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Increasing the Physically Effective Fiber Content of Dairy Cow Diets May Lower Efficiency of Feed Use[1]

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ABSTRACT

Barley silages varying in theoretical chop length were used to evaluate the effects of physically effective (pe) neutral detergent fiber (NDF) content of dairy cow diets on nutrient intakes, site and extent of digestion, microbial protein synthesis, and milk production. The experiment was designed as a replicated 3 × 3 Latin square using 6 lactating dairy cows with ruminal and duodenal cannulas. During each of 3 periods, cows were offered 1 of 3 diets (low, medium, and high peNDF) obtained using barley silage that varied in particle length: fine (theoretical chop length of 4.8 mm), medium (equal proportions of long and fine silages), and long (theoretical chop length of 9.5 mm). The peNDF contents were determined by multiplying the proportion (dry matter basis) of feed retained on the 2 screens (8 and 19 mm) of the Penn State Particle Separator by the NDF content of the diet, and were 10.5, 11.8, and 13.8% for the low, medium, and high diets, respectively. Increased forage particle length linearly increased intake of peNDF but intakes of dry matter, organic matter, starch, and N were highest for cows fed the medium peNDF diet. Digestibilities of organic matter, NDF, and acid detergent fiber in the total tract were linearly decreased with increasing dietary peNDF, although total digestibility of starch and N was not affected by the treatments. Nevertheless, decreased digestibility due to increased dietary peNDF did not reduce milk production or milk composition because the cows were in mid to late lactation. Ruminal microbial protein synthesis and microbial efficiency were numerically higher with the low peNDF than with the medium or high peNDF diets. These results indicate that increasing the peNDF content of a diet containing barley silage decreases fiber digestibility in the total tract and lowers microbial efficiency. Therefore, the benefits of increasing dietary particle size, expressed as peNDF, on reducing the risk of ruminal acidosis should be weighed against potentially negative effects on efficiency of feed use.

Key words: physically effective neutral detergent fiber, digestion, microbial protein synthesis, site of digestion

INTRODUCTION

Digestibility of nutrients is an important aspect of feed quality. The physical characteristics of feeds such as particle length can affect rumen digestion, passage rate, and microbial protein synthesis, and thus postruminal or total digestion. Reducing forage particle length (**FPL**) in dairy cow diets may enhance feed intake by increasing the passage rate of digesta through the digestive tract (Udén, 1987). However, smaller forage particles spend less time in the rumen, thus ruminal digestibility, particularly of fiber, can be reduced (Udén, 1987). Consequently, fiber digestibility in the total tract may be lowered by decreasing the chop length of alfalfa hay (Le Liboux and Peyraud, 1999). In addition, efficiency of ruminal microbial protein synthesis and digestion of CP in the rumen or in the total tract are typically improved with increasing FPL (Rode et al., 1985; Yang et al., 2002).

The physical form of specific feeds can be quantitatively assessed by various sieving methods (Murphy and Zhu, 1997). However, the variety of methods used to measure particle length has made it difficult to compare results from different laboratories or compile such data into a form that is useful for diet formulation. It is, therefore, imperative that a validated unit or measure be established (Mertens, 1997).

Physically effective NDF (**peNDF**) is a measure that reflects the ability of physical characteristics of fiber, mainly particle size, to stimulate chewing and saliva buffering in the rumen (Mertens, 1997). The term peNDF is used as a means of formulating diets to provide fiber of adequate particle size to reduce subacute ruminal acidosis. The Penn State Particle Separator (**PSPS**) is a quick and cost-effective method to estimate particle size of forage and TMR, and is widely used on-farm to evaluate peNDF (Lammers et al., 1996). Based on measurements using the PSPS, several studies have recently shown that increased intake of peNDF increased chewing activity and ruminal pH (Krause et al., 2002b; Kononoff and Heinrichs, 2003a; Beauchemin

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Table 1. Chemical composition and particle size distribution of barley silage measured using the Penn State Particle Separator

Item	Barley silage			Effect
	Short cut	Long cut	SE	$P <$
Chemical composition				
DM, %	37.9	39.8	1.3	0.05
OM, % of DM	89.8	88.1	1.0	NS
NDF, % of DM	42.6	43.2	0.5	0.05
ADF, % of DM	23.7	24.3	0.7	NS
Starch, % of DM	21.9	21.6	0.8	NS
N, % of DM	2.30	2.35	0.03	0.10
Particles, % of DM retained				
>19.0 mm	1.5	4.1	0.1	0.01
19.0 to 8.0 mm	66.9	80.0	1.6	0.01
<8.0 mm	31.6	16.0	1.6	0.01
pef[1]	0.68	0.84	0.02	0.01
peNDF,[2] % of DM	29.1	36.4	1.2	0.01

[1]pef = Physical effectiveness factor determined as the proportion of particles retained by both sieves of the Penn State Particle Separator.

[2]peNDF = Measured as the NDF content of the silage (DM basis) multiplied by the pef.

et Yang, 2005), improved total digestibility (Kononoff and Heinrichs, 2003b; Yansari et al., 2004; Yang and Beauchemin, 2005), and increased milk fat content (Yang et al., 2001; Kononoff and Heinrichs, 2003b). However, other studies have demonstrated either no effects of peNDF on digestibility and milk composition (Fernandez et al., 2004), or negative effects on digestibility (Krause et al., 2002b; Kononoff and Heinrichs, 2003a). The optimum concentration of peNDF in dairy cow diets is uncertain, because there is a paucity of information on the effects of peNDF on digestibility and milk production for a range of forages and concentrates.

