDF content decreased from 33.4 to 29.3%. The latter diet was associated with a significant decline in the total tract NDF digestibility

from 59 to 51%, although DMI was maintained at 20 kg/d throughout the study.

Although increases in DMI are associated with proportional increases in the amount of peNDF and RDSG intakes, the backward elimination procedure showed that increasing DMI may promote fermentation rather than neutralization processes in the rumen, and hence development of SARA. However, this result should be interpreted with caution because of a possible interaction between DMI and other predictors of the model, particularly with RDSG. In fact, ruminal pH reflects the balance between acid production (i.e., VFA and lactate) in the rumen and acid removal through neutralization and absorption within the rumen (Allen, 1997). In this regard, Shaver (2002) estimated that the flow of salivary buffers remained almost constant when increasing daily intake of rumen-fermentable OM from 4 to 16 kg/d, whereas fermentation acids produced in the rumen increased linearly, which in turn may increase the risk of SARA in high-producing dairy cows. Firkins et al. (2001) and Stone (2004) concluded that high-yielding dairy cows are at increased risk of SARA due simply to an increased DMI. Oetzel (2000) also suggested limiting the DMI as a strategy to reduce the risk of SARA and improve feed efficiency in high-yielding dairy cows. However, results of our study showed that the risk of SARA could be lowered without limiting the DMI, but rather by varying the content of peNDF and RDSG in the diet. Results also suggest that a ratio of peNDF to RDSG in the diet less than 1.5 should be avoided.

The observation that rumen-degradable starch from forages did not affect ruminal pH in this study was unexpected, as forage sources like corn silage have high content of starch (18 to 35%), and its ruminal degradability is evaluated to be as high as 85% (Offner et al., 2003). However, this can be explained by the fact that the ruminal degradability of starch from corn silage is strongly affected by the variety, maturity, inoculant inclusion, and kernel processing (Johnson et al., 2002). In fact, none of these variables were accounted for in the analysis of this study as appropriate data were missing, and hence this aspect warrants further research.

Total-Tract Fiber Digestibility and Rumen Conditions

Because ruminal pH has profound effects on microbial populations, it is considered a critical factor in the normal and stable functioning of the rumen. As shown in the present study, variables of rumen conditions (i.e., ruminal pH or outflow rate of digesta from reticulorumen) have the potential to affect total fiber degradation.

Similarly, Yang et al. (2002) demonstrated that decreasing daily mean ruminal pH from 6.18 to 5.78, associated with an increased outflow rate of digesta out of reticulorumen from 2.5 to 3.4 %/h, decreased NDF digestibility in the rumen and in total tract (from 40 to 37% and 52 to 42%, respectively). By increasing the outflow rate of particulate digesta out of reticulorumen from 2.7 to 4.0 %/h, which was associated with a decreased ruminal mat consistency, Zebeli et al. (2007b) showed a decreased total tract NDF digestibility from 55 to 50%. Similarly, Boddugari et al. (2001) reported that low digesta consistency in the reticulorumen due to high concentrate levels in the diet was associated with lower entrapment of small particles, increased outflow rate of solid digesta, and decreased ruminal NDF digestibility in dairy cows.

Production Responses to Diet Composition and Dietary Fiber Adequacy

This modeling approach revealed that increasing peNDF content up to about 32% slightly reduced DMI and actual milk yield; however, FCM, milk fat yield, and MEE were significantly increased. In fact, the effects of dietary peNDF on DMI in high-producing dairy cows are often controversially discussed. Because of the effects on ruminal physical fill, low peNDF content in the diet is believed to increase feed intake in dairy cows (Dado and Allen, 1995). However, diets low in peNDF and high in readily fermentable carbohydrates may result in increased fermentation intensity and particularly propionate production in the rumen (Zebeli et al., 2007a), which is reported to stimulate plasma insulin response, and this may result in a depression of DMI (Bradford and Allen, 2007) or milk fat synthesis (Reynolds, 2006).

That the content of peNDF up to 32% in the diet had low constraining effect on DMI in this study may also be explained by a variable DMI capacity of high-yielding dairy cows and by a low constraining effect of peNDF on rumen fill when diets are high in concentrates (>45% in DM basis; Allen, 2000). Feeding diets based on corn silage and ground corn with about 32% peNDF, Kononoff et al. (2003b) and Kononoff and Heinrichs (2003a) reported an average DMI of about 27 kg/d, and milk yield ranged from 41 to 48 kg/d and milk fat content averaged $\geq 3.5\%$. In contrast, feeding diets with about 26% peNDF and replacing corn silage with chopped alfalfa haylage, Kononoff and Heinrichs (2003b) reported a lower DMI (about 23 kg/d), milk yield (35 kg/d), and milk fat content (3.3 to 3.4%). Increasing peNDF content from about 29 to 33% in a TMR based on alfalfa silage and steam-rolled barley, Yang and Beauchemin (2007b) reported a decreased DMI and milk yield of

about 2 and 3 kg/d, respectively. In contrast, milk fat content was increased from 3.4 to 3.8% resulting in similar amounts of 4% FCM among treatments and decreased milk efficiency (i.e., FCM/DMI) from 1.40 to 1.28 with increasing peNDF content.

