Pelleted Beet Pulp Substituted for High-Moisture Corn: 2. Effects on Digestion and Ruminal Digestion Kinetics in Lactating Dairy Cows

J. A. Voelker and M. S. Allen

Department of Animal Science, Michigan State University,
East Lansing 48824-1225

ABSTRACT

The effects of increasing concentrations of dried, pelleted beet pulp substituted for high-moisture corn on digestion and ruminal digestion kinetics were evaluated using eight ruminally and duodenally cannulated multiparous Holstein cows in a duplicated 4×4 Latin square design with 21-d periods. Cows were 79 ± 17 (mean $\pm$ SD) d in milk at the beginning of the experiment. Experimental diets with 40% forage (corn silage and alfalfa silage) and 60% concentrate contained 0, 6.1, 12.1, or 24.3% beet pulp substituted for high-moisture corn on a dry matter basis. Diet concentrations of neutral detergent fiber (NDF) and starch were 24.3 and 34.6% (0% beet pulp), 26.2 and 30.5% (6% beet pulp), 28.0 and 26.5% (12% beet pulp), and 31.6 and 18.4% (24% beet pulp), respectively. Ruminal dry matter pool decreased and NDF turnover rate increased as dietary beet pulp content increased. Potentially digestible NDF was digested more extensively and at a faster rate in the rumen with increasing beet pulp, resulting in increased total tract NDF digestibility. Passage rates of potentially digestible NDF and of indigestible NDF were not affected by treatment. True ruminal digestibility of starch decreased with increasing beet pulp substitution. This was caused by a linear increase in starch passage rate, possibly because of increasing ruminal fill, and a linear decrease in digestion rate of starch in the rumen, possibly because of reduced amylolytic enzyme activity for lower-starch diets. Although true ruminal starch digestibility decreased when more beet pulp was fed, whole tract starch digestibility was not affected because of compensatory digestion of starch in the intestines. Due to more thorough digestion of fiber in diets containing more beet pulp, whole-tract digestibility of organic matter increased linearly, and intake of digestible organic matter was not affected. Partially

replacing high-moisture corn with beet pulp in low-forage diets increased fiber digestibility without reducing whole-tract starch digestibility.

(**Key words:** beet pulp, high-moisture corn, site of digestion, starch digestion)

Abbreviation key: BP = dried, pelleted beet pulp, 0BP = 0% beet pulp treatment, 6BP = 6% beet pulp treatment, 12BP = 12% beet pulp treatment, 24BP = 24% beet pulp treatment, HMC = high-moisture corn, INDF = indigestible NDF, NSC = nonstructural carbohydrate, pdNDF = potentially digestible NDF.

INTRODUCTION

Because starch usually is more completely digested than NDF, replacing forage with grain is expected to increase diet digestibility. However, fiber digestibility can be reduced by increased starch concentration. Depressed fiber digestibility can be caused by several factors: decreased mastication and slower particle size reduction, a reduction in ruminal pH resulting from increased VFA production and decreased flow of saliva buffers (Strobel and Russell, 1986), and inhibition of fiber digestion independent of effects of mastication or pH (Grant and Mertens, 1992).

Carbohydrate sources exist that are more extensively degraded than forage NDF and mimic some of its beneficial effects but do not bring the same negative effects as starch fermentation. When low-forage, high-grain diets are fed, adding carbohydrate from these sources can improve the overall digestion and absorption of nutrients. Beet pulp contains approximately 40% NDF and is unique in its high concentration of neutral-detergent soluble fiber, especially pectic substances (~25% of DM). The NDF in beet pulp can be digested more quickly than forage NDF (Bhatti and Firkins, 1995), and pectin is degraded more rapidly than cellulose and hemicellulose (Marounek et al., 1985). Unlike starch, pectin fermentation does not inhibit cellulose and hemicellulose digestion, primarily because pectinolytic bacteria also are inhibited at low pH (Marounek et al., 1985).

Received November 12, 2002.

Accepted June 2, 2003

Corresponding author: M. S. Allen; e-mail: allenm@pilot.msu.edu.

Therefore, substituting beet pulp for high-moisture corn (HMC) grain in a diet with a low forage content should, at some rate of inclusion, improve NDF digestion and possibly increase overall nutrient digestion in the whole tract. Starch digestion kinetics might also be altered, changing the proportion of starch digested in the rumen and intestines, although the direction of that shift cannot be predicted. The objective of this experiment was to measure the effects of substituting beet pulp for high-moisture corn at four concentrations (0, 6, 12, and 24% of diet DM) on ruminal, postruminal, and whole tract digestion of NDF, starch, DM, and OM.

