Nutrient Demand Interacts with Forage Family to Affect Intake and Digestion Responses in Dairy Cows

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ABSTRACT

The effect of feed intake in the preliminary period on responses to diets containing alfalfa silage or orchardgrass silage was evaluated using 8 ruminally and duodenally cannulated Holstein cows in a crossover design experiment with a 14-d preliminary period and two 15-d treatment periods. Responses measured were DMI, rates of fiber digestion and passage, and milk production. Cows were 139 ± 83 (mean $\pm$ SD) d in milk at the beginning of the preliminary period. During the preliminary period, 3.5% fat-corrected milk yield ranged from 23.9 to 47.6 kg/d (mean = 36.9 kg/d) and preliminary voluntary DMI (pVDMI) ranged from 14.2 to 21.3 kg/d (mean = 18.6 kg/d). The 2 treatments were a diet containing alfalfa silage as the sole forage (AL) and a diet containing orchardgrass silage as the sole forage (OG). Alfalfa silage contained 43% neutral detergent fiber (NDF; dry-matter basis) and orchardgrass silage contained 48% NDF; diets contained ~23% forage NDF and 27% total NDF, so forage-to-concentrate ratio was 53:47 for AL and 48:52 for OG. Digestibility of NDF was lower for AL in the rumen and whole tract compared with OG, and milk fat concentration tended to be greater for OG than for AL. Mean 3.5% fat-corrected milk yield and DMI were not different between AL and OG. Response of DMI to forage family depended on pVDMI, as indicated by a significant interaction between treatment and pVDMI in predicting DMI. As pVDMI increased, DMI increased when cows were fed AL but not when they were fed OG. That is, as appetite increased, intake was more restricted for the more physically filling OG than for the less physically filling AL. This more positive DMI response to AL over OG among high-pVDMI cows is corroborated by interactions between treatments and pVDMI for both ruminal NDF turnover rate and indigestible NDF passage rate response. Therefore, the effects of alfalfa and orchardgrass forages on intake and fiber digestion de-

pended on the extent to which fill limited feed intake of an individual cow.

Key words: nutrient demand, grass, legume, digestion kinetics

INTRODUCTION

A meta-analysis of data from experiments using dairy cows demonstrated lower voluntary DMI (**VDMI**) and milk yield for grass-based diets than for legume-based diets, across maturities, despite greater NDF digestibility for grass (Oba and Allen, 1999b). Although grass NDF usually is more digestible than alfalfa NDF, grass NDF is digested more slowly than alfalfa NDF, and grass particles are more resistant to breakdown than are alfalfa particles (Wilson and Hatfield, 1997). Therefore, we hypothesize that the reduction in VDMI seen for grass-based diets is because of the filling effect caused by slower particle breakdown and slower passage rate in grass forages.

However, individual nutrient demand influences both feed intake responses to forage characteristics and the extent to which physical or metabolic factors limit VDMI (Mertens, 1994; Allen, 1996). The effects on feed intake of diet characteristics (such as forage family) that influence ruminal passage rate of digesta will depend on the extent to which physical filling effects limit feed intake in an individual animal. As a result, testing only overall treatment mean differences may mask important responses in intake, digestion, and production (Allen, 2000). Because cows are now frequently grouped and fed according to milk yield or other major factors affecting nutrient demand, models that predict the effects of nutrient demand on response to diet are even more necessary. We developed and have successfully used an experimental model to evaluate effects of preliminary VDMI (**pVDMI**), an index of nutrient demand, on animal responses to dietary treatments (Oba and Allen, 1999a; Burato et al., 2001; Voelker et al., 2002; Harvatine and Allen, 2002; Bradford and Allen, 2004). Preliminary VDMI was selected to represent nutrient demand because it can be measured directly and accurately and because it represents multiple factors that drive nutrient demand. This model was utilized to test

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Table 1. Status of 8 cows during the final 4 d of the 14-d preliminary period, when cows were fed a common diet

Parameter	Mean	Standard deviation
Parity	4.0	2.6
BW, kg	538	17
BCS	2.5	0.4
DIM	139	83
3.5% FCM yield, kg/d	36.9	9.8
DMI, kg/d	18.6	2.8

our hypothesis that pVDMI and forage family interact in affecting responses of VDMI and digesta passage rate to diets containing orchardgrass silage or alfalfa silage as the sole forage.