In fact, milk fat content is often used as an indicator for health and fiber adequacy in dairy cows. According to De Brabander et al. (2002), a reduction of milk fat content of about 0.6% in 1 wk could be considered an indicator for a fiber deficiency in the diet of dairy cows. That the response of milk fat content to dietary peNDF was somewhat lower than the response of ruminal pH in this study could be explained with a lower sensitivity of milk fat concentration to dietary fiber in cows in early lactation (Allen, 1997; Mertens, 2000), which typically are in a negative energy balance (NRC, 2001). When cows are in a negative energy balance, contribution from mobilized fatty acids increases in direct proportion to the extent of the energy deficit (Bauman and Griinari, 2001), and hence milk fat content may increase regardless of a low milk fat synthesis. In fact, milk fat content was quadratically decreased with increasing DMI in this study. In addition, there was a break-point of peNDF (i.e., $20 \pm 3.2\%$), beyond which milk fat content became more responsive to dietary peNDF (Figure 5A). In a recent study, Mertens (2007) also found that increasing the content of dietary peNDF from 19 to 23% by adding 5% wheat straw in the diet was insufficient to alleviate milk fat depression (2.69 vs. 3.30% milk fat) in dairy cows. Other results of the current study showed that milk fat content depends also on rumen-degradable starch in the diet (Table 6). Feeding a high barley starch-based diet, Silveira et al. (2007) reported that 29% peNDF was insufficient to maintain a milk fat content of 3.4%, and this was associated with lowered daily mean ruminal pH, acetate to propionate ratio, and butyrate proportion in the rumen fluid. In contrast, when increasing the peNDF content of about 32 to 33% and reducing the content of degradable starch, milk fat content exceeded an average of 3.5%, although diets were based on barley grains (Silveira et al., 2007; Yang and Beauchemin, 2007b) and cows were in early (Yang and Beauchemin, 2007b) or mid lactation (Silveira et al., 2007). This indicates that the balance between dietary peNDF and degradable starch from grains has the capacity to affect fat concentration in the milk by dairy cows by affecting rumen fermentation and metabolism.

Inadequate balance between peNDF and RDSG levels in the diet may alter microbial populations and ruminal biohydrogenation (Weimer et al., 2007), whereby alterations in the pathways of rumen biohydrogenation results in the production of fatty acid intermediates that inhibit fatty acid synthesis in the mammary gland

(Bauman and Griinari, 2003). In addition, the alteration of microbial species in the rumen may also lead to a reduction of acetate and butyrate production, hence resulting in lower lipogenic factors for de novo synthesis of fatty acids in the mammary gland. Indeed, in a recent study, AlZahal et al. (2007) reported that cows experiencing SARA showed lower de novo synthesis of fatty acids (<16C) and increased *trans* 18:1 fatty acids, which are considered intermediate products of ruminal biohydrogenation, and this was associated with milk fat depression.

Although milk fat content linearly increases also when diets exceeded 32% peNDF, this study showed that more than $32 \pm 1.8\%$ peNDF in the diet is not justified because this may be related to a lower DMI potential and may reduce MEE due likely to lower milk production and milk fat yield. In terms of ruminal pH and maximization of the MEE in dairy cows, results of the present modeling approach support the inclusion of a maximal content of about 30 to 33% peNDF in the TMR of lactating dairy cows. However, using the equations developed in the present study, the content of peNDF required to stabilize ruminal pH and maintain milk fat content without compromising MEE can be arranged based on grain or starch sources included in the diet, DMI, and DIM of the cows.

CONCLUSIONS

This study showed that to minimize the risk of SARA, a daily mean ruminal pH lower than 6.16 and a time length in which ruminal pH is <5.8 is longer than 5.24 h/d should be avoided. Increasing dietary peNDF up to $31.2 \pm 1.6\%$ (DM basis) or the ratio of peNDF to RDSG up to 1.45 ± 0.22 linearly increased daily mean ruminal pH, of which the asymptotic plateau was achieved at a pH of 6.20 to 6.27. This study also showed that digestibility of NDF in the total tract depends on ruminal pH and outflow rate of digesta from reticulorumen; thereby both variables explained 62% of the variation of NDF digestibility. Feeding diets with a peNDF content from 21.6 to $31.9 \pm 1.97\%$ slightly decreased DMI and actual milk yield; however, FCM, milk fat yield, and MEE were increased. In conclusion, a level of about 30 to 33% peNDF in TMR may be considered as the general optimal level of peNDF to minimize the risk of SARA without impairing production responses in high-yielding dairy cows.