MATERIALS AND METHODS

This paper is one of three papers in a series from one experiment that evaluated effects of the substitution of dried, pelleted beet pulp for HMC. This paper discusses treatment effects on ruminal, postruminal, and whole-tract digestion, and the companion papers focus on feed intake and milk production (Voelker and Allen, 2003a), and ruminal fermentation, including efficiency of microbial nitrogen production (Voelker and Allen, 2003b). Experimental procedures were approved by the All University Committee on Animal Use and Care at Michigan State University.

Treatments and Cows

Eight multiparous Holstein cows (79 ± 17 DIM; mean $\pm$ SD) from the Michigan State University Dairy Cattle Teaching and Research Center were randomly assigned to a duplicated 4×4 Latin square balanced for carryover effects in a dose-response arrangement of treatments. Treatment periods were 21 d, with the final 10 d used to collect samples and data. Treatments were diets containing dried, pelleted beet pulp (BP) substituted for HMC at 0 (0BP), 6 (6BP), 12 (12BP), and 24% (24BP) of diet DM. Cows were cannulated ruminally and duodenally before calving. Duodenal cannulas were soft gutter type made of Tygon and vinyl tubing (Crocker et al., 1998). The duodenum was fistulated proximal to the pylorus region and before the pancreatic duct, and the cannulas were placed between 10th and 11th ribs as described by Robinson et al. (1985). Both ruminal and duodenal surgeries were performed at the Department of Large Animal Clinical Science, College of Veterinary Medicine, Michigan State University. At the beginning of the experiment, empty BW (ruminal digesta removed) of cows was 516 ± 64 kg (mean $\pm$ SD).

Nutrient composition for HMC and BP are shown in Table 1. Experimental diets contained 40% forage (50:50 corn silage: alfalfa silage), HMC, BP at 0 to 24% of diet DM, a premixed protein supplement (soybean

Table 1. Nutrient composition of high-moisture corn and dried, pelleted beet pulp.

Nutrient (DM, % as fed)	High-moisture corn (71.5)	Beet pulp (84.9)
	% of DM	
NDF	10.0	39.9
CP	8.3	8.9
Indigestible NDF	3.8	8.0
Starch	70.5	3.9
Ether extract	4.7	0.7
Ash	1.0	7.8

meal, corn distillers' grains, and blood meal), and a mineral and vitamin mix (Table 2). All diets were formulated for 18% dietary CP concentration and fed as TMR.

Data and Sample Collection

Cows were housed and fed as described previously (Voelker and Allen, 2003a). Chromic oxide was used as a marker to estimate nutrient digestibility in the rumen and in the total tract. Gelatin capsules (1.5 oz., Tropac Inc., Airfield, NJ) containing 5 g of chromic oxide and spelt hulls (Wiley Mill, 2-mm screen; Arthur H. Thomas, Philadelphia, PA) were dosed through the ruminal cannula at 0300, 1100, and 1900 h (total of 15 g of $\text{Cr}_2\text{O}_3/\text{d}$) from 7 to 14 d with a priming dose of $3 \times$ on d 7. Duodenal samples (1000 g), fecal samples (500 g), and rumen fluid samples (100 ml) were collected every 9 h from d 12 to 14 so that eight samples were taken for each cow each period, representing every 3 h of a 24-h period to account for diurnal variation. Rumen fluid samples were obtained by combining and straining digesta from five different sites in the rumen. Fluid pH was immediately recorded. All samples were immediately frozen at -20°C .

Ruminal contents were evacuated manually through the ruminal cannula at 1500 h (4 h after feeding) on d 20 and at 0900 h (2 h before feeding) at the end of d 21 of each period. Total ruminal content mass and volume were determined. During evacuation, 10% aliquots of digesta were separated to allow accurate sampling. Aliquots were squeezed through a nylon screen (1-mm pore size) to separate into primarily solid and liquid phases. Samples were taken from both phases for determination of nutrient pool size.

Sample and Statistical Analysis

Diet ingredients and orts were processed as previously described (Voelker and Allen, 2003a), and feces were processed similarly. Dried, ground fecal samples were combined on an equal DM basis into one sample

Table 2. Ingredient and nutrient composition of experimental diets.

	0% BP	6% BP	12% BP	24% BP
Ingredients	% of DM			
Corn silage ¹	20.1	20.1	20.1	20.1
Alfalfa silage ²	19.9	19.9	19.9	19.9
Protein mix ³	19.5	19.5	19.5	19.5
Mineral vitamin mix ⁴	4.8	4.8	4.8	4.8
Dried, pelleted beet pulp	0	6.1	12.1	24.3
High-moisture corn	35.6	29.5	23.5	11.4
Nutrient				
DM	50.2	50.5	50.8	51.6
Starch	34.6	30.5	26.5	18.4
NDF	24.3	26.2	28.0	31.6
Indigestible NDF	9.4	9.6	9.8	10.2
Forage NDF	17.1	17.1	17.1	17.1
CP	18.0	18.0	18.0	18.1
Rumen-undegraded CP ⁵	11.6	11.4	11.3	10.9
% Starch from				
high-moisture corn	72.7	68.3	62.6	43.7
% NDF from forage	70.2	65.3	61.1	54.1
% NDF from beet pulp	0.0	9.3	17.3	30.7

¹Corn silage contained 36.2% DM (as fed) and (DM basis) 43.5% NDF, 7.6% CP, 13.4% indigestible NDF, 28.5% starch, and 3.8% ash. BP = beat pulp.