MATERIALS AND METHODS

Cows and Treatments

Experimental procedures were approved by the All University Committee on Animal Use and Care at Michigan State University. Eight multiparous Holstein cows from the Michigan State University Dairy Cattle Teaching and Research Center were assigned randomly to treatment sequence in a crossover design experiment with a 14-d preliminary period and two 15-d treatment periods. These 8 cows were 139 ± 83 (mean $\pm$ SD) DIM at the beginning of the preliminary period (Table 1) and were selected deliberately to provide a wide, uniform distribution of preliminary milk yield and DMI (Figure 1). During the 14-d preliminary period, 3.5% fat-cor-

Table 2. Chemical characterization of alfalfa silage and orchardgrass silage

Characteristic	Alfalfa silage	Orchardgrass silage
DM (% as fed)	30.6	35.3
Nutrient, % DM		
OM	88.7	89.2
NDF	42.6	48.0
Indigestible NDF	25.2	13.1
Potentially digestible NDF	17.4	34.9
Starch	4.0	2.3
CP	20.5	20.4
30-h in vitro NDF digestibility, %	29.4	61.1

rected milk yield (**FCMY**) ranged from 23.9 to 47.6 kg/d (mean = 36.9 kg/d) and pVDMI ranged from 14.2 to 21.3 kg/d (mean = 18.6 kg/d). Cows were cannulated ruminally and duodenally before calving. Surgery was performed at the Department of Large Animal Clinical Sciences, College of Veterinary Medicine, Michigan State University. Cows were housed in tie-stalls and fed once daily (1100 h) at 110% of expected intake.

The 2 treatments were a diet containing alfalfa silage as the sole forage (**AL**) and a diet containing orchardgrass silage as the sole forage (**OG**). Alfalfa and orchardgrass forages were produced at the campus farm at Michigan State University (East Lansing) and ensiled in Ag-Bags (Ag-Bag Systems Inc., St. Nazianz, WI). Alfalfa was harvested at early bud stage, chopped at 0.95 cm theoretical length of cut, and ensiled at 36% DM. Orchardgrass was harvested at early boot stage, chopped at 0.64 cm theoretical length of cut, and ensiled at 37% DM. Cut lengths were selected to yield similar particle size distributions using the Pennsylvania State Particle Size Separator (Nasco, Fort Atkinson, WI). Proportions of fresh-chopped forage retained on the top pan varied greatly by sample batch and averaged 20.1% for alfalfa and 28.1% for orchardgrass. Mean total mass retained on the top and middle pans were similar for alfalfa (62%) and orchardgrass (58%).

During the sample collection periods, alfalfa silage contained 43% NDF (DM basis) and orchardgrass silage contained 48% NDF (Table 2). Diets AL and OG were formulated to contain 23% forage NDF and 27% total NDF, so forage-to-concentrate ratios (DM basis) were 53:47 for AL and 48:52 for OG (Table 3). The diet fed during the preliminary period was formulated so that alfalfa silage and orchardgrass silage each contributed 50% of forage NDF (Table 3). Diets also contained dry ground corn, soybean meal (48% CP), SoyPlus (West Central Soy, Ralston, IA.), a vitamin-mineral premix, and blood meal; limestone, urea, and bloodmeal were used to compensate for lower measured CP and anticipated Ca concentrations in orchardgrass silage than in alfalfa silage. All diets were formulated for 18% dietary

Figure 1. Distribution of voluntary DMI (VDMI) and 3.5% fat-corrected milk yield (FCMY) of 8 cows during the final 4 d of the 14-d preliminary period, when cows were fed a common diet.

Table 3. Ingredient and nutrient composition of preliminary diet and treatment diets: one diet (AL) containing alfalfa silage and another diet (OG) containing orchardgrass silage

Ingredient	% of DM		
	Preliminary	AL	OG
Alfalfa silage	25.4	53.0	—
Orchardgrass silage	21.5	—	47.9
Dry ground corn	39.8	36.3	40.3
Soybean meal (48% CP)	6.1	6.5	7.0
Vitamin mineral mix ¹	4.4	4.2	4.2
SoyPlus ²	1.6	1.3	1.3
Bloodmeal	0.4	0.3	0.9
Limestone	0.6	—	0.4
Urea	0.2	—	0.2
Nutrient			
DM (% as fed)	46.4	43.6	50.6
	% of DM		
	Preliminary	AL	OG
OM	91.4	91.5	91.5
NDF	25.8	26.7	27.5
Forage NDF	21.1	22.5	23.0
Indigestible NDF	10.8	14.8	7.9
Potentially digestible NDF	15.0	11.9	19.7
Starch	33.1	30.2	32.1
CP	18.7	18.3	18.8
Rumen-undegraded CP ³	6.0	5.6	6.3