Whole crop barley silage (**BS**) is used extensively as forage for dairy cows in certain areas of Canada, Europe, and the United States. However, limited information is available on its peNDF content for dairy cows (Kononoff et al., 2000; Einarson et al., 2004; Leonardi et al., 2005). The objectives of the present study were to determine the effects of increasing the peNDF concentration of a diet containing BS and a rapidly fermentable concentrate source on feed intake, site and extent of digestion, microbial protein synthesis, and milk yield and composition of lactating dairy cows. The effects on chewing activity, ruminal pH, and fermentation were measured and reported separately (Yang and Beauchemin, 2006).

MATERIALS AND METHODS

Barley Silage

Whole-plant barley was harvested at 60% moisture content from a single field, and ensiled on the same day in large silo bags (200-t capacity) for 2 mo before being used. A forage harvester (model 6910, John Deere, West Bend, WI), equipped with a 37-tooth sprocket and 8 knives, was used to obtain silage chopped at a theoretical chop length (**TCL**) of 4.8 and 9.5 mm for short- and long-cut silage, respectively. Two kilograms of each BS (short and long) was obtained weekly, and immediately subdivided into 3 portions for determining DM content, particle size, and chemical composition, respectively (Table 1). Particle size distribution of the silage was determined using the PSPS (Lammers et al., 1996) containing 2 sieves (8 and 19 mm) and a pan. The 1.18-mm screen was not used because it retains almost the entire sample of most forages (Kononoff and Heinrichs, 2003a), and thus, does not distinguish silages of varying chop length. Hence, in this study, the original PSPS was used to measure particle size distribution. The DM content was determined by oven drying at 55°C for 48 h. The third portion was composited by experimental period and retained for determination of chemical composition.

Cows and Diets

Six lactating Holstein cows were used in an experiment to investigate the effects of peNDF content of BS-based diets on feed intake, passage rate of liquid and solids from the rumen, site and extent of digestion, microbial protein synthesis, and milk production. Three cows fitted with ruminal cannulas and 3 cows fitted with ruminal and duodenal cannulas were separately assigned to a 3×3 Latin square. The ruminal cannulas measured 10 cm in diameter and were constructed of soft plastic (Bar Diamond, Parma, ID). Duodenal cannulas were T-shaped and were placed proximal to the common bile and pancreatic duct, approximately 10 cm distal to the pylorus. Cows were housed in individual tie stalls and offered a TMR 3 times daily at 0600, 1500, and 1800 h for ad libitum intake. Cows, averaging 652 ± 118 kg of BW and 189 ± 39 DIM, and were cared for according to the Canadian Council on Animal Care Guidelines (Ottawa, ON, Canada).

Cows were offered 1 of 3 diets that contained approximately 53% concentrate and 47% BS (Table 2) and differed in peNDF level: low, medium, and high. The 3 dietary peNDF levels were obtained using BS differing in particle length: 100% short silage (low), 50% short silage + 50% long silage (medium), and 100% long silage (high). The diets were formulated using the Cornell-Penn-Miner system (CPMDairy, Version 2.23, Cornell University, Ithaca, NY; University of Pennsylvania, Kennett Square, PA; and William H. Miner Agricultural Research Institute, Chazy, NY) to supply adequate ME and MP for a 600-kg cow producing 30 kg/d

Table 2. Ingredients, chemical composition, and particle size distribution of the diets differing in physically effective fiber (peNDF) content

	Dietary peNDF				Effect
	Low	Medium	High	SE	Linear
Ingredients, %					
Barley silage, long cut	—	23.3	46.6	—	—
Barley silage, short cut	46.6	23.3	—		
Barley grain, steam-rolled[1]	37.4	37.4	37.4	—	—
Corn gluten meal	3.01	3.01	3.01	—	—
Heat-treated canola meal (Alberta Gold)[2]	5.01	5.01	5.01	—	—
Soybean meal	4.51	4.51	4.51	—	—
Beet molasses	0.50	0.50	0.50	—	—
Calcium carbonate	0.70	0.70	0.70	—	—
Dicalcium phosphorus	0.45	0.45	0.45	—	—
Vitamin-mineral mix[3]	1.15	1.15	1.15	—	—
Canola oil	0.50	0.50	0.50	—	—
Binding agent	0.15	0.15	0.15	—	—
Chemical composition					
DM, %	52.4	52.9	53.0	0.2	NS
CP, % of DM	17.4	17.5	17.7	0.6	NS
NDF, % of DM	32.1	32.1	33.3	0.9	NS
NDF from forages, % of DM	19.8	20.0	20.2	0.2	NS
ADF, % of DM	15.6	15.5	15.3	0.3	NS
Starch, % of DM	31.3	31.5	30.8	0.4	NS
NE_L, Mcal/kg	1.70	1.69	1.68	0.2	NS
Particle size distribution and effective fiber, % DM retained on sieve					
>19.0 mm	0.7	1.4	2.0	0.1	0.01
19.0-8.0 mm	32.0	35.6	39.2	1.2	0.01
<8.0 mm	67.4	63.1	58.8	0.9	0.01
pef[4]	0.33	0.37	0.41	0.01	0.01
peNDF,[5] % of DM	10.5	11.8	13.8	0.3	0.01

[1]Chemical composition of barley grain (DM basis) was 90.2%, 23.6%, 6.8% and 11.3% for OM, NDF, ADF, and CP, respectively.