²Alfalfa silage contained 34.6% DM (as fed) and (DM basis) 41.8% NDF, 19.5% CP, 26.1% indigestible NDF, 3.0% starch, and 8.1% ash.

³Protein mix contained 75% soybean meal, 20% corn distillers' grains (with solubles), and 5% blood meal.

⁴Mineral vitamin mix contained 10.4% trace mineral premix, 0.4% vitamin D, 0.4% vitamin A, 2.7% magnesium oxide, 22.3% dicalcium phosphate, and 63.8% dry ground corn as a carrier.

⁵Rumen-degraded protein estimated using values from NRC (2001).

per cow per period. Ruminal digesta samples were lyophilized (Tri-Philizer MP, FTS Systems, Stone Ridge, NY). Duodenal samples were thawed, combined, and filtered into primarily solid and liquid phases using nylon mesh (1 mm pore size) to minimize sampling errors due to segregation of samples into solid and liquid phases. Both phases were weighed, and subsamples were taken from each phase. Liquid and solid subsamples were lyophilized, ground, and recombined by weight according to the original ratio of solid and liquid DM. All dried samples were analyzed for DM, ash, NDF, 120-h in vitro indigestible NDF (**INDF**), potentially digestible NDF (**pdNDF**; 1 - **INDF**), CP, and starch, as previously described (Voelker and Allen, 2003a).

Diet ingredients, duodenal digesta, and feces were analyzed for concentrations of chromium. Samples were digested with phosphoric acid (Williams et al., 1962), and chromium was quantified by flame atomic absorption spectrometry (SpectraAA 220, Varian, Victoria, Australia) according to manufacturer's recommendation. Nutrient intake was calculated using the composition of feed offered and refused. Duodenal flow of microbial OM was determined as described by Oba and Allen (2003b), and true ruminally degraded OM was calculated by subtracting duodenal flow of nonmicrobial OM from OM intake. Ruminal pool sizes (kg) of OM, NDF, **INDF**, **pdNDF**, and starch were determined by multiplying the concentration of each component by the rumi-

nal digesta DM mass (kg). Turnover rate in the rumen, passage rate from the rumen, and ruminal digestion rate of each component (%/h) were calculated by the following equations:

Turnover rate in the rumen (%/h) =

$100 \times (\text{intake of component} / \text{ruminal pool of component}) / 24$

Passage rate from the rumen (%/h) =

$100 \times (\text{duodenal flow of component} / \text{ruminal pool of component}) / 24$; and

Digestion rate in the rumen (%/h) =

turnover rate in the rumen (%/h) - passage rate from the rumen (%/h).

To determine differences between treatments, all data were analyzed using the fit model procedure of JMP (Version 4, SAS Institute, Cary, NC) according to the following model:

$$Y_{ijk} = \mu + C_i + P_j + T_k + e_{ijk},$$

where

μ = overall mean,

C_i = random effect of cow ($i = 1$ to 8),

P_j = fixed effect of period ($j = 1$ to 4),

T_k = fixed effect of treatment ($k = 1$ to 4), and

e_{ijk} = residual, assumed to be normally distributed.

Table 3. Effects of substitution of pelleted beet pulp for high-moisture corn on ruminal digestion kinetics.

	Treatment LSM ¹				P ²			
	0% BP	6% BP	12% BP	24% BP	SE	Trt	L	Q
Ruminal turnover rate, %/h								
DM	9.1	9.8	9.4	9.3	0.6	0.34	0.20	0.20
OM	9.4	10.2	9.6	9.6	0.6	0.25	0.24	0.24
NDF	4.5	5.5	5.2	5.9	0.4	<0.01	<0.01	0.24
pdNDF	5.9	7.6	7.2	8.6	0.6	<0.01	<0.01	0.38
Starch	29.0	29.6	28.3	25.4	2.3	0.49	0.87	0.56
Ruminal passage rate, %/h								
pdNDF ³	3.16	3.29	2.74	2.89	0.36	0.49	0.29	0.76
INDF	3.09	3.78	3.44	3.67	0.28	0.11	0.16	0.26
Starch	15.90	19.31	18.33	23.50	2.99	0.07	0.01	0.96
Ruminal digestion rate, %/h								
pdNDF ³	2.71	4.29	4.43	5.86	0.47	<0.01	<0.01	0.23
Starch	11.30	10.36	9.45	1.91	3.06	0.02	<0.01	0.27

¹Treatments were beet pulp (BP) substituted for high-moisture corn as 0, 6, 12, and 24% of diet DM.