¹Vitamin mineral mix contained (DM basis) 11.7% dicalcium phosphate, 11.1% trace-mineral premix, 8.8% sodium bicarbonate, 2.3% magnesium oxide, 134.3 kIU/kg of vitamin A, 35.53 kIU/kg of vitamin D, 895.5 kIU/kg of vitamin E, and 65.2% ground corn grain as a carrier.

²West Central Soy, Ralston, IA. Nutrient composition: 85% DM, 7% ash, 16% NDF, 5% starch, 49% CP.

³Estimated using values from NRC (2001).

CP and fed once daily as totally mixed rations. During the experimental periods, orchardgrass silage CP concentration was similar to alfalfa silage CP concentration, so dietary CP was 0.5% higher on a diet DM basis in OG than in AL.

Data and Sample Collection

Amounts of feed offered and orts were weighed for each cow daily. Samples of all dietary ingredients (0.5 kg) and orts from each cow (12.5% of orts) were collected daily on d 11 to 13 and combined into one sample per period. Cows were milked twice daily in a milking parlor (0300 and 1500 h); milk yield was measured, and milk was sampled at each milking on d 11 to 13. Rumen-empty BW was measured after evacuation of ruminal digesta on d 14 of the preliminary period, and on d 15 of each experimental period. Body condition score was determined on the same days by 3 trained investigators blinded to treatments (Wildman et al., 1982; 5-point scale where 1 = thin and 5 = fat).

Duodenal samples (1,000 g), fecal samples (500 g), and rumen fluid samples for pH (100 mL) were collected every 9 h from d 11 to 13 so that 8 samples were taken

for each cow in each period, representing every 3 h of a 24-h period to account for diurnal variation. Rumen fluid was obtained by combining digesta from 5 different sites in the rumen and straining it through a layer of nylon mesh (~1 mm pore size). Fluid pH was recorded immediately. All samples were stored at -20°C.

Ruminal contents were evacuated manually through the ruminal cannula at 1600 h (5 h after feeding) on d 14 and at 0700 h (4 h before feeding) on d 15 of each period. Total ruminal content mass and volume were determined. To ensure accurate sampling, every tenth handful of digesta (10%) was separated for a subsample throughout evacuation. This sub-sample was squeezed through a nylon screen (1-mm pore size) to separate it into primarily solid and liquid phases. Both phases were weighed and sampled (350 mL) for determination of nutrient pool size. All samples were stored at -20°C.

Sample and Statistical Analyses

Diet ingredients, orts, and feces were dried in a 55°C forced-air oven for 72 h. All dried samples were ground with a Wiley mill (1-mm screen; Arthur H. Thomas, Philadelphia, PA). Dried, ground fecal samples were combined on an equal DM basis into one sample per cow per period. Frozen duodenal samples for each cow period (n = 8) were chopped finely using a commercial food processor (84142 Food cutter, Hobart Manufacturing Co., Troy, OH) and subsampled in the frozen state to obtain representative samples. These duodenal subsamples and the 350 mL of ruminal solid and liquid samples were lyophilized (Tri-Philizer MP, FTS Systems, Stone Ridge, NY) and ground as described above. Dried ruminal solid and liquid samples were recombined according to the original ratio of solid and liquid DM. Samples were analyzed for ash, NDF, indigestible NDF (**iNDF**), CP, and starch. Ash concentration was determined after 5 h combustion at 500°C in a muffle furnace. Concentrations of NDF were determined according to Van Soest et al. (1991, method A). Indigestible NDF was estimated as NDF residue after 120-h in vitro fermentation (Goering and Van Soest, 1970). Ruminal fluid for the in vitro incubations was collected from a nonpregnant dry cow fed only alfalfa hay. Fraction of potentially digestible NDF (**pdNDF**) was calculated by difference (1.00 - iNDF). Crude protein was analyzed according to Hach et al. (1987). Starch was measured by an enzymatic method (Karkalas, 1985) after samples were gelatinized with sodium hydroxide. Glucose concentration was measured using a glucose oxidase method (Glucose kit #510, Sigma Chemical Co., St. Louis, MO), and absorbance was determined with a micro-plate reader (SpectraMax 190, Molecular Devices Corp., Sunnyvale, CA). Concentrations of all nutrients

except DM were expressed as percentages of DM determined by drying at 105°C in a forced-air oven for more than 8 h. Milk samples were analyzed for fat, true protein, and lactose with infrared spectroscopy by Michigan DHIA (East Lansing).

