J. Dairy Sci. 102:5161–5171
https://doi.org/10.3168/jds.2018-15634

Diet starch concentration and starch fermentability affect energy intake and energy balance of cows in the early postpartum period

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ABSTRACT

Our objective was to evaluate the effects of diet starch concentration and fermentability on energy intake and energy balance during the early postpartum (PP) period. Fifty-two multiparous Holstein cows were used in a randomized block design experiment with a 2 × 2 factorial arrangement of treatments. Treatment rations were formulated to 22% or 28% starch concentration (LS and HS, respectively) with dry ground corn (DGC) or high moisture corn (HMC) as the primary starch source. Rations were formulated for 22% forage neutral detergent fiber (NDF) and 17% crude protein and fed from 1 to 23 d PP. Starch concentration was adjusted by altering concentrations of corn grain and soyhulls. Dry matter intake and milk yield were measured daily, and milk components, milk composition, body condition score (BCS), body weight (BW), and back fat thickness (BFT) were measured weekly. Feeds and refusals as well as fecal samples were collected, and digestibility was determined weekly. High moisture corn (HMC) decreased dry matter and net energy (NE_L) intakes compared with DGC more when included in an HS diet (3.9 kg/d and 3.2 Mcal/d) than in an LS diet (0.9 kg/d and 0.6 Mcal/d). The HMC treatment decreased NDF digestibility 3.7 percentage units compared with DGC when included in the HS diet but had little effect when included in an LS diet. Compared with DGC, HMC increased weekly BW and BFT loss when included in an HS diet (−34.7 vs. −8.4 kg/wk and −0.12 vs. −0.10 cm/wk) and decreased weekly BW loss but increased weekly BFT loss when included in an LS diet (−18.9 vs. −21.4 kg/wk and −0.11 vs. −0.02 cm/wk). Weekly BCS loss increased for HMC compared with DGC (−0.33 vs. −0.23 unit/wk). High moisture corn also decreased milk NE_L output compared with DGC (28.2 vs. 31 Mcal/d), but had little effect on energy balance, which was improved by HS compared with LS (−14.7 vs. −16.8 Mcal/d). Over time, concentrations of milk de novo fatty acids (<16 carbons) increased and concentration of milk preformed fatty acids (>16 carbons) decreased for all treatments, but yields of both sources as well as yield of mixed fatty acids (C16:0 plus C16:1 *cis*-9 and *iso*-C16:0) decreased over time with increased SF. Feeding HMC decreased energy intake and milk energy output, but it had little effect on energy balance during the early PP period.

Key words: postpartum period, starch concentration, fermentability, energy balance

INTRODUCTION

The early postpartum (**PP**) period is characterized by depressed feed intake and increased nutrient demand to sustain milk production and other bodily functions. Decreased energy intake and increased energy output results in negative energy balance, predisposing cows to health disorders and decreased performance. Increasing energy density of the diet by increasing the concentration of starch, which provides glucose and glucose precursors, is a strategy commonly used to increase energy intake in dairy cows. However, diet starch concentration (**SC**) and starch fermentability (**SF**) affect cow production and metabolism differently depending on stage of lactation (Oba and Allen, 2003a; Albornoz and Allen, 2018), and these effects are likely associated with cow's blood insulin concentration and insulin response to glucose (Bradford and Allen, 2007; Allen et al., 2009), degree of lipolysis (Piantoni et al., 2015), and rate of propionate production and absorption (Oba and Allen, 2003b; Maldini and Allen, 2018). We demonstrated that feeding a highly fermentable starch source (e.g., high moisture corn, **HMC**) depressed DMI and milk production compared with a starch source of moderate ruminal fermentability (e.g., dry ground corn, **DGC**) during the early PP period, and effects were exacerbated when included in a high starch (**HS**) diet with the same forage NDF (**fNDF**)

Received September 1, 2018.
Accepted February 17, 2019.
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concentration as a low starch (**LS**) diets (Albornoz and Allen, 2018). Likely, the more fermentable starch source increased propionate production and absorption, which can increase oxidation of fuels in the liver that triggers a satiety signal consistent with the hepatic oxidation theory (Allen et al., 2009).

Feeding HS diets was previously shown to increase concentrations of blood plasma glucose and insulin (Oba and Allen, 2003a; McCarthy et al., 2015b). However, the decrease in plasma insulin concentration and insulin sensitivity in adipose tissue during the peripartum period promotes lipolysis (Drackley, 1999), which can exacerbate hypophagic effects of propionate (Piantoni et al., 2015).