²Trt: treatment effect, L: linear effect, Q: quadratic effect.

³Potentially digestible NDF.

Period $\times$ treatment interaction was originally evaluated, but it was removed from the statistical model because it was not significant. Linear and quadratic dose-response effects were evaluated using the same model with diet percent BP (0, 6, 12, and 24) in place of the fixed effect of treatment. Pearson's correlation coefficients were determined between cow-period observations for some parameters. Treatment effects, linear and quadratic responses, and correlations were declared significant at $P < 0.05$, and tendencies were declared at $P < 0.10$. For reasons previously described (Voelker and Allen, 2003a), data from two cow-periods were excluded from statistical analysis.

RESULTS AND DISCUSSION

Ruminal NDF Digestion

Turnover rate of NDF (Table 3) increased linearly with added BP ($P < 0.01$). A faster turnover rate can result from increased passage rate, increased digestion rate, or both. Passage rates of pdNDF and INDF were not affected by treatment (Table 3). However, digestion rate of pdNDF more than doubled, from 2.71 to 5.86%/h ($P < 0.0001$), from 0BP to 24BP.

As BP was substituted for HMC up to 24% of diet DM, the proportion of NDF from forage decreased from approximately 70 to 54% of total NDF, and the proportion of NDF from BP increased from 0 to approximately 31% of total NDF (Table 2). Beet pulp NDF has a shorter lag time and more rapid digestion rate than most other sources of fiber (Bhatti and Firkins, 1995) partly because it has been previously soaked in hot water (Bichsel, 1988). Therefore, increasing the contribution of BP NDF to total NDF can increase the overall rate of NDF

digestion, independent of any associative effects of BP NDF on the digestion of NDF from other sources.

Substituting the readily degraded pectin and NDF of BP for HMC may also increase the rate of digestion of other dietary fiber through associative effects of both fiber and starch. Adding BP might have increased the population of fibrolytic bacteria and fibrolytic enzyme activity by providing excess available substrate for fiber degraders. Dilution of the concentration of dietary starch would also reduce the negative effects of starch fermentation on cellulolytic bacteria. Measurements of ruminal pH over 96 h in this study are reported in a companion paper (Voelker and Allen, 2003b). As mean and minimum daily pH were not different among treatments, the improvement in fiber digestion with added BP was not caused by increased mean pH. However, reduction of NDF digestion by the addition of starch can occur even when pH is held constant (Grant and Mertens, 1992).

Ruminal pH and NDF Digestion

Increased rate of NDF digestion with added BP was not the result of increased mean pH among treatments. However, correlations between cow-period observations for ruminal pH characteristics and rate of ruminal fiber digestion show that greater daily mean pH was correlated with more rapid digestion of pdNDF (Figure 1; $R = 0.41$, $P < 0.05$), as was greater minimum ruminal pH (Table 4; $R = 0.55$, $P < 0.01$). Interestingly, although 0BP, 12BP, and 24BP appear to demonstrate positive relationships between mean ruminal pH and pdNDF digestion rate, 6BP appears to demonstrate a slightly negative relationship. Lower mean or minimum rumi-

Figure 1. Relationship between rate of digestion of potentially digestible NDF (%/h) and mean ruminal pH. pdNDF rate of digestion = $-11.1 + 2.5 \text{ mean pH}$ ($R = 0.41$; $P < 0.05$). $\circ$ denotes 0% beet pulp, $+$ denotes 6% beet pulp, $\blacksquare$ denotes 12% beet pulp, and $\bullet$ denotes 24% beet pulp (%diet DM) substituted for high-moisture corn.

nal pH and greater variability in pH probably slowed fermentation of NDF because low pH (especially below 6.0) slows growth of fibrolytic bacteria, perhaps due to intracellular accumulation of VFA and anion toxicity (Russell and Wilson, 1996). Although higher pH mean and minimum were associated with more rapid fiber digestion, they were not related to ruminal fiber digestibility ($P > 0.30$), because higher pH was also associated with increased passage rate of INDF from the rumen (Table 4). Therefore, ruminal pH was related to the rate but not the extent of ruminal NDF digestion, and the correlation between mean pH and rate of pdNDF digestion was independent of treatment effects for the two variables.

Whole-Tract NDF Digestion

As NDF intake and the rate of ruminal NDF digestion increased with BP replacing HMC, the amount of NDF

digested in the rumen also increased ($P < 0.01$; Table 5). Ruminal digestibility of total NDF was not affected ($P > 0.10$), but pdNDF was more completely digested with added BP ($P < 0.01$). There was no compensatory postruminal NDF digestion, so the diets with the greatest ruminal NDF digestibility also had the greatest whole-tract NDF digestibility ($P < 0.001$).