Indigestible NDF was used as an internal marker to estimate nutrient digestibility in the rumen and in the total tract (Cochran et al., 1986), to estimate rates of passage for iNDF, pdNDF, and starch, and to estimate rates of digestion for pdNDF and starch. Nutrient intake was calculated using the composition of feed offered and refused. Ruminal pool sizes (kg) of OM, NDF, iNDF, pdNDF, and starch were determined by multiplying the concentration of each component by the ruminal digesta DM mass (kg). Duodenal flows (kg/d) of OM, total NDF, pdNDF, and starch were determined using iNDF as an internal marker; iNDF intake (kg/d) was multiplied by the ratio between the component and iNDF in duodenal digesta. Turnover rates in the rumen of OM, NDF, iNDF, pdNDF, and starch were calculated using the following equation:

$$\text{Turnover rate in the rumen (\%/h)} = 100 \times (\text{intake of component/ruminal pool of component})/24.$$

Passage rates from the rumen (k_p) of iNDF, pdNDF, and starch were calculated using the following equation:

$$\text{Passage rate from the rumen (\%/h)} = 100 \times (\text{duodenal flow of component/ruminal pool of component})/24.$$

Ruminal digestion rates (k_d) of pdNDF and starch were calculated using the following equation:

$$\text{Digestion rate in the rumen (\%/h)} = \text{turnover rate in the rumen (\%/h)} - \text{passage rate from the rumen (\%/h)}.$$

Preliminary VDMI was calculated as the mean of DMI values on d 11 to 14 of the 14-d preliminary period. The hypothesis was tested using the following model:

$$Y_{ijk} = \mu + C_i + P_j + T_k + P T_{jk} + \text{pVDMI}_i + T \text{pVDMI}_{ki} + e_{ijk},$$

where μ = overall mean, C_i = random effect of cow ($i = 1$ to 8), P_j = fixed effect of period ($j = 1$ or 2), T_k = fixed effect of treatment ($k = 1$ or 2), PT_{jk} = period $\times$ treatment, pVDMI_i = effect of pVDMI, $T \text{pVDMI}_{ki}$ = treatment $\times$ pVDMI, and e_{ijk} = residual, which was assumed to be normally distributed.

Significance for main effects or interactions was declared at or below $P = 0.05$, and tendencies were declared at or below $P = 0.15$. In the above prediction equation for response Y, the term used to test the hypothesis is treatment $\times$ pVDMI. Both the significance of the treatment $\times$ pVDMI term and the signs of the coefficients for that interaction term (when significant) are reported and discussed.

The original sample size was 13 cows; data from 5 cows were excluded from statistical analysis. One cow developed hypocalcemia during the experiment, 2 were removed from the trial due to duodenal cannula malfunction, one was excluded because feed intake decreased by 50% on d 11 of period 2 for undetermined reasons (intake slowly returned to normal on the same diet), and one was excluded because several key digestion parameters were outside the 95% confidence interval. None of the causes for removal or exclusion were determined to be associated with either of the 2 treatments. Among the remaining 8 cows, each of the 2 treatment sequences was represented by 4 cows. Data in Table 1 and Figure 1 are for the 8 cows used in the statistical analysis.

RESULTS AND DISCUSSION

In Vivo and In Vitro NDF Digestibility

Enhanced NDF digestibility of forages usually improves DMI in high-producing dairy cows (Oba and Allen, 1999b). The alfalfa silage used in this experiment was of moderate quality (Table 2), containing 42.6% NDF and 25.2% iNDF (% DM). The orchardgrass was high-quality, containing 48.0% NDF and 13.1% iNDF. In vitro NDF digestibility (30-h) was much greater for orchardgrass silage (61.1%) than for alfalfa silage (29.4%; Table 2). Digestibility of NDF was greater for OG than for AL in both the rumen (57.4 vs. 37.8%; $P < 0.01$) and the whole gastrointestinal tract (55.8 vs. 32.7%; $P < 0.001$; Table 4). This is consistent with previous comparisons of the digestion of grasses and legumes in lactating cows (Weiss and Shockey, 1991; Holden et al., 1994; Hoffman et al., 1998).