Increasing diet SC or SF can affect rumen microbial populations and rumen pH. Reduced ruminal pH can decrease fiber digestibility and increase production of *trans* fatty acid (**FA**) intermediates that could increase the risk for diet-induced milk fat depression (Jenkins et al., 2003; Lascano et al., 2016). The combined effect of diet SC and SF on energy intake and energy balance and the risk for milk fat depression during the early PP period have not been investigated.

Our objective was to evaluate the combined effects of diet SC and SF for cows in the early PP period on energy intake, energy balance, glucose metabolism, and milk FA composition. The starch treatments were corn grain harvested as high moisture (high ruminal fermentability) or dry (moderate ruminal fermentability). Starch concentration of diets was adjusted by altering concentrations of corn grain and soyhulls, keeping fNDF and the filling effect of diets constant. We hypothesized that rations with highly fermentable starch will decrease energy intake and affect metabolism involved in energy conservation by cows during the early PP period compared with rations with moderate starch fermentability, and effects will be greater for diets with greater starch concentration.

MATERIALS AND METHODS

Animal Care

This study was conducted from February 1 to November 15, 2015, at the Dairy Cattle Research and Teaching Center at Michigan State University, with all experimental procedures approved by the Michigan State University Institutional Animal Care and Use Committee (East Lansing, MI; AUF 11/13-254-00). Additional descriptions of experimental procedures and results have been included in our companion paper (Albornoz and Allen, 2018). Cows were housed individually in tiestalls, allowing for daily records of feed offered and refused, and fed once a day (0800 h) at 115% of expected intake and milked in a parlor twice a day (0400 and 1430 h). All cows were in apparent good health at the beginning of the experiment and standard farm health and reproductive protocols were maintained during this study. Signs for ketosis (e.g., depressed feed intake and milk yield and change in normal behavior) were monitored daily and diagnosis was aided with the use of a urine ketone test (Ketostix, Bayern Corp., Elkhart, IN). Confirmed cases were administered 300 mL of propylene glycol for 3 to 5 d.

Experimental Design and Treatments

Fifty-two multiparous Holstein cows were used in a completely randomized block design experiment with 2 × 2 factorial arrangement of treatments with 13 cows per treatment. Blocking criteria included BCS observed within 1 wk before expected calving date (up to 1-unit difference within block using a 5-point scale, where 1 = thin and 5 = fat; Wildman et al., 1982), previous lactation 305-d mature-equivalent milk production (up to 5,000-kg difference within block) and calving date (up to 60 d within block). A common close-up diet was fed from 21 d before expected calving date until calving. This diet contained corn silage, mature grass hay, dry ground corn, soybean meal, SoyChlor (West Central Soy, Ralston, IA), and a mineral and vitamin mix, and it was formulated to contain 42.5% NDF, 38.3% fNDF, 21.5% starch, and 13.5% CP.

Treatments included diet SC (22%, LS; 28%, HS) and diet SF (DGC or HMC). At calving, cows within each block were randomly assigned to 1 of the 4 diet treatment combinations (LS-DGC, LS-HMC, HS-DGC, HS-HMC). Dry ground corn grain was stored in a covered gravity wagon and HMC was ground and ensiled in a bag (Ag-Bag Plastic, Cottage Grove, MN) for at least 4 mo after harvest before utilization. Differences in SF were confirmed by 7-h in vitro starch digestibility analysis (Goering and Van Soest, 1970) before and throughout the experiment (44.1 and 61.9% for DGC and HMC, respectively; Albornoz and Allen, 2018). Starch concentration of treatment diets was adjusted by partially replacing the main starch source with soyhulls to maintain the same fNDF concentration across treatment diets. Treatment diets contained alfalfa silage, grass hay, corn grain treatments, soyhulls, soybean meal, minerals, and vitamins and were formulated to 17% CP and 22% fNDF. Cows received their respective diets beginning at day of calving if they calved before feeding time (0800 h) or at the following morning's feeding until 23 d PP. Dry matter concentration of fermented feeds was determined twice per week throughout the experiment and diets were adjusted accordingly. All rations were formulated to meet or

Table 1. Ingredient and nutrient composition of treatment diets[1]