Ruminal Starch Digestion Kinetics

Corresponding to diet composition and DMI, starch intake decreased from 8.2 kg/d for 0BP to 4.0 kg/d for 24 BP (Table 6; $P < 0.0001$). Ruminal starch turnover rate was not affected by treatment (Table 3; $P > 0.40$) due to opposing changes in ruminal rates of both passage and digestion of starch. As HMC was replaced by BP, passage rate of starch increased linearly ($P = 0.01$) and ruminal starch digestion rate decreased linearly from 11.3%/h for 0BP to 1.9%/h for 24BP ($P < 0.01$). As the dietary concentration of HMC decreased, the proportion of starch from HMC decreased (Table 2), and starch from other sources (such as corn silage) probably was degraded less rapidly than starch from HMC due to differences in processing and preservation (Oba and Allen, 2003a). Rate of starch digestion also might have been reduced by lower amylase activity in rumen fluid, because of a smaller population of amylolytic microbes and possibly because of depressed enzyme activity of the population as a result of reduced substrate and high dilution rate.

Site of Starch Digestion

Large differences in starch intake, rapid passage of starch from the rumen for the high-BP diets, and a sharp decrease in ruminal starch digestion rate resulted in much lower true ruminal starch digestibility as BP replaced HMC ($P < 0.01$; Table 6). Reducing dietary starch content by only 4%, from 34.6 to 30.5% of diet DM (0BP to 6BP) resulted in a 31% decrease in true ruminal starch digestion (from 46.5 to 32.3%). From 0BP to 24BP, dietary starch content was reduced by 48%, the amount of starch truly digested in the rumen decreased 82% (3.8 to 0.7 kg), and the percentage

Table 4. Correlation coefficients for fiber digestion kinetics and ruminal pH.

	pdNDF^1 digestion rate	pdNDF^1 passage rate	INDF^2 passage rate
Mean ruminal pH	0.41 ³	0.34 ³	0.52 ³
Minimum ruminal pH	0.55 ³	0.40	0.64 ³

¹Potentially digestible NDF.

²Indigestible NDF.

³Correlation is significant ($P < 0.05$).

Table 5. Effects of substitution of pelleted beet pulp for high-moisture corn on digestion of total NDF and potentially digestible NDF (pdNDF).

	Treatment LSM ¹				P ²			
	0% BP	6% BP	12% BP	24% BP	SE	Trt	L	Q
NDF								
Intake, kg/d	5.7	6.2	6.6	6.9	0.2	<0.01	0.01	0.15
Ruminally digested								
kg/d	2.1	2.1	2.3	2.9	0.2	0.04	<0.01	0.39
%	35.9	34.5	34.5	42.5	3.5	0.32	0.14	0.23
Passage to duodenum, kg/d	3.7	4.1	4.3	4.0	0.3	0.37	0.08	0.11
Postruminally digested								
kg/d	0.68	0.72	0.99	0.88	0.18	0.56	0.33	0.47
% of intake	12.0	11.7	15.3	12.7	3.0	0.81	0.54	0.59
% of duodenal passage	16.7	17.6	24.3	22.7	3.8	0.40	0.17	0.50
Total tract digested								
kg/d	2.5	2.9	3.5	3.9	0.22	<0.01	<0.01	0.13
% of intake	43.4	47.3	53.4	57.2	2.1	<0.01	<0.01	0.31
pdNDF³								
Intake, kg/d	3.2	3.6	4.0	4.3	0.1	<0.01	<0.01	0.17
Ruminally digested								
kg/d	1.6	2.0	2.3	2.8	0.1	<0.01	<0.01	0.37
%	46.1	56.8	60.3	67.3	3.4	<0.01	0.02	0.20
Passage to duodenum, kg/d	1.6	1.6	1.6	1.4	0.1	0.51	0.81	0.86
Postruminally digested								
kg/d	0.36	0.45	0.49	0.35	0.11	0.77	0.34	0.30
% of intake	10.9	12.6	12.1	8.0	2.9	0.70	0.57	0.40
% of duodenal passage	22.3	17.6	26.7	24.9	7.6	0.82	0.90	0.99
Total tract digested								
kg/d	1.9	2.4	2.8	3.2	0.1	<0.01	<0.01	0.03
% of intake	60.2	67.0	71.6	75.4	1.7	<0.01	<0.01	0.03

¹Treatments were beet pulp (BP) substituted for high-moisture corn as 0, 6, 12, and 24% of diet DM.²Trt: treatment effect, L: linear effect, Q: quadratic effect.³Potentially digestible NDF.

of starch truly digested in the rumen decreased 64% (46.5 to 16.9%). Replacing ground corn grain with soyhulls as 0, 10, 20, 30, and 40% of diet DM (Ipharraguerre et al., 2002) also altered apparent ruminal digestibility of nonstructural carbohydrates (NSC).