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APPENDIX

Table A1. Publications included in the database used in modeling the responses of ruminal pH and milk production to diet composition

Allen and Grant (2000)	Gulmez and Turkmen (2007)	San Emeterio et al. (2000)
Bal et al. (2000)	Junck et al. (2004)	Schwab et al. (2002)
Beauchemin et al. (1997)	Khezri et al. (2005)	Silveira et al. (2007)
Beauchemin et al. (2003a)	Kleinschmit et al. (2007)	Soita et al. (2000)
Bezerra et al. (2002)	Kononoff and Heinrichs (2003a)	Soita et al. (2005)
Bhandari et al. (2006)	Kononoff and Heinrichs (2003b)	Tafaj et al. (2005)
Bhandari et al. (2007)	Kononoff et al. (2003)	Tafaj et al. (2006)
Birick et al. (2007)	Krause and Combs (2003)	Weber et al. (2006)
Calberry et al. (2003)	Krause et al. (2002a)	Yang and Beauchemin (2006b)
Clark and Armentano (1997)	Krause et al. (2002b)	Yang and Beauchemin (2007a)
Clark and Armentano (1999)	Krause et al. (2003)	Yang and Beauchemin (2007b)
Clark and Armentano (2002)	Le Liboux and Peyrand (1998)	Yang et al. (2001a)
Couderc et al. (2006)	Le Liboux and Peyrand (1999)	Yang et al. (2001b)
Dann et al. (2007)	Leonardi et al. (2005)	Yang et al. (2002)
Einarson et al. (2004)	Mertens (2007)	Yansari et al. (2004)
Fernandez et al. (2004)	Onetti et al. (2003)	Zebeli (2006)
Gencoglu and Turkmen (2006)	Penner et al. (2007)	Zebeli et al. (2007)
Gencoglu et al. (2007)	Plaizier (2004)	Zebeli et al. (2008)
Grant et al. (1990a)	Rustomo et al. (2006a)	Zebeli et al. (unpublished results) ¹
Grant et al. (1990b)		

¹Q. Zebeli, K. Frick, and J. Streicher, Univ. Hohenheim, Stuttgart, Germany.

Table A2. Publications included in the database used in modeling the relationship between daily mean and fluctuation of ruminal pH

AlZahal et al. (2007a)	Kenelly et al. (1999)	Reis et al. (2001)
Bach et al. (2007)	Keunen et al. (2002)	Robinson et al. (1997)
Beauchemin and Yang (2005)	Keunen et al. (2003)	Rustomo et al. (2006a)
Beauchemin et al. (2000)	Khorasani and Kennelly (2001)	Rustomo et al. (2006b)
Beauchemin et al. (2001)	Khorasani et al. (2001a)	San Emeterio et al. (2000)
Beauchemin et al. (2003a)	Khorasani et al. (2001b)	Schwab et al. (2002)
Beauchemin et al. (2003b)	Koenig et al. (2003)	Schwarzkopf et al. (2004)
Bevans et al. (2005)	Kononoff and Heinrichs (2003a)	Silveira et al. (2007)
Bowman et al. (2003)	Kononoff and Heinrichs (2003b)	Tafaj et al. (2004)
Cottee et al. (2004)	Krajcarski-Hunt et al. (2002)	Tafaj et al. (2005)
Cruywagen et al. (2007)	Krause and Combs (2003)	Tafaj et al. (2006)
Dado and Allen (1995)	Krause and Oetzel (2005)	Taylor and Allen (2005)
Dohme et al. (2007b)	Krause et al. (1998)	Voelker and Allen (2003)
Douglas et al. (2007)	Krause et al. (2002)	Weidner and Grant (1994)
Fairfield et al. (2007)	Krause et al. (2003)	Weber et al. (2006)
Fernandez et al. (2004)	Krehbiel et al. (1995)	Yang and Beauchemin (2006a)
Gencoglu and Turkmen (2006)	Le Liboux and Peyraud (1998)	Yang and Beauchemin (2006b)
Ghorbani et al. (2002)	Le Liboux and Peyraud (1999)	Yang and Beauchemin (2007)
Gozho et al. (2005)	Leonardi et al. (2005)	Yang et al. (1997)
Gozho et al. (2006)	Maekawa et al. (2002a)	Yang et al. (2000)
Gozho et al. (2007)	Maekawa et al. (2002b)	Yang et al. (2001a)
Graf et al. (2005a)	Mutswanga et al. (2002)	Yang et al. (2007)
Graf et al. (2005b)	Oba and Allen (2000)	Zebeli (2006)
Gulmez and Turkmen (2007)	Osborne et al. (2004)	Zebeli et al. (2007)
Harvatin and Allen (2006)	Penner et al. (2007)	Zebeli et al. (2008)
Johnson et al. (2002)	Reis and Combs (2000a)	Zebeli et al. (unpublished results) ¹
Johnson et al. (2003)	Reis and Combs (2000b)	

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Table A3. Publications included in the database used in modeling the incidence of subacute ruminal acidosis

AlZahal et al. (2007a)	Douglas et al. (2007)	Keunen et al. (2003)
AlZahal et al. (2007b)	Goad et al. (1998)	Khafipoor et al. (2007a)
Cottee et al. (2004)	Gozho et al. (2005)	Khafipoor et al. (2007b)
Chiquette et al. (2007)	Gozho et al. (2006)	Krajcarski-Hunt et al. (2002)
DeFraen et al. (2002)	Gozho et al. (2007)	Krause and Oetzel (2005)
Dohme et al. (2007a)	Keunen et al. (2002)	

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