Item	LS		HS	
	DGC	HMC	DGC	HMC
Ingredient, % of DM				
Alfalfa silage	37.0	37.1	37.7	37.0
Grass hay	8.25	8.35	8.35	8.21
DGC	27.5	—	35.4	—
HMC	—	28.1	—	36.2
Soyhulls	11.0	11.0	1.87	2.18
Soybean meal	11.7	11.1	12.2	12.4
Mineral-vitamin mix[2]	2.02	2.02	2.02	2.02
Limestone	0.55	0.55	0.55	0.55
Sodium bicarbonate	0.95	0.95	0.95	0.95
Dicalcium phosphate	0.95	0.95	0.95	0.95
Nutrient composition, % of DM				
DM	58.4	55.2	59.2	53.1
OM	89.5	89.4	89.8	89.6
NDF	33.0	33.0	28.3	27.6
Forage NDF	22.4	22.8	22.6	22.2
CP	17.2	16.7	17.3	16.9
Starch	21.4	21.9	27.1	27.8
Ash	10.5	10.5	10.2	10.3
Gross energy, Mcal/kg	4.21	4.21	4.25	4.25

[1]LS = low starch (22% starch); HS = high starch (28% starch); DGC = dry ground corn, HMC = high moisture corn.

[2]On a DM basis, mineral-vitamin mix contained 25.6% NaCl, 10.0% Ca, 2.0% Mg, 2.0% P, 30 mg/kg of Co, 506 mg/kg of Cu, 20 mg/kg of I, 2,220 mg/kg of Fe, 2,080 mg/kg of Mn, 15 mg/kg of Se, 2,030 mg/kg of Zn, 300 kIU/kg of vitamin A, 50 kIU/kg of vitamin D, and 1,500 kIU/kg of vitamin E.

exceed the cows' predicted requirements for protein, minerals, and vitamins according to NRC (2001), and ingredient and nutrient composition of treatment diets is reported in Table 1.

Data and Sample Collection

Feed offered, orts, and milk yield were recorded on a daily basis throughout the experiment. Samples and measurements were collected or recorded on the same day of the week ± 3 d relative to expected calving date prepartum or relative to day of calving during the PP period. Back fat thickness (**BFT**), BCS, BW, feed ingredients, fecal samples, and PM milk samples were collected on the same day of the week (5, 12, 19 d PP), with a.m. milk, fecal, and orts samples collected the following morning. Also, an additional measurement of BFT was performed within a week before calving and BCS and BW were determined at calving to determine the change in those variables during the first week PP. A glucose tolerance test (**GTT**) was performed on d 14 PP according to Bradford and Allen (2007).

Representative samples (0.5 kg) of feed ingredients and orts from each cow were collected weekly throughout the experiment and stored at −20°C for later analysis of DM and nutrient composition. Fecal samples (0.5 kg) were collected from the rectum every 8 h of a 24-h period to account for diurnal variation. Feces were stored in sealed plastic cups at −20°C until dried. Milk samples were collected weekly at each milking and stored with preservative (Bronopol, D&F Control Systems, San Ramos, CA) at 4°C for component and SCC analysis (Universal Lab Services, East Lansing, MI). An additional milk sample was collected without preservative and stored at −20°C for milk FA analysis. Body condition was scored by 3 trained investigators on a 5-point scale, as described by Wildman et al. (1982). Subcutaneous cross-section measurements of BFT were performed on the right side of the cow between the 12th and 13th rib by ultrasonography (Aloka SSD-500V monitor and UST-5044 3.5-MHz probe, Aloka Co. Ltd., Tokyo, Japan). Back fat thickness was determined by performing an average of 2 measurements that were within 0.1 cm difference.

Sample Analysis

Feed ingredients, orts, and fecal samples were dried in a 55°C forced-air oven for 72 h, analyzed for DM concentration, and ground with a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA). Fecal samples were composited by cow by day on an equal DM basis before analysis. All feed ingredients, orts, and fecal composites for each cow were analyzed by week for DM, ash, NDF, CP, starch, and gross energy concentration. Nutrients were expressed as percentages of

DM, determined by drying at 105°C in a forced-air oven for more than 8 h. Ash concentration was determined after 5 h of oxidation at 500°C in a muffle furnace. Concentration of NDF was determined according to Mertens (2002) and CP was determined according to Hach et al. (1987). The NDF residue after 240 h of in vitro fermentation (indigestible NDF; Goering and Van Soest, 1970) was used as an internal marker to estimate fecal output and nutrient digestibility (Cochran et al., 1986). Flasks for incubation contained rumen fluid from a nonpregnant dry cow fed dry hay only and were reinoculated at 120 h to ensure a viable microbial population. Gross energy was determined by bomb calorimetry according to manufacturer's instructions (Parr Instrument Inc., Moline, IL). Starch was measured by gelatinization with sodium hydroxide and subsequent hydrolysis to glucose using an enzymatic method (Karkalas, 1985). Glucose was then measured with a glucose oxidase method (PGO Enzyme Product No. P7119; Sigma Chemical Co., St. Louis, MO) and by determination of absorbance with a microplate reader (SpectraMax 190; Molecular Devices Corp., Sunnyvale, CA).