The reduction of ruminal starch digestibility with added BP was compensated for by intestinal digestion. The percentage of starch consumed that was digested postruminally increased from 45.7 to 77.5% ($P = 0.02$) as dietary starch content decreased from 34.6 to 18.4%,

Table 6. Effects of substitution of pelleted beet pulp for high-moisture corn on digestion of starch.

	Treatment LSM ¹				P ²			
	0% BP	6% BP	12% BP	24% BP	SE	Trt	L	Q
Intake, kg/d	8.2	7.3	6.4	4.0	0.2	<0.01	<0.01	0.21
Apparently ruminally digested								
kg/d	3.5	2.1	1.6	0.4	0.6	<0.01	<0.01	0.32
%	42.2	27.9	26.1	9.7	10.0	0.03	<0.01	0.74
Truly ruminally digested								
kg/d	3.8	2.4	1.9	0.7	0.6	<0.01	<0.01	0.32
%	46.5	32.3	31.2	16.9	9.8	0.05	<0.01	0.68
Passage to duodenum, kg/d	4.7	5.2	4.8	3.7	0.6	0.11	0.40	0.14
Apparent postruminal digested								
kg/d	3.7	4.1	4.0	3.1	0.6	0.32	0.27	0.14
% of intake	45.7	57.2	62.6	77.5	9.5	0.02	<0.01	0.77
% of duodenal passage	78.0	77.4	83.2	85.0	2.6	0.02	<0.01	0.96
Apparent total tract digested								
kg/d	7.2	6.2	5.7	3.5	0.2	<0.01	<0.01	0.30
%	88.0	86.2	88.6	87.5	1.6	0.49	0.99	0.97

¹Treatments were beet pulp (BP) substituted for high-moisture corn as 0, 6, 12, and 24% of diet DM.²Trt: treatment effect, L: linear effect, Q: quadratic effect.

and digestibility of starch passing into the duodenum increased from 78.0 to 85.0% ($P = 0.02$). Ipharraguerre and co-workers (2002) may also have increased the proportion of NSC digested postruminally by feeding soyhulls, which suggests that adding fibrous byproducts to high-concentrate diets might frequently shift starch digestion from the rumen to the intestines. Because digestion of starch in the small intestine results in the absorption of glucose into intestinal cells, which is more energetically efficient than starch fermentation to VFA (Owens et al., 1986) and should spare plasma glucose that would otherwise be used by intestinal cells, cows might obtain energy from starch more efficiently when fed diets containing less starch. Because these cows were not ileally cannulated, the proportions of starch digested and absorbed as glucose in the small intestine or fermented and absorbed as VFA in the large intestine could not be measured. As a result of compensatory postruminal starch digestion, total tract digestibility of starch was the same across BP treatments ($P > 0.40$) even though the amount of starch digested in the total tract decreased from 7.2 to 3.5 kg/d ($P < 0.0001$) as starch intake decreased. Replacing corn with soyhulls only reduced whole-tract NSC digestibility when soyhulls comprised 40% of diet DM (Ipharraguerre et al., 2002), which is well outside the range of treatments in the present experiment.

Source of starch can affect ruminal and intestinal starch digestion. The rate and extent of starch digestion might be expected to be greater for rolled HMC than for kernels in corn silage, the second most significant starch source in these diets, because of greater surface area:weight in the rolled HMC. As HMC was increasingly replaced by BP, the percentage of dietary starch derived from HMC decreased from 73 to 44% (Table 2). It would be conceivable that ruminal rate of starch digestion (%/h) decreased as dietary BP increased because corn silage grain was digested more slowly than the rolled HMC, and corn silage kernels comprised a greater proportion of total starch as dietary BP increased. However, whole-tract starch digestibility was similar among treatments (Table 7), so starch reaching the duodenum was as digestible, if not more digestible, when HMC starch comprised a smaller percentage of total dietary starch. Undegraded starch in corn silage kernels was probably more resistant to intestinal digestion than undegraded starch in HMC, so it is not likely that a greater proportion of corn-silage grain resisted ruminal degradation for high-beet-pulp diets (thus reducing ruminal starch digestion rate) and then was digested in the intestines to the same extent as the starch in low-BP diets. Whereas the ruminal digestion of silage kernels probably was affected by dietary starch concentration, the treatment effects detected were not

Table 7. Effects of substitution of pelleted beet pulp for high-moisture corn on digestion of DM and OM.