[2]Canbra Foods Ltd., Lethbridge, AB, Canada.

[3]Contained 51.97% NaCl, 35.98% Dynamate (Pitman Moore, Inc., Mundelein, IL; 18% K, 11% Mg, 22% S, 1000 mg Fe /kg), 2% $ZnSO_4 \cdot H_2O$, 2.4% $MnSO_4 \cdot 4H_2O$, 0.01% $CoSO_4 \cdot 6H_2O$, 0.009% Na_2SeO_3, 0.012% ethylenediamine dihydroiodide, 0.8% $CuSO_4 \cdot 5H_2O$, 680,000 IU/kg of vitamin A, 160,000 IU/kg of vitamin D and 2,000 IU/kg of vitamin E.

[4]pef determined as the proportion of DM retained by both sieves of the Penn State Particle Separator.

[5]peNDF measured as the NDF content of the TMR (DM basis) multiplied by the pef.

NS = $P > 0.15$.

of milk with 3.5% fat and 3.2% protein. For the purpose of diet formulation, a single chemical composition and peNDF value was used for BS thereby ensuring that diet composition, other than the BS, was the same in all 3 diets.

Each period consisted of 11 d of adaptation to diets and 10 d of experimental measurements. Because diets differed only in particle size, and not in chemical composition, a short adaptation phase was deemed acceptable. Feed offered and orts were measured and recorded daily during the last 10 d of the period to calculate feed intake. Feed samples including BS and TMR were collected once weekly, and orts were collected daily and composited weekly for particle length and DM determination. Samples were then composited by period, dried in an oven at 55°C for 48 h, and then ground through a 1-mm diameter screen (standard model 4, Arthur Thomas Co., Philadelphia, PA) for analysis of OM, NDF, ADF, starch, and CP. Milk production was recorded daily, a.m. and p.m., and sampled on 5 consecutive days during the last 10 d of the period for milk fat, CP, and lactose determination using an infrared analyzer (Milko-Scan 605, Foss Electric, Hillerød, Denmark).

Rate of Passage

Passage rate of digesta from the rumen or the postruminal tract was measured during d 12 to 16 of the period using Cr-mordanted NDF and Co-EDTA as forage and liquid markers, respectively. Fiber from long- and short-chopped silage was separately prepared by washing in a washing machine twice with detergent and then boiling for 4 h in diluted detergent solution until the NDF content of the material exceeded 85%. Methods used to mordant Cr to plant cell walls and to prepare CoEDTA were those of Udén et al. (1980). Two hundred fifty grams of Cr-mordanted NDF and 300 mL of solution containing 15 g of CoEDTA were introduced in the rumen via the ruminal cannulas. Fecal samples were collected from the rectum at 0, 6, 9, 12, 15, 18, 24, 30,

36, 48, 72, 96, and 120 h after dosing with the markers. A double compartmental model, represented by 2 exponential constants and a time delay (Grovum and Williams, 1973), was fitted using the nonlinear regression procedure of SAS (SAS Institute, 1996).

Duodenal Flow and Apparent Digestion

Duodenal flow and apparent digestion of nutrients in the total tract or at the different sites of the digestive tract were determined using $YbCl_3$ (Rhône-Poulenc Inc., Shelton, CT). Ammonia ^{15}N ($[^{15}NH_4]_2SO_4$, 10.6% atom percent ^{15}N; Isotec, Miamisburg, OH) was used as a ruminal microbial marker. Marker solution was continuously infused into the rumen via ruminal cannulas using an automatic pump (model 60 rpm/7524-10, Masterflex L/S Microprocessor pump drive, Vernon Hills, IL) during the last 11 d of the period. Daily amounts infused were 2.6 g of Yb and 140 mg of ^{15}N dissolved in 800 mL of water for each cow. Six ruminal samples were collected from the 3 duodenal cannulated cows during 3 d of collection for ruminal bacterial pellet preparation. Duodenal and fecal samples were collected 4 times daily every 6 h, moving ahead 2 h each day for the last 3 d of infusion. This schedule provided 12 representative samples of duodenal and fecal contents taken at 2-h intervals. A ruminal and a duodenal sample taken before marker infusion from each cow during the first period were used to determine background concentration of ^{15}N in samples.

Ruminal samples were processed immediately to separate ruminal bacteria. The samples were squeezed through 4 layers of cheesecloth and the particles obtained by squeezing were blended (400 g of particles plus 400 mL of 0.9% NaCl) in a Waring blender (Waring Products Division, New Hartford, CT) for 1 min and then squeezed through 4 layers of cheesecloth. Both filtrates from squeezed and strained homogenate were mixed, centrifuged ($800 \times g$ for 15 min at 4°C) to remove protozoa and feed particles, and the supernatant was centrifuged ($27{,}000 \times g$ for 30 min at 4°C) to obtain a mixed ruminal bacteria pellet. Bacterial pellets were accumulated by period, freeze-dried, ground using a mortar and pestle, and then further ground using a ball mill (Mixer Mill MM2000; Retsch, Haan, Germany) to a fine powder for determination of N content and ^{15}N enrichment.

Duodenal samples were subdivided using an electric drill fitted with a shaft and propeller. Each sample was split into 3 fractions that were pooled by cow within period and retained for ammonia analysis, DM determination after oven drying at 55°C, or for chemical analysis after freeze-drying. For fecal samples, the sample from each sampling time was mixed and divided into 2 subsamples (about 100 g each). One was pooled by cow within period, then dried at 55°C and ground through a 1-mm screen (standard model 4) for chemical analysis. The other subsample was immediately used to measure pH with a pH meter by preparing of slurry of feces and distilled water.