Intakes of DE and ME were calculated according to NRC (2001):

$$\text{DE intake} = \text{gross energy intake (Mcal/d)} \times \text{gross energy digestibility},$$

$$\text{ME intake} = [1.01 \times (\text{DE} - 0.45)] \times \text{DMI (kg/d)},$$

$$\text{NE}_\text{L} \text{ intake} = [(0.703 \times \text{ME}) - 0.19] \times \text{DMI (kg/d)}.$$

Energy balance was determined according to NRC (2001):

$$\text{NE}_\text{L} \text{ balance (Mcal/d)} = \text{NE}_\text{L} \text{ intake (Mcal/d)} - \text{NE maintenance (Mcal/d)} - \text{NE}_\text{L} \text{ (Mcal/d)},$$

where NE_L intake was calculated from DE through ME according to NRC (2001); NE maintenance (Mcal/d) = 0.08 Mcal/kg × BW $(\text{kg})^{0.75}$ (NRC, 2001); and NE_L (Mcal/d) = milk yield (kg/d) × [(fat % × 0.0929) + (true protein % × 0.0563) + (lactose % × 0.0395)] (NRC, 2001).

Milk samples were analyzed for fat, true protein, and lactose by mid-infrared spectroscopy (AOAC International, 1997) by the Michigan Herd Improvement Association (Universal Lab Services). Additional PM and AM milk samples for FA analysis were composited by milk yield for each collection day for each cow. Fat cakes from composites were obtained by centrifugation at 1,300 × *g* for 20 min at 4°C before freezing. Fatty acid profile was determined as described by Rico and Harvatine (2013) with slight modifications. Briefly, lipid extraction was performed according to Hara and Radin (1978) using hexane–isopropanol. Fatty acid methyl esters were prepared by base-catalyzed transmethylation according to Chouinard et al. (1999). Fatty acid methyl esters were quantified by GC using an Agilent 6890A gas chromatograph (Agilent Technologies, Palo Alto, CA) equipped with a fused-silica capillary column (SP-2560, 100 m × 0.25 mm i.d. with 0.2-μm film thickness; Supelco Inc., Bellefonte, PA) and a flame-ionization detector with hydrogen as the carrier gas. Initial oven temperature was 80°C, which was increased by 2°C/min to 190°C and held for 15 min. Inlet and detector temperatures were 250°C with a 100:1 split ratio. Constant gas flows were 1 mL/min for hydrogen carrier, 25 mL/min for detector hydrogen, 400 mL/min for detector airflow, and 40 mL/min for detector nitrogen plus carrier. Fatty acid peaks were identified using FAME standards (GLC 461, GLC 780, and pure CLA *trans*-10,*cis*-12 and CLA *cis*-9,*trans*-11, NuChek Prep Inc., Elysian, MN; Bacterial Acid Methyl Ester Mix, 47080-U, Sigma-Aldrich; and GLC 110 mixture, Matreya LLC, State College, PA). Recovery of individual FA were determined using an equal weight reference standard (GLC 461; NuChek Prep Inc.). Correction factors for individual FA and calculation of milk FA yield were carried out as described by Rico and Harvatine (2013).

Plasma samples from GTT were analyzed for glucose using a glucose oxidase method (PGO Enzyme Product No. P7119; Sigma Chemical Co.) and insulin with a commercial kit (Coat-A-Count RIA kit; Siemens Healthcare Diagnostics, Deerfield, IL). Area under the curve for glucose and insulin was calculated using the trapezoidal rule.

Statistical Analysis

All data were analyzed using the Fit Model procedure of JMP Pro (version 13, SAS Institute, Cary, NC) according to the following model:

$$Y_{ijosf} = \mu + B_i + C(B_i)_j + J + O_o + S_s + F_f + S_sF_f + T + S_sT + F_fT + S_sF_fT + e_{ijosf},$$

where Y_{ijosf} = response variable; μ = overall mean; B_i = random effect of block (i = 1 to 13); $C(B_i)_j$ = random effect of cow (j = 1 to 4) within block; J = random effect of Julian date; O_o = days offset from fixed weekly sampling day (o = −3 to +3); S_s = fixed effect of SC (s = 1 to 2); F_f = fixed effect of SF (f = 1 to 2); S_sF_f

= interaction between SC and SF; T = fixed effect of sampling day PP; S_sT = interaction between SC and day PP; F_fT = interaction between SF and day PP; S_sF_fT = interaction between SC, SF, and day PP; and e_{ijosf} = residual error.