	Treatment LSM ¹				P ²			
	0% BP	6% BP	12% BP	24% BP	SE	Trt	L	Q
DM								
Intake, kg/d	23.7	23.8	23.9	21.8	0.7	0.11	<0.05	0.15
Apparently ruminally digested								
kg/d	6.4	5.3	3.7	4.7	1.1	0.29	0.09	0.16
%	27.4	22.2	16.2	21.9	4.8	0.38	0.10	0.15
Passage to duodenum, kg/d	17.2	18.6	20.2	17.1	1.5	0.35	<0.10	0.08
Apparent total tract digested								
kg/d	16.1	15.9	16.7	15.4	0.5	0.28	0.35	0.22
%	68.4	66.9	70.6	70.8	1.3	<0.10	0.07	0.87
OM								
Intake, kg/d	22.3	22.4	22.4	20.2	0.7	0.06	0.50	0.15
Apparently ruminally digested								
kg/d	7.0	5.4	5.9	5.7	0.8	0.30	0.21	0.32
%	31.2	23.8	26.7	27.9	3.5	0.34	0.22	0.27
Truly ruminally digested								
kg/d	11.4	9.7	10.2	9.4	0.8	0.15	0.85	0.95
%	50.7	42.9	45.9	46.4	3.6	0.34	0.69	0.60
Passage to duodenum, kg/d	16.2	17.0	16.4	14.5	1.0	0.21	0.16	0.12
Apparent postruminal digested								
kg/d	9.5	9.7	10.0	8.6	0.9	0.69	0.50	0.36
% of intake	38.9	43.8	45.0	42.9	3.8	0.67	0.24	0.29
% of duodenal passage	57.8	58.0	60.7	59.7	2.6	0.77	0.51	0.64
Apparent total tract digested								
kg/d	15.6	15.4	16.0	14.6	0.4	0.19	0.37	0.19
%	69.9	68.7	72.2	72.5	1.3	0.09	0.05	0.90

¹Treatments were beet pulp (BP) substituted for high-moisture corn as 0, 6, 12, and 24% of diet DM.

²Trt: treatment effect, L: linear effect, Q: quadratic effect.

Figure 2. Relationship between starch digestibility (% duodenal flow) and duodenal starch flow [Starch digested postruminally (% duodenal flow) = $74.1 + 1.4$ duodenal starch flow; $R = 0.35$, $P < 0.07$]. ○ denotes 0% beet pulp, ■ denotes 6% beet pulp, + denotes 12% beet pulp, and ● denotes 24% beet pulp (%diet DM) substituted for high-moisture corn.

only the result of changing proportions of starch sources but were also caused by treatment effects on rates of starch digestion and passage.

If the amount of duodenal enzyme activity limits the amount of starch digested in the small intestine, then extent of digestion should decrease as duodenal starch flow increases (Owens et al., 1986), and the amount of starch digested in the small intestine should reach a plateau as enzyme becomes limiting. However, across cow-period observations, the amount of starch digested in the intestines (kg/d) increased linearly ($R = 0.98$, $P < 0.0001$) but not quadratically ($P > 0.85$), so starch digestion did not reach a plateau as duodenal starch flow increased. Intestinal starch digestibility (percentage of duodenal flow) also tended to increase as duodenal starch flow increased ($R = 0.34$, $P = 0.07$; Figure 2a), whereas it would be expected to decrease if enzyme was limiting. Similar responses in intestinal starch digestion were reported in a study in which treatments were dietary starch concentration and degradability of corn grain (Oba and Allen, 2003a). Because greater flow was not associated with lower intestinal digestibility, starch digestion in the small intestine was probably limited by physical or chemical characteristics of starch escaping ruminal digestion, rather than by enzyme activity (Oba and Allen, 2003a). However, the relationships between starch flow and digestibility or amount digested may also reflect increased amylase secretion with increased duodenal starch flow (Owens et al., 1986).

Digestion of DM and OM

Substituting highly degradable fiber for rapidly fermentable starch radically altered ruminal digestion and passage of starch and fiber, probably through both physical and microbial changes in the rumen environment. This resulted in a tendency for decreased apparent ruminal DM digestion ($P = 0.10$) but did not affect apparent or true ruminal OM digestion (Table 7).

Because compensatory postruminal starch digestion took place as the concentration of BP increased, apparent total tract OM digestibility increased, and DM digestibility tended to increase. Thus, although DMI decreased linearly with added BP, quantities of DM and OM apparently digested in the whole tract were not affected by treatment. Therefore, substituting highly digestible NDF for rapidly degraded starch in a high-concentrate diet did not reduce the amount of digested DM, but increased total diet digestibility by increasing NDF digestibility.

SUMMARY

Increasing the substitution rate of pelleted beet pulp for HMC decreased the rate of ruminal starch digestion and increased starch passage rate, drastically shifting the site of starch digestion to the intestines. Adding beet pulp greatly increased the rate at which potentially digestible NDF was digested in the rumen and also increased whole-tract NDF digestibility. Partially replacing a highly fermentable starch source with beet pulp was accomplished without reducing apparent DM digestibility because adding beet pulp increased fiber digestibility without reducing total tract starch digestibility. Therefore, substitution of beet pulp for highly fermentable grain can reduce the risk of ruminal acidosis for animals fed diets low in forage NDF.