Chemical Analyses

Feed DM was determined by oven drying at 55°C for 48 h. Analytical DM content of the samples was determined by drying at 135°C for 3 h (AOAC, 1990). The OM content was calculated as the difference between DM and ash contents, with ash determined by combustion at 550°C overnight. The NDF and ADF contents were determined using the methods described by Van Soest et al. (1991) with amylase and sodium sulfite used in the NDF procedure. Starch was determined by enzymatic hydrolysis of α-linked glucose polymers as described by Rode et al. (1999). Contents of digestive markers in the duodenal and fecal samples were determined using inductively coupled plasma optical emission spectroscopy according to the AOAC method (1990) modified such that no $CaCl_2$ for Co and Cr or no KCl for Yb determination was used during sample digestion. Content of N in the samples was determined by flash combustion (model 1500; Carlo Erba Instruments, Milan, Italy) and enrichment of ^{15}N in the rumen bacterial and duodenal samples was analyzed with isotope ratio mass spectrometry (VG Isotech, Middlewich, UK). Particle size distributions of BS, TMR, and orts were determined using the PSPS. Physical effectiveness factors (**pef**) for silage, TMR, and orts were calculated as the sum of the proportions of the materials retained on the 8- and 19-mm sieves of the PSPS. The peNDF content of the diets was determined by multiplying the pef of the TMR by the NDF content (DM basis) of the diet.

Calculations and Statistical Analyses

Flows of DM to the duodenum and DM excreted in feces were calculated by dividing Yb infused (grams of Yb per day) by Yb concentration (grams of Yb per kilogram of DM) in the duodenal digesta or feces, respectively. Flows of other nutrients to the duodenum or feces were calculated by multiplying DM flow by their concentration in duodenal or fecal DM. Ruminal microbial protein synthesis for each cow was estimated by the ratio of ^{15}N flow at the duodenum to ^{15}N concentration of mixed ruminal bacteria.

Data were analyzed using the MIXED procedure of SAS (SAS Institute, 1996) to account for effects of square, period within square, cow within square, and treatment. The treatment was considered a fixed effect;

square, period within square, and cow within square were considered random effects. For variables of site of digestion and microbial protein synthesis, data from a single square were analyzed. In that case, the mixed model accounted for effects of period, cow, and treatment. The treatment was considered a fixed effect; period and cow were considered random effects. Data for particle distribution, pef, and peNDF of forages and diets were averaged by period and analyzed by including particle length as a fixed effect and period as a random effect. The estimation method was the restrictive maximum likelihood (REML) and the degrees of freedom method was Kenward-Rogers. All variables were tested for linear and quadratic effects in relation to the peNDF content of the diets. Effects of the treatments were declared significant at $P < 0.05$ unless otherwise noted and trends were discussed at $P < 0.15$.

RESULTS

Particle Size Distribution and peNDF of Feeds

Nutrient composition and particle size distribution of BS including short- and long-cut silages are presented in Table 1. Although contents of DM, NDF, and N of short-cut BS were statistically lower than those of long-cut BS, the differences were small. As expected, the particles retained on the 8- and 19-mm sieves increased as the TCL of BS was increased from 4.8 to 9.5 mm, and as a result, pef and peNDF were increased by 20%. Fermentation characteristics of these BS are reported in detail elsewhere (Yang and Beauchemin, 2006), but most importantly, pH and concentration of organic acids were similar across silages. Therefore, the comparisons among diets in this study reflected differences in particle size of silages rather than differences in their fermentation quality.

The diets were similar in chemical composition because the same formulation and ingredients were used, with the exception of BS differing in TCL (Table 2). Dietary particle size distribution reflected the proportion of long-cut BS in the diets. Increased proportion of long-cut BS in the diets increased the DM retained on 8- and 19-mm sieves but decreased the DM on the pan of the PSPS. As such, pef and peNDF linearly increased with increasing proportion of long-cut BS in the diets.

Intake, BW, and Apparent Digestion in the Total Tract

Body weight averaged 682 kg across the treatments although it was numerically higher ($P < 0.15$) for cows fed the medium peNDF diet than for the other 2 treatments (Table 3). Intakes of DM, OM, starch, and N tended to be higher ($P < 0.08$) for cows fed the medium peNDF diets than for cows fed the low or high peNDF diets. However, correcting DMI for differences in BW eliminated the effects of diet on intake. Intakes of digestible OM tended ($P < 0.08$) to decrease with increasing dietary peNDF. Furthermore, intakes of NDF and ADF were not different across the treatments but intake of digestible NDF tended ($P < 0.11$) to be lower for the medium peNDF diet than for the other diets.

Increased dietary peNDF content tended to linearly reduce digestibilities of DM ($P < 0.14$), OM ($P < 0.10$), and NDF ($P < 0.10$) and linearly decrease ADF digestibility in the total tract (Table 3). In addition, digestibilities of NDF and ADF tended ($P < 0.11$) to quadratically decrease with increasing dietary peNDF. However, digestibilities of starch and N in the total tract were not affected by the treatments. Fecal pH averaged from 7.11 to 7.15 and was not affected by the treatments. High fecal pH indicates minimal fermentation occurred in the large intestine.