Intake and Ruminal NDF Kinetics

Despite greater NDF digestibility of grass in many studies, VDMI and milk yield (MY) of lactating dairy cows are usually lower for grass-based diets than for legume-based diets (Oba and Allen, 1999b). However, in this experiment, mean DMI (20.5 kg/d), and NDF intake (5.4 kg/d) were not different between AL and OG ($P \geq 0.25$; Table 4). Feed intake is regulated by a combination of mechanisms, including physical filling effects and metabolic satiety, and the dominant limiting

Table 4. Least squares means of feed intake, digestion, and production responses in response to diets containing alfalfa (AL) or orchardgrass (OG)

Response	Treatment LSM ¹		<i>P</i> ²			Interaction coefficient	
	AL	OG	Trt	pVDMI	Trt × pVDMI	AL	OG
Yield, kg/d							
Milk	27.7	27.9	0.77	0.42	0.35		
3.5% fat-corrected milk	29.9	32.2	0.27	0.38	0.78		
Fat	1.11	1.25	0.21	0.36	0.95		
Milk composition, %							
Fat	3.98	4.39	0.07	0.36	0.67		
BW change, kg/15 d	1.58	−14.7	0.06	0.70	0.19		
BCS change, /15 d	0.11	−0.01	0.32	0.90	0.83		
Intake, kg							
DM	20.9	20.0	0.25	0.54	0.03	+0.46	−0.46
NDF	5.5	5.4	0.59	0.65	0.07	+0.11	−0.11
iNDF ³	3.1	1.6	<0.001	0.40	0.02	+0.053	−0.053
Forage NDF	4.7	4.6	0.50	0.54	0.04	+0.10	−0.10
Rumen pool, kg							
DM	10.5	11.4	0.38	0.64	0.94		
NDF	5.6	5.1	0.31	0.41	0.69		
iNDF	4.4	2.7	<0.01	0.54	0.94		
Ruminal NDF turnover time, h	25.0	22.8	0.22	0.84	0.06	−0.80	+0.80
Passage rate from rumen, %/h							
iNDF ³	2.9	2.4	0.01	0.95	0.06	+0.052	−0.052
pdNDF ⁴	1.3	1.4	0.82	0.46	0.46		
Starch	10.4	11.3	0.70	0.87	0.19	+0.67	−0.67
Ruminal digestion rate, %/h							
pdNDF	7.5	5.8	0.12	0.75	0.70		
Starch	22.4	19.5	0.46	0.34	0.43		
NDF digested in the rumen							
kg	2.1	3.1	0.02	0.44	0.71		
%	37.8	57.4	<0.01	0.51	0.39		
NDF digested in the whole tract							
kg	1.8	3.0	<0.01	0.77	0.43		
%	32.7	55.8	<0.001	0.98	0.51		

¹Treatment least squares means.²*P*-values for effects of treatment (Trt), preliminary voluntary DMI (pVDMI), and the interaction between them (Trt × pVDMI).³Indigestible NDF.⁴Potentially digestible NDF = NDF − iNDF.

factor varies depending on nutrient demand. These cows represented a wide range in pVDMI, which was used as an estimate of nutrient demand, and their DMI responses to forage family depended on pVDMI, as indicated by the significant treatment × pVDMI interaction for DMI ($P = 0.03$; Table 4). The positive coefficient for the interaction when the treatment is AL (+ 0.46) indicates that increasing pVDMI results in greater predicted DMI when AL is the treatment. By contrast, the negative coefficient for the treatment × pVDMI interaction indicates that increasing pVDMI results in decreasing predicted DMI when OG is the treatment. As pVDMI increased, DMI increased when cows were fed AL ($P = 0.05$) but not when they were fed OG ($P = 0.73$; data not shown). This suggests that the mechanism by which cows are able to increase feed intake was more impaired among cows with increasing pVDMI when they were fed OG. This was caused, at least in part,

by inhibition of NDF disappearance from the rumen. Response to treatment for turnover time of NDF in the rumen tended to depend on pVDMI ($P = 0.06$), with a negative interaction coefficient for AL and a positive interaction coefficient for OG (Table 4). For AL, predicted NDF turnover time decreased as pVDMI increased, but for OG, predicted NDF turnover time increased as pVDMI increased. A shorter ruminal retention time of NDF in the rumen as pVDMI increased when cows were fed AL reduced the physical filling effects more for NDF from AL than was possible for NDF from OG.