Day PP was included in the model as continuous measure and linear and quadratic interactions between main effects and sampling day PP were evaluated. Interactions with time were removed from the model for GTT data analysis, and when they were nonsignificant, a reduced model was used to determine treatment effects. However, all interactions were included in the tables for informational purposes. Normality of the residuals was checked with normal probability and box plots and homogeneity of variances with plots of residuals versus predicted values. Goodness of normal fit was also tested with Shapiro-Wilk. Because of storage issues with milk samples for FA analysis for the first 3 blocks (12 cows), this analysis was performed on the subsequent 10 blocks (40 cows). All cows were included for the analysis of all other variables. Treatment effects were declared significant at $P < 0.05$ and tendencies at $P < 0.10$. Interactions were declared significant at $P < 0.10$ and tendencies at $P < 0.15$.

RESULTS

Digestibility and Energy Balance

Dry matter, NDF, CP, and starch intakes increased over time for both starch sources, but more for DGC compared with HMC throughout the treatment period ($P = 0.12$, $P = 0.02$, $P = 0.03$, and $P = 0.04$, linear, respectively; Table 2). The LS diets decreased starch intake (1.1 kg/d) and increased NDF intake (0.88 kg/d) compared with HS diets ($P < 0.01$). The HMC treatment decreased daily intake of DM, NDF, CP, and starch compared with DGC ($P < 0.02$ for all), but the decrease was greater when included in the HS (3.9, 1.06, 0.65, and 0.89 kg/d, respectively) than the LS diet (0.9, 0.20, 0.18, and 0.15 kg/d; interaction, $P = 0.07$, $P = 0.11$, $P = 0.12$, and $P = 0.10$, respectively).

The HS treatment increased total-tract digestibility of DM, OM, and gross energy by 2.5, 2.3, and 2.4 percentage units compared with LS, respectively ($P < 0.01$; Table 2). The HMC treatment decreased NDF digestibility by 3.7 percentage units compared with DGC when included in the HS diet but had little effect when included in the LS diet (interaction $P = 0.10$).

Table 2. Effects of diet starch concentration (SC) and starch fermentability (SF) on DMI, body reserves, apparent total-tract digestibility, and energy balance[1]

	LS		HS			*P*-value[2]					
Variable	DGC	HMC	DGC	HMC	SEM	SC	SF	SC × SF	SC × time	SF × time	SC × SF × time
Intake, kg/d											
DM	18.6	17.7	20.2	16.3	0.80	0.96	<0.01	0.07	0.97	0.12^{L}	0.84
NDF	5.98	5.78	5.53	4.48	0.28	<0.01	0.02	0.11	0.80	0.02^{L}	0.98
CP	3.19	3.00	3.44	2.79	0.16	0.90	0.01	0.12	0.95	0.03^{L}	0.94
Starch	4.02	3.86	5.46	4.57	0.22	<0.01	0.02	0.10	0.18	0.04^{L}	0.90
Body reserves											
BCS change,[3] unit/wk	−0.25	−0.30	−0.20	−0.36	0.06	0.91	0.08	0.33	0.88	0.06^{Q}	0.14^{Q}
BW change, kg/wk	−21.4	−18.9	−8.37	−34.7	4.80	0.77	0.02	<0.01	0.80	0.04^{L,Q}	<0.01^{L,Q}
BFT change,[4] cm/wk	−0.02	−0.11	−0.10	−0.12	0.03	0.14	0.14	0.03	0.01^{Q}	0.51	0.49
Total-tract digestibility, %											
DM	61.5	61.7	63.4	64.8	0.71	<0.01	0.27	0.43	0.79	0.91	0.61
OM	63.0	64.0	65.2	66.4	0.73	<0.01	0.16	0.86	0.63	0.98	0.79
Gross energy	60.5	61.7	62.9	64.0	0.77	<0.01	0.12	0.96	0.73	0.89	0.93
NDF	38.9	39.6	36.2	32.5	1.33	<0.01	0.25	0.10	0.56	0.86	0.90
CP	63.2	64.5	64.3	66.1	1.42	0.32	0.27	0.89	0.79	0.79	0.86
Starch	95.0	96.6	95.0	97.4	0.62	0.34	<0.01	0.35	0.35	0.82	0.75
Energy intake, Mcal/d											
Digestible energy	47.5	45.9	53.3	44.6	1.88	0.22	0.01	0.06	0.71	0.45	0.15^{L}
ME	39.4	38.4	44.7	37.7	1.57	0.14	0.01	0.06	0.67	0.52	0.12^{L}
NE_L	24.2	23.6	27.6	23.4	0.95	0.09	0.01	0.06	0.64	0.56	0.12^{L}
Production, Mcal/d											
Maintenance NE	10.9	10.9	11.1	10.7	0.09	0.97	0.01	0.05	0.89	0.08^{Q}	0.01^{L,Q}
Milk NE_L	30.7	29.1	31.3	27.5	1.30	0.65	0.02	0.32	0.86	0.01^{L}	0.78
Energy balance, Mcal/d	−17.2	−16.4	−14.4	−15.1	1.03	0.05	0.93	0.44	0.56	0.01^{L}	1.00