Site and Extent of Digestion

Data for site and extent of nutrient digestion were obtained from a single 3×3 Latin square using 3 primiparous lactating dairy cows fitted with ruminal and duodenal cannulas. Thus, results must be cautiously interpreted because of the limited replication. Intakes of DM (range of 16.9 to 17.6 kg/d) as well as of other nutrients (Table 4) were lower than the averages for all cows (Table 3) because primiparous cows of smaller frame size were used in this group. In contrast to the observation from all 6 cows, there were no effects of dietary peNDF on intakes of DM, OM, fiber, and starch. Similarly, no differences in duodenal nutrient flows were detected across the treatments. Microbial OM flow at the duodenum represented about 22% of the total duodenal OM flow and was not statistically different between the treatments.

Digestibilities (% of intake) of OM (truly), NDF, and ADF in the rumen were not affected by the treatments, but ruminal starch digestibility was numerically higher ($P < 0.11$) for the low peNDF than for the high or medium peNDF diets (Table 4). In the intestine, digestibility (% of intake) of OM was about 26% higher for the low peNDF than for the medium or high peNDF diets likely due to the numerically higher fiber digestion of the low peNDF diet. In contrast, starch digestibility of the medium and high peNDF diets was higher than that of the low peNDF diet. Thus, lower ruminal starch digestion of the medium and high peNDF diets was compensated for by higher intestinal starch digestion, such that starch digestibility in the total tract was only

Table 3. Effects of increasing dietary physically effective NDF (peNDF) on intake and digestibility of nutrients in the total tract of lactating dairy cows (n = 6)

	Dietary peNDF				Effects	
	Low	Medium	High	SE	Linear	Quadratic
BW, kg	679	689	678	65	NS	0.15
Intake						
DM, kg/d	19.6	20.8	19.4	2.2	NS	0.08
DM, % of BW	2.9	3.0	2.9	0.2	NS	NS
OM, kg/d	17.8	18.9	17.5	2.0	NS	0.07
Digestible OM, kg/d	13.2	13.4	12.4	1.7	0.08	NS
NDF, kg/d	7.0	7.3	7.4	0.8	NS	NS
Digestible NDF, kg/d	3.8	3.5	3.7	0.5	NS	0.11
ADF, kg/d	3.0	3.2	2.9	0.3	NS	NS
Starch, kg/d	6.1	6.4	5.9	0.7	NS	0.08
N, g/d	526.5	569.4	526.8	64.5	NS	0.06
Digestibility, % of intake						
DM	70.7	68.3	68.0	1.7	0.14	NS
OM	73.8	71.5	71.0	2.0	0.10	NS
NDF	54.7	48.1	50.4	2.3	0.10	0.11
ADF	35.3	25.7	24.5	3.8	0.01	0.10
Starch	96.1	95.6	94.9	0.9	NS	NS
N	68.1	68.5	67.1	2.5	NS	NS
Fecal pH	7.11	7.15	7.11	0.14	NS	NS

NS = $P > 0.15$.

Table 4. Effects of increasing dietary physically effective NDF (peNDF) on intake, duodenal flow, and site and extent of digestion of nutrients in lactating dairy cows (n = 3)

	Dietary peNDF				Effects	
Item	Low	Medium	High	SE	Linear	Quadratic
Intake, kg/d						
DM	16.9	17.0	17.6	1.6	NS	NS
OM	15.5	15.2	15.9	1.4	NS	NS
NDF	6.1	6.2	6.7	0.7	NS	NS
ADF	2.6	2.5	2.7	0.3	NS	NS
Starch	5.3	5.2	5.2	0.4	NS	NS
Duodenal flow, kg/d						
OM						
Total	9.0	8.7	8.8	1.8	NS	NS
Microbial	2.1	1.8	1.9	0.2	NS	NS
NDF	3.7	3.7	3.9	0.7	NS	NS
ADF	1.9	2.0	2.1	0.3	0.02	0.09
Starch	1.8	2.1	2.0	0.9	NS	NS
RFOM,[1] kg/d	8.5	8.8	8.9	0.7	NS	NS
Digestibility, % of intake						
Rumen						
OM (truly)	57.0	55.4	57.3	8.2	NS	NS
NDF	40.0	41.1	42.7	6.6	NS	NS
ADF	26.7	26.6	22.1	5.4	NS	NS
Starch	69.1	61.6	63.5	6.2	0.11	NS
Intestine						
OM	29.7	23.8	23.4	5.6	0.03	NS
NDF	13.2	5.4	5.5	6.7	NS	NS
ADF	13.0	2.7	6.1	5.8	NS	NS
Starch	27.0	33.2	31.3	5.4	0.03	0.04
Total						
OM	73.1	68.7	68.7	1.9	0.06	0.14
NDF	53.2	46.3	48.2	2.3	NS	NS
ADF	39.8	29.5	28.2	1.6	0.01	0.11
Starch	96.1	94.6	94.8	1.2	0.12	NS

[1]RFOM = Ruminally fermented OM.

NS = $P > 0.15$.