Changes in NDF turnover time may result from an altered digestion rate, passage rate, proportion of digestible NDF, or a combination of these. In this case, the treatment × pVDMI interaction for turnover time was caused primarily by the tendency for a treatment × pVDMI interaction in response of iNDF k_p ($P = 0.06$;

Table 4). For AL, predicted iNDF k_p increases as pVDMI increases (positive interaction coefficient); for OG, predicted iNDF k_p decreases as pVDMI increases (negative interaction coefficient). Less severe physical filling effects for AL permitted k_p to increase as pVDMI increased, but more severe physical filling effects for OG prevented an increase in k_p as pVDMI increased. Therefore, among cows with a greater drive to eat (greater pVDMI), mechanisms permitting greater passage rate of NDF for AL probably allowed actual DMI to more closely match demand in cows fed AL. Among the same animals, when they were fed OG, NDF passage rate could not be increased to allow DMI to match demand.

Passage rate from the rumen can be increased by increased reticular contractions (Okine and Mathison, 1991), and this does occur with greater ruminal distention (Dado and Allen, 1995), which would likely be greater in animals with greater nutrient demand. Reticular contractions were not measured in this experiment. Rumen pools of DM and NDF were similar both between treatments and across the range of pVDMI ($P > 0.30$; Table 4). Rumen pool of iNDF was greater ($P < 0.01$) for AL (4.4 kg) than for OG (2.7 kg), and response to treatment did not depend on pVDMI. The rumen pool treatment responses reflect intake responses; both intake and pool of iNDF were greater for AL than for OG (Table 4). Although intake responses depended on pVDMI, rumen pool responses did not; rumen pool sizes were the same regardless of pVDMI. This suggests that cows with greater appetite were unable to increase rumen pool size to allow greater feed intake. Therefore, physical fill likely was a primary factor limiting feed intake among cows with greater appetite. Without an increase in ruminal pool, the only mechanism that could increase feed intake is an increase in rate of either passage or digestion, or both. As described above, passage rate increased with increasing pVDMI on AL, but not on OG. This is likely because of anatomical and chemical differences between legume and grass forages that affect their escape from the rumen.

Primary limitations to escape of particles from the rumen are particle size and particle density (Welch, 1986). Both rate of particle size reduction and rate of increase in particle specific gravity are likely faster in legume forages than in grasses. Particles of legume forage, and specifically alfalfa, have been demonstrated to be more fragile than particles of grass (Chai et al., 1984; Waghorn et al., 1989). Therefore, both rate of NDF digestion and rate of particle size reduction usually are greater, and retention time usually is shorter, in legumes than in grasses (Waghorn et al., 1989; Hoffman et al., 1993; Holden et al., 1994). In addition, particle density likely increases more slowly in grass particles than in legume particles because of more slowly

digested pdNDF in grass compared with alfalfa fiber (Allen, 1996).

Anatomical and chemical characteristics that lead to slower particle size reduction and slower increase in particle density explain the greater ruminal filling effects observed for the grass compared with the legume in this experiment. Therefore, grass-based diets have little negative effect on cows that have lower nutrient demand and for whom intake is less likely to be limited by fill. Animals with greater nutrient demand, however, need to compensate for greater ruminal NDF retention time. These animals could increase chewing when fed grass and thus increase the rate of particle size reduction, but that apparently did not occur in this experiment. Chewing behavior was not measured in this study, and previous comparisons of chewing time for grasses and legumes are rare and have not utilized high-producing dairy cows for whom total chewing time might be a primary limiting factor (McLeod et al., 1990; Beauchemin and Iwaasa, 1993).