[1]LS = low starch (22% starch); HS = high starch (28% starch); DGC = dry ground corn; HMC = high moisture corn.

[2]Time = day postpartum. Polynomial interactions are identified with superscripts: L = linear and Q = quadratic.

[3]Change represents the difference between final and initial measurement at each week postpartum.

[4]BFT= back fat thickness.

High moisture corn increased starch digestibility 2.0 percentage units compared with DGC ($P < 0.01$) but digestibility of CP was not affected by treatment.

Intakes of DE, ME, and NE_L all tended to increase over time, but the rate of increase was less for LS-HMC than the other treatments (interactions; $P = 0.15$, $P = 0.12$, and $P = 0.12$, all linear, respectively; Figure 1A). The HMC treatment decreased DE, ME, and NE_L intakes compared with DGC ($P < 0.01$ for all), and the decrease was greater when included in the HS diet (8.7, 7.0, and 4.2 Mcal/d, respectively) than the LS diet (1.6, 1.0, and 0.6 Mcal/d, respectively; all interactions $P = 0.06$). The HMC treatment decreased the energy required for maintenance compared with DGC in the HS diet (10.7 vs. 11.1 Mcal/d), but did not differ between SF treatments when included in the LS diet (10.9 Mcal/d; interaction $P = 0.05$). Over time, all treatments decreased energy required for maintenance following change in BW, but HS-HMC had a more pronounced decrease during the second week PP compared with the rest of the treatments ($P = 0.01$, quadratic). Milk energy output increased over time for DGC but decreased for HMC ($P = 0.01$, linear; Figure 1B), and HMC decreased milk energy output 2.7 Mcal/d compared with DGC over the treatment period. Energy balance was negative for all treatments during the treatment period, but HS improved energy balance compared with LS (−14.7 vs. −16.8, $P = 0.05$), and HMC decreased energy balance during the first week PP and increased thereafter compared with DGC ($P = 0.01$, linear; Figure 1C).

Body Reserves

Body condition score decreased over each week, but the pattern of loss varied by treatment, with a greater loss for the HS-HMC and smaller loss for the HS-DGC treatments compared with the other treatments until the second week PP and then smaller loss for the HS-HMC and greater loss for HS-DGC compared with the other treatments for the remainder of the treatment period ($P = 0.14$, quadratic, Table 2). Overall, HMC tended to increase weekly BCS loss compared with DGC ($P = 0.08$), with both treatments reaching similar values by the third week PP ($P = 0.06$, quadratic). Body weight also decreased each week through the treatment period, with patterns among treatments over time similar to those for BCS. The HS-HMC treatment combination increased and HS-DGC decreased BW loss compared with the other treatments until wk 2, but HS-HMC decreased and HS-DGC increased BW loss compared with the other treatments for the remainder of the treatment period ($P < 0.01$, quadratic). Over the treatment period, HMC increased BW loss com-