Table 5. Effects of increasing dietary physically effective NDF (peNDF) on intake and metabolism of N in the digestive tract of lactating dairy cows (n = 3)

	Dietary peNDF				Effects	
Item	Low	Medium	High	SE	Linear	Quadratic
Intake, g/d	448.5	467.0	472.8	57.1	NS	NS
Flow to duodenum						
Total						
g/d	446.4	426.9	460.1	72.8	NS	NS
% of intake	99.3	92.8	95.9	7.1	NS	NS
NAN						
g/d	436.3	418.3	450.6	72.5	NS	NS
% of intake	97.1	90.9	93.8	7.1	NS	NS
Feed + endogenous						
g/d	232.0	249.7	263.1	66.1	NS	NS
% of intake	49.8	51.8	53.7	9.8	NS	NS
Microbial						
g/d	204.3	181.1	187.6	18.3	NS	NS
% of intake	47.3	38.2	40.2	5.3	0.08	NS
g/kg of RFOM[1]	23.9	20.5	21.5	1.9	0.15	NS
Digestibility						
Ruminal (truly), %	50.2	48.2	46.3	9.9	NS	NS
Postruminal						
% of intake	65.2	56.3	61.5	6.2	NS	NS
% of flow to duodenum	64.7	60.1	63.1	2.6	NS	NS
ADTT,[2] % of intake	65.8	63.8	65.6	2.2	NS	0.05

[1]RFOM = Ruminally fermented OM.

[2]ADTT = Apparently digested in the total tract.

NS = $P > 0.15$.

numerically higher ($P < 0.12$) for the low peNDF diet than for the other 2 diets. Although DMI was lower, digestibility in the total tract of the 3 duodenally cannulated primiparous cows was similar to that of the 6 cows. Furthermore, total digestibility linearly decreased for OM ($P < 0.06$) and ADF with increasing dietary peNDF. Digestibility of NDF in the total tract was higher ($P < 0.08$) for the low peNDF than for the medium peNDF diet, but was not different from the high peNDF diet.

N Metabolism

Intake and duodenal flows of total, NAN, and rumen undegradable N (measured as the feed plus endogenous fraction) were not affected by dietary peNDF (Table 5). However, the flow of microbial N to the duodenum tended to linearly decrease with increasing dietary peNDF when expressed as percentage of N intake ($P < 0.08$) or as grams per kilogram of rumen-fermentable OM ($P < 0.15$). Furthermore, although statistically not significant, it is notable that the amount of microbial N arriving at the duodenum for the low peNDF diet was increased by 13 or 9% compared with the medium or high peNDF diets, respectively. Digestibility of feed N either in the rumen or in the intestine was not affected by the treatments, but the digestibility in the total tract was 2 percentage units lower for cows fed the medium peNDF diet.

Rate of Passage

Rumen liquid dilution rate averaged 9.5%/h and was not affected by dietary peNDF (Table 6). In contrast, passage rate of rumen solids was higher ($P < 0.07$) for the high peNDF than for the medium or low peNDF diets with similar postruminal transit times among treatments. The mean retention time of solid particles in the total digestive tract linearly decreased ($P < 0.07$) with increasing dietary peNDF.

Milk Production and Composition

Milk yield and 4% FCM were similar across the treatments, averaging 27.1 and 24.6 kg/d, respectively (Table 7). However, the variability in milk production responses to diet among cows was high (CV = 13.6%), but typical of cows at various stages of lactation. Yield of milk fat was not affected by dietary peNDF because milk fat content was similar for all treatments. Although milk protein content tended ($P < 0.06$) to be lower for the high peNDF than for the medium and low peNDF diets, milk protein yield was not different. Milk efficiency was not affected by the treatments.

DISCUSSION

The NRC (2001) does not specify requirements for physically effective fiber for dairy cows due to a paucity

Table 6. Effects of increasing dietary physically effective NDF (peNDF) on passage rate and retention time[1] of particles and liquid in the gastrointestinal tract of dairy cows (n = 6)

	Dietary peNDF				Effects	
Item	Low	Medium	High	SE	Linear	Quadratic
Liquid						
LORR,[2] %/h	9.5	9.0	10.0	1.0	NS	NS
Mean retention time, h	25.3	24.3	24.7	2.1	NS	NS
Forage particles						
PORR,[3] %/h	3.9	3.8	4.5	0.3	0.07	NS
Transit time, h	9.5	9.6	10.1	0.5	NS	NS
Mean retention time, h	44.0	40.7	37.1	3.0	0.07	NS

[1]Markers: liquid, CoEDTA; solids, Cr-mordanted NDF. The two-compartmental fecal model of Grovum and Williams (1973) was used for calculation.

[2]LORR = Liquid outflow rate from the reticulorumen.

[3]PORR = Particulate outflow rate from the reticulorumen.

NS = $P > 0.15$.

of information. However, it is generally understood by nutritionists that the physical characteristics of the diet, including forage chop length, are important considerations in ration formation particularly as related to reducing the risk of acidosis (Shaver, 2002). However, in developing recommendations for peNDF in dairy cow diets it is important to consider the effects on intake, digestion, and microbial protein synthesis in addition to chewing time and ruminal fermentation.

In the present study, the peNDF content of the diet had only small effects on feed intake. The trend for higher ($P < 0.08$) starch intake with the medium peNDF diet primarily reflected its higher ($P < 0.08$) DMI rather than a particle-selecting effect (Yang and Beauchemin, 2005). Effects of sorting by cows in favor of coarse particles is less pronounced for BS-based diets (Yang and Beauchemin, 2006) than for corn silage-based diets (Yang and Beauchemin, 2005).

The present results for intake are in agreement with some studies that reported no effect of FPL on DMI (Soita et al., 2000; Yang et al., 2001), but are in contrast to other studies in which DMI was decreased with increasing peNDF content (Soita et al., 2002; Einarson et al., 2004). In the studies in which increasing peNDF lowered DMI, either a high-forage diet (100% BS; Soita et al., 2002) or a forage with long FPL (TCL = 19 mm; Einarson et al., 2004) was used.