Milk Production

Milk yield averaged 27.8 kg/d and was similar across treatments ($P = 0.77$; Table 4). Mean FCMY was numerically, but not statistically ($P = 0.27$), greater when cows were fed OG (32.2 kg/d) than when they were fed AL (29.9 kg/d; Table 4). This is in contrast with the increase commonly seen in MY or FCMY when legume forage is substituted for grass forage (Oba and Allen, 1999b), and it occurred because milk fat concentration tended to be greater for OG (4.39%) than for AL (3.98%; $P = 0.07$; Table 4). Milk fat concentration response has varied in previous comparisons of grass- and legume-based diets (Zimmerman et al., 1991; Hoffman et al., 1998; Broderick et al., 2002; Dewhurst et al., 2003a; Al-Mabruk et al., 2004), probably because of differences in forage NDF concentrations, total dietary NDF concentration, dietary concentration of forage NDF, and milk yield or stage of lactation of cows. Most diets comparing forages are formulated to contain equal forage-to-concentrate ratios, equal total dietary NDF, or equal estimated NE_L , or are fed as separate components. All of these eliminate the possibility of directly comparing the specific effects of forage fiber on intake and production parameters.

In this experiment, 2 potential mechanisms exist for the effect of treatment on milk fat concentration. First, cows tended ($P = 0.06$) to lose BW when fed OG (−14.7 kg over 15 d) and to maintain a similar BW on AL (+1.58 kg over 15 d). Some of the additional fatty acids mobilized by cows fed OG might have been taken up by the mammary gland and incorporated into milk fat. A second possible mechanism would result from

changes in the profile of fatty acids removed from blood by the mammary gland (Bauman and Griinari, 2003). Although the fatty acid concentrations of grass and alfalfa forages are very low, and their fatty acid profiles are quite similar (Dewhurst et al., 2003a), faster passage rate of some digesta fractions for alfalfa-based diets relative to grass-based diets (as discussed above) likely result in greater escape of rumen biohydrogenation intermediates for alfalfa-based diets (Harvatiné and Allen, 2006). Milk fatty acid profiles were not measured in this experiment, but Dewhurst et al. (2003a,b) reported greater concentrations of the intermediates of ruminal fatty acid biohydrogenation in milk from cows fed legumes, including alfalfa, compared with milk from cows fed grass. Several fatty acid isomers produced by ruminal biohydrogenation have inhibited milk fat synthesis (Bauman and Griinari, 2003) and may have caused the reduction in milk fat concentration observed for cows fed alfalfa-based diets. That is, the effect of forage type on milk fat concentration may have been mediated by diet effect on passage rate and ruminal retention time through their effects on biohydrogenation. In this experiment, milk fat concentration was linearly correlated with starch passage rate ($P = 0.03$) but not with iNDF passage rate, pdNDF passage rate, or NDF turnover time (data not shown). It is likely that both mechanisms contributed to the increased milk fat concentration in cows fed OG compared with AL.

Because treatment and pVDMI interacted to affect DMI and k_p , they might be expected to interact in affecting milk production and milk fat concentration. However, milk yield, FCMY, and milk fat concentration responses to treatment did not depend on pVDMI ($P \geq 0.35$; Table 4).

Summary

As hypothesized, DMI on AL became increasingly greater than DMI on OG with greater pVDMI. This occurred because NDF turnover time in the rumen decreased more for AL than for OG as pVDMI increased. The faster ruminal disappearance of NDF on diet AL, caused primarily by a greater increase in passage rate of iNDF on AL with increasing pVDMI, reduced the physical filling effects for AL more than was possible for OG. This likely was caused by differences in both rate of particle size reduction and rate of increase in particle specific gravity, which have been demonstrated to be faster in legume forages than in grass forages.

CONCLUSIONS

Cows with the greatest drive to eat, as estimated by pVDMI, responded the most positively in feed intake

and digesta passage rate to alfalfa versus orchardgrass as the primary dietary fiber source. These results corroborate previous research suggesting that intake is more limited by physical fill effects both for animals with greater nutrient demand and for grass forages compared with legume forages.

Many models of feed intake, digestion, and metabolism in dairy cows may be improved by incorporating the quantified effects of nutrient demand and feed sources on feed intake and passage rate. These quantified effects can be provided by this experiment and future experiments testing other important variations in diet characteristics. Finally, the results of this experiment reinforce the need to provide separate diets for cows with higher and lower nutrient demand to maximize the efficiency of nutrient utilization among the whole herd.

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