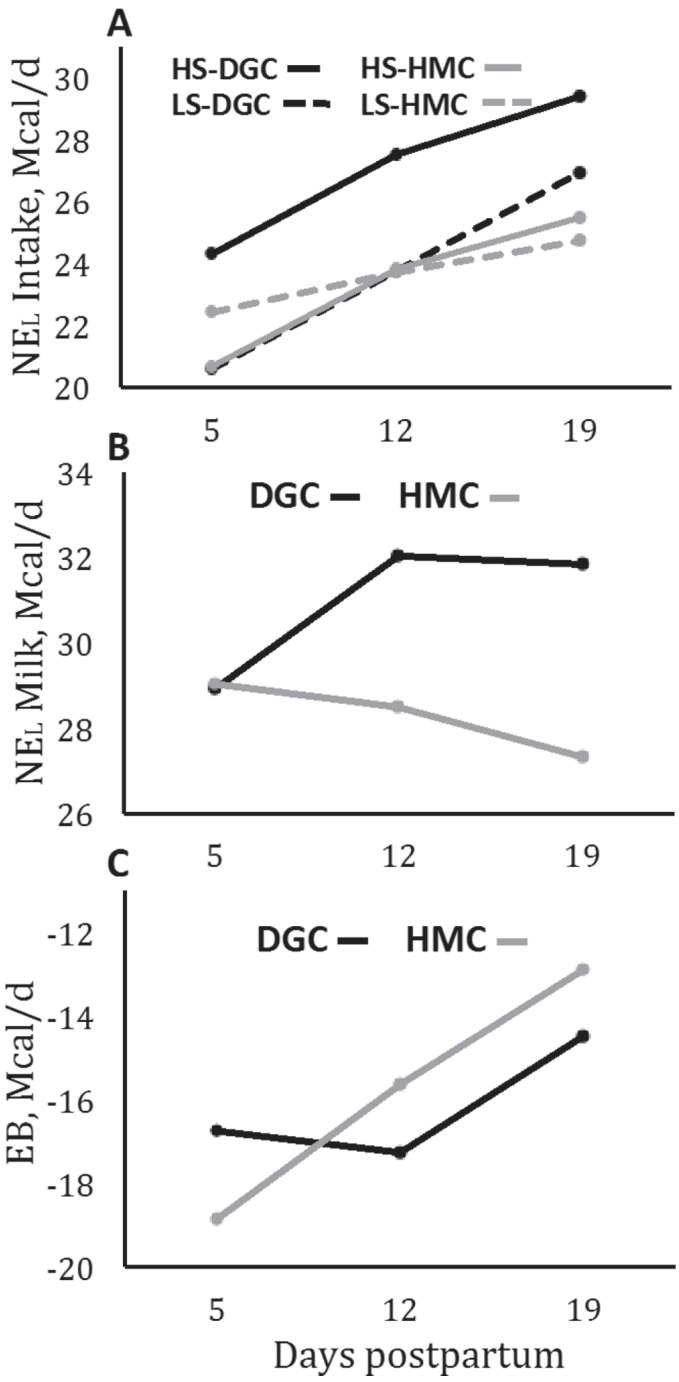

Figure 1. Effects of diet starch concentration (SC) and fermentability (SF) on (A) NE_L intake and effects of diet SF on (B) milk NE_L and (C) energy balance (EB). For (A), treatments are 28% starch with dry ground corn (HS-DGC), 22% starch with dry ground corn (LS-DGC), 28% starch with high moisture corn (HS-HMC), and 22% starch with high moisture corn (LS-HMC). For (B) and (C), treatments are dry ground corn (DGC) and high moisture corn (HMC). Interactions among SC, SF, and day postpartum are represented for NE_L intake ($P = 0.12$, linear) and interactions between SF and day postpartum for (B) milk NE_L ($P = 0.01$, linear) and (C) EB ($P = 0.01$, linear).

pared with DGC for HS (−34.7 vs. −8.4 kg/wk) but decreased BW loss compared with DGC for LS (−18.9 vs. −21.4 kg/wk; $P < 0.01$), with the greatest difference at the second week ($P = 0.04$, quadratic). Back fat thickness decreased for all treatments during the treatment period but HMC increased BFT loss more compared with DGC for LS (−0.11 vs. −0.02 cm/wk) than HS (−0.12 vs. −0.10; $P = 0.03$; Table 2) and HS increased loss more during the second week PP, with similar loss rate during the first and third week PP compared with LS treatments ($P = 0.01$, quadratic).

Glucose Tolerance Test

Starch concentration and SF interacted to affect baseline (pre-glucose infusion) glucose concentration, with HMC increasing glucose concentration compared with DGC for HS (47.7 vs. 42.1 mg/dL) and decreasing glucose concentration for LS (40.7 vs. 44.2 mg/dL, $P = 0.02$; Table 3). However, treatment did not affect maximum glucose concentrations or time required to reach it. The HMC treatment tended to increase the rate of increase in glucose concentration from 10.2 to 11.0 mg/dL per minute ($P = 0.09$) compared with DGC but the amount of time required to achieve baseline glucose concentrations post infusion and the area under the curve were not different between treatments.

High starch diets increased baseline insulin concentration compared with LS diets (3.59 vs. 2.22 μIU/mL, $P = 0.01$), but treatment did not affect maximum insulin concentration, time required to reach it, or rate of increase in insulin concentration. The HS treatment reduced the amount of time required to reach baseline insulin concentrations post infusion (88.5 vs. 98.7 min, $P = 0.03$), but area under the curve did not differ among treatments.