Whether peNDF affects DMI may depend upon which factors limit intake. In a review of the effects of diet on short-term regulation of feed intake by lactating dairy cattle, Allen (2000) concluded that, at the high concentrate inclusion level (>50%), metabolic, rather than physical constraints, are typically rate-limiting. The lack of effect of peNDF on intake observed in the present study may signify that metabolic, rather than physical effects, limited intake. Consequently, despite higher passage rate of particles from the rumen of cows fed the high peNDF diet, DMI was not increased.

The effects of FPL on digestibility in the total tract of dairy cows are inconclusive and somewhat contradic-

Table 7. Effects of increasing dietary physically effective NDF (peNDF) on milk production and composition from lactating dairy cows (n = 6)

	Dietary peNDF				Effects	
Item	Low	Medium	High	SE	Linear	Quadratic
Milk yield, kg/d						
Actual	26.6	27.6	27.2	3.7	NS	NS
4% FCM	24.8	24.2	24.9	3.0	NS	NS
Component yield, kg/d						
Fat	0.94	0.88	0.93	0.12	NS	NS
Protein	0.91	0.93	0.90	0.11	NS	NS
Lactose	1.16	1.22	1.20	0.18	NS	NS
Milk component, %						
Fat	3.64	3.51	3.54	0.36	NS	NS
Protein	3.48	3.50	3.37	0.20	0.06	NS
Lactose	4.30	4.32	4.36	0.11	NS	NS
Milk/DMI	1.40	1.35	1.39	0.25	NS	NS

NS = $P > 0.15$.

tory in the literature. The linear decrease in total digestibility of OM and fiber with increasing dietary peNDF are consistent with several reports (Soita et al., 2002; Kononoff and Heinrichs, 2003a), but in contrast to other findings (Le Liboux and Peyraud, 1998; Yang et Beauchemin, 2005). Higher total digestibility of the low peNDF diet was likely due to increased surface area available for microbial attack combined with slower particulate passage rate from the rumen. Kononoff and Heinrichs (2003a) observed that highest NDF digestibility occurred for the shortest diet even though mean ruminal pH was lowest. Krause et al. (2002a) also reported that diets resulting in the lowest ruminal pH had numerically the highest fiber digestion. It appears that the effect of low rumen pH on fiber digestion is less drastic for mixed rumen microorganisms than for pure cultures. Furthermore, ruminal pH was not increased with increasing dietary peNDF in the present study (Yang and Beauchemin, 2006).

The negative effect of increased dietary peNDF on digestibility in the total tract was more pronounced for fiber digestion, especially for ADF digestion, than for starch digestion (Table 3). Although starch digestibility was about 10% lower ($P < 0.11$) in the rumen for the medium and high peNDF diets than for the low peNDF diets, starch was 19% more digestible in the intestine. Thus, compensatory digestion in the intestine lessened the negative effects of increasing peNDF content of the diet on total tract starch digestion. The present result confirms the previous finding that low starch digestion in the rumen can be partly or wholly compensated for by high intestinal digestion (Beauchemin et al., 2001; Yang et al., 2002). A shift of starch digestion from the rumen to the intestine is beneficial for alleviating ruminal acidosis, especially for diets containing barley grain, which is rapidly digested in the rumen following ingestion.

It is not clear whether the effects of peNDF on site of starch digestion are consistent among forages other than BS. In support of the observations of the present study, Fernandez et al. (2004) reported that increased FPL of corn silage reduced starch digestion in the rumen, but increased postruminal digestion such that starch digestion in the total tract was not affected. However, when the corn silage was subjected to rolling before ensiling, starch digestibility in the rumen was not affected by FPL (Yang and Beauchemin, 2005). For BS, it was reported that reduced FPL increased ruminal molar proportion of propionate (Soita et al., 2002; Einarson et al., 2004) but there is a paucity of data on the effects of chop length of BS on site and extent of starch digestion. In the present study, numerically higher starch digestion in the rumen for the low peNDF diet mostly likely resulted from increased retention time of feed in the rumen, because retention time increased as FPL decreased. It is also possible that ruminal starch digestion increased because of more extensive breakage of kernels with more extensive particle size reduction of forage during harvesting; however, there was no evidence of increased kernel damage upon visual inspection of the silage.

In contrast to starch, the proportion of ingested fiber that can be digested in the intestine is limited. The proportion digested in the intestine ranged from 11 to 25% of the total digestible NDF compared with an average of 32% for starch (Table 4). Similarly, Overton et al. (1995) reported that the proportion of total NDF digestion that occurred as intestinal NDF digestion ranged from 6 to 26% for diets based on corn, barley, or a mix of the 2 grains.

Higher fiber digestibility of low peNDF diets was also reported in other studies using BS (Soita et al., 2002) or alfalfa silage (Kononoff and Heinrichs, 2003a). Increased total fiber digestion with reduced dietary peNDF (Table 3) resulted from numerically increased intestinal digestion because ruminal digestion was generally similar across treatments (Table 4). Intestinal NDF digestibility was 140% higher for the low peNDF than for the high and medium peNDF diets although it was not statistically significant due to high variation when sampling at the duodenum combined with the limited power of a single 3×3 Latin square. Lack of significant differences in ruminal digestion of OM, fiber, and starch across treatments was supported by the ruminal fermentation results in which molar proportions of acetate and propionate were not affected by the treatments (Yang and Beauchemin, 2006). Ruminal NDF digestibility is normally depressed when ruminal pH is decreased or feed intake and passage rate are increased due to reduced FPL (Shaver et al., 1988). In the current study, ruminal pH including mean, area between the curve and a horizontal line drawn at pH 5.8 or 5.5, and time that pH was below 5.8 or 5.5 were not affected by peNDF content of diets (Yang and Beauchemin, 2006). In addition, the coarse particles in the high and medium peNDF diets might have been efficiently reduced in size due to increased mastication as a result of increased chewing time (Yang and Beauchemin, 2006). Faster particulate passage rate (Table 6) apparently had minimal effects on ruminal digestion of fiber.