ACKNOWLEDGMENTS

The authors wish to thank D. G. Main, R. A. Longuski, Y. Ying, M. Oba, C. S. Mooney, R. A. Kreft, and the staff of the Michigan State University Dairy Cattle Teaching and Research Center for their assistance in this experiment, and N. K. Ames of the Department of Large Animal Clinical Science in the College of Veterinary Medicine at Michigan State University for performing the cannulation surgeries.

REFERENCES

- Allen, M. S., L. E. Armentano, M. N. Pereira, Y. Ying, and J. Xu. 2000. Method to measure fractional rate of volatile fatty acid absorption from the rumen. Proc. 2000 Rumen Function Conference, Chicago 25:24. (Abstr.)

- Bhatti, S. A., and J. L. Firkins. 1995. Kinetics of hydration and functional specific gravity of fibrous feed by-products. *J. Anim. Sci.* 73:1449–1458.
- Bichsel, S. E. 1988. An overview of the U. S. beet sugar industry. Pages 1–8 in *Chemistry and Processing of Sugarbeet and Sugar-cane*. M. A. Clarke and M. A. Godshall, eds. Elsevier, New York, NY.
- Crocker, L. M., E. J. DePeters, J. G. Fadel, H. Prez-Monti, S. J. Taylor, J. A. Wyckoff, and R. A. Zinn. 1998. Influence of processed corn grain in diets of dairy cows on digestion of nutrients and milk composition. *J. Dairy Sci.* 81:2394–2407.
- Goering, H. K., and P. J. Van Soest. 1970. *Forage Fiber Analysis (Apparatus, Reagents, Procedures, and Some Applications)*. Agric. Handbook No. 379. ARS-USDA, Washington, DC.
- Grant, R. J., and D. R. Mertens. 1992. Influence of buffer pH and raw corn starch addition on in vitro fiber digestion kinetics. *J. Dairy Sci.* 75:2762–2768.
- Hach, C. C., B. K. Bowden, A. B. Lopelove, and S. V. Brayton. 1987. More powerful peroxide Kjeldahl digestion method. *J. AOAC* 70:783–787.
- Ipharraguerre, I. R., Z. Shabi, J. H. Clar, and E. E. Freeman. 2002. Ruminant fermentation and nutrient digestion by dairy cows fed varying amounts of soyhulls as a replacement for corn grain. *J. Dairy Sci.* 85:2890–2904.
- Karkalas, J. 1985. An improved enzymatic method for the determination of native and modified starch. *J. Sci. Food Agric.* 36:1019–1027.
- Marounek, M., S. Bartos, and P. Brezina. 1985. Factors influencing the production of volatile fatty acids from hemicellulose, pectin and starch by mixed culture of rumen microorganisms. *Z. Tierphysiol. Tierernähr. Futtermittelk.* 53:50–58.
- Oba, M., and M. S. Allen. 2003a. Effects of corn grain conservation method on ruminal digestion kinetics for lactating dairy cows at two dietary starch concentrations. *J. Dairy Sci.* 86:184–194.
- Oba, M., and M. S. Allen. 2003b. Effects of diet fermentability on efficiency of microbial nitrogen production in lactating dairy cows. *J. Dairy Sci.* 86:195–207.
- Owens, F. N., R. A. Zinn, and Y. K. Kim. 1986. Limits to starch digestion in the ruminant small intestine. *J. Anim. Sci.* 63:1634–1648.
- Robinson, P. H., C. J. Sniffen, and D. F. Smith. 1985. Development of a one-piece reentrant cannula for the proximal duodenum of dairy cows. *J. Dairy Sci.* 68:986–995.
- Russell, J. B., and D. B. Wilson. 1996. Why are ruminal cellulolytic bacteria unable to digest cellulose at low pH? *J. Dairy Sci.* 79:1503–1509.
- Strobel, H. J., and J. B. Russell. 1986. Effect of pH and energy spilling on bacterial protein synthesis by carbohydrate-limited cultures of mixed rumen bacteria. *J. Dairy Sci.* 69: 2941–2947.
- Voelker, J. A., and M. S. Allen. 2003a. Pelleted beet pulp substituted for high-moisture corn: 1. Effects on feed intake, chewing behavior, and milk production in lactating dairy cows. *J. Dairy Sci.* 86:3542–3552.
- Voelker, J. A., and M. S. Allen. 2003b. Pelleted beet pulp substituted for high-moisture corn: 3. Effects on ruminal fermentation, pH, and microbial protein efficiency in lactating dairy cows. *J. Dairy Sci.* 86:3562–3570.
- Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583–3597.
- Williams, C. H., D. J. David, and O. Iismaa. 1962. The determination of chromic oxide in feces samples by atomic absorption spectrophotometry. *J. Agric. Sci.* 59:381–385.