The mechanism whereby reducing peNDF intake numerically increased intestinal NDF digestibility is not clear, but most likely can be attributed to increased surface area for microbial attachment. In agreement with the present results, Le Liboux and Peyraud (1999) reported higher digestibility of NDF and ADF in the intestine for ground than for chopped alfalfa hay, but ruminal fiber digestibility was lower for ground hay.

The supply of NAN to the duodenum depends upon the flow of dietary N (feed + endogenous) and ruminal microbial N. Similar flows of NAN to the duodenum across the treatments were attributed to the combined trend of increased ($P > 0.15$) dietary N flow and decreased ($P > 0.08$) microbial N (% of N intake) flow with increasing dietary peNDF (Table 5). The numerical increase in dietary N flow to the duodenum was likely due to the small decrease in CP degradation in the rumen with increasing dietary peNDF (Table 5). The present results are consistent with other observations that feeding short FPL rather than long FPL to dairy cows increased the rate of degradation of forage protein in the rumen and thus, increased its RDP content and reduced its RUP content (Yang and Beauchemin, 2004). The numerically increased microbial N synthesis with reducing dietary peNDF in the present study was consistent with the results of Le Liboux and Peyraud (1999) who explained that the effect was from less recycling of microbial N in the rumen because there was a significant reduction of protozoal biomass in the rumen when chopped alfalfa hay was replaced with ground alfalfa. Krause et al. (2002a) reported that microbial N supply depended on starch intake, which in turn was affected by dietary FPL. In another study, we found that the highest microbial N production occurred on a high-forage diet formulated with short FPL (Yang and Beauchemin, 2004). It can be concluded that FPL, and consequently, dietary peNDF, can be a crucial factor influencing the supply of feed N or microbial N, and thus the supply of NAN, to the duodenum. Lower total digestibility of N with the medium peNDF diet was consistent with the higher ammonia concentration reported by Yang and Beauchemin (2006), indicating low microbial efficiency.

Dietary peNDF did not affect milk yield, which is not surprising considering the lack of DMI (% of BW) response and the fact that the cows were either in mid or late lactation. Similarly, milk production did not respond to FPL in other metabolism studies that used BS (Kononoff et al., 2000; Soita et al., 2000; Einarson et al., 2004), corn silage (Kononoff and Heinrichs, 2003b; Yang and Beauchemin, 2005) or alfalfa silage (Kononoff and Heinrichs, 2003a). Responses in milk production primarily reflect changes in DMI or starch intake (Krause et al., 2002a) when FPL is altered. Low milk efficiency (milk/DMI <1.4) was expected because half of the cows were in late lactation during which cows divert more DMI to BW gain, fetal growth, and growth in young cows than to milk production.

Lack of effect of dietary peNDF on milk fat content suggests that the diets contained adequate fiber to maintain milk fat percentage above 3.5%. Kononoff et al. (2000) suggested that diets based on BS and barley grain with a dietary peNDF of 13.7% are adequate to maintain milk fat level above 3.5% for cows in early to midlactation. That peNDF level (13.7%) is greater than the values for the medium and low peNDF diets in the present study. However, the peNDF values in the Kononoff et al. (2000) study are higher than those in the present study because peNDF values were determined based on particles retained on a 1.18-mm sieve rather than on an 8-mm sieve as in the present study. For barley grain-based diets, the diets used in the present study closely met the recommendation of NDF and starch for lactating dairy cows by Beauchemin and Yang (2003). Although NDF from forage sources (Table 2) was 1 percentage unit lower than the minimum recommendation (21 to 23% NDF from forage), starch content (31%) was also lower than the recommended maximum (33%).

CONCLUSIONS

Increasing particle length of BS linearly increased the intake of peNDF as expected, but had minimal effects on intake, expressed as a function of BW. Digestibility in the total tract, especially for fiber, was decreased with increasing intake of peNDF. Decreased total fiber digestion with higher peNDF was due to decreased intestinal digestion rather than decreased ruminal digestion. Interestingly, increased intake of peNDF tended to shift starch digestion from the rumen to the intestine, which is particularly beneficial for reducing ruminal acidosis when cows are fed barley-based diets. Microbial N production and efficiency were improved with the low peNDF diet but mechanisms by which dietary peNDF affects ruminal microbial production need to be further investigated. Dietary particle size, expressed as peNDF, was associated with nutrient digestibility but not with milk production because cows were in mid to late lactation. A dietary peNDF of 10% of DM, measured using the PSPS with 8- and 19-mm screens, was adequate to maintain 3.5% milk fat for mid to late lactating dairy cows fed barley-based diets. The benefits of further increasing peNDF intake of dairy cows to increase chewing time and minimize acidosis must be considered in relation to possible losses in efficiency due to decreased feed digestion and reduced microbial protein synthesis.

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