Milk Fatty Acids

Treatments had no main effects on FA concentrations, but they interacted with each other and time for concentrations of certain individual FA and total de novo, mixed, or preformed milk FA (Table 4). The proportions of mixed FA were not affected by treatments, but treatments interacted with time to affect proportion of de novo FA, which increased over time ($P = 0.02$, linear), and proportion of preformed FA, which decreased over time ($P = 0.10$, linear; Table 4; Supplemental Figure S1; https://doi.org/10.3168/jds.2018-15634). Overall, SC and SF interacted to affect concentration of C14:1 *cis*-9 and C18:1 *cis*-11, with HMC decreasing their concentrations for LS (0.55 vs. 0.65% and 1.06 vs. 1.10%) but increasing their concentrations for HS (0.71 vs. 0.62% and 1.18 vs. 1.03%; $P = 0.03$ and $P = 0.08$, respectively). Over time, concentration of C14:1 *cis*-9 and C18:1 *cis*-11 were higher for LS-DGC and HS-HMC compared with LS-HMC and HS-DGC, with the greatest difference in concentration observed during wk 2 PP, with less difference among treatments by the third week PP ($P = 0.05$, quadratic and $P = 0.06$, linear, respectively). Treatments interacted to affect concentrations of *iso*-C16:0, C18:1 *trans*-11, and C18:0, with HMC increasing their concentrations for LS (0.21 vs. 0.18%, 0.76 vs. 0.65%, and 13 vs. 11.9%) but decreasing their concentrations for HS (0.18 vs. 0.21%, 0.68 vs. 0.76%, and 11.7 vs. 12.5%; $P = 0.10$, $P = 0.03$, and $P = 0.02$, respectively). Treatments also interacted with time to affect concentration of *iso*-C16:0

Table 3. Effects of diet starch concentration (SC) and starch fermentability (SF) on response to glucose tolerance test[1]

	LS		HS			*P*-value		
Variable	DGC	HMC	DGC	HMC	SEM	SC	SF	SC × SF
Glucose								
Baseline, mg/dL	44.2	40.7	42.1	47.7	2.19	0.20	0.59	0.02
Maximum, mg/dL	151	151	148	158	4.40	0.64	0.28	0.25
Time to maximum, min	10.8	10.0	11.5	10.0	0.86	0.66	0.19	0.66
Rate, mg/dL × min	10.4	11.0	9.92	11.0	0.48	0.69	0.09	0.65
Time to baseline, min	91.5	83.1	78.5	74.6	6.64	0.12	0.36	0.73
AUC,[2] mg/dL × min	4,388	4,279	4,225	3,688	271	0.19	0.26	0.45
Insulin								
Baseline, μIU/mL	2.34	2.10	3.73	3.45	0.59	0.01	0.61	0.98
Maximum, μIU/mL	61.5	65.1	69.7	72.5	6.23	0.21	0.61	0.95
Time to maximum, min	13.8	12.5	13.1	15.4	1.36	0.46	0.73	0.21
Rate, μIU/mL × min	4.72	5.52	5.68	4.87	0.64	0.82	1.00	0.23
Time to baseline, min	99.2	98.1	89.2	87.7	4.87	0.03	0.77	0.96
AUC, μIU/mL × min	2,289	2,407	2,353	2,435	235	0.84	0.66	0.94

[1]LS = low starch (22% starch); HS = high starch (28% starch); DGC = dry ground corn; HMC = high moisture corn.
[2]AUC = area under the curve, calculated with the trapezoidal rule.

Table 4. Effects of diet starch concentration (SC) and starch fermentability (SF) on profile and yield of milk fatty acids (FA)[1]

	LS		HS			*P*-value[2]					
Variable	DGC	HMC	DGC	HMC	SEM	SC	SF	SC × SF	SC × time	SF × time	SC × SF × time
Profile,[3] %											
De novo[4]	19.9	18.0	20.2	18.3	1.26	0.82	0.18	1.00	0.43	0.42	0.02^{L}
Mixed[4]	27.4	28.0	27.3	27.7	0.41	0.62	0.20	0.76	0.71	0.67	0.72
Preformed[4]	49.5	51.1	49.7	50.9	1.93	0.97	0.30	0.87	0.21	0.64	0.10^{L}
C14:1 *cis*-9	0.65	0.55	0.62	0.71	0.04	0.12	0.93	0.03	0.07^{L}	0.09^{L}	0.05^{Q}
iso-C16:0	0.18	0.21	0.21	0.18	0.01	1.00	0.94	0.10	0.41	0.01^{L}	0.06^{Q}
C18:1 *trans*-11	0.65	0.76	0.76	0.68	0.04	0.70	0.71	0.03	0.54	0.15^{Q}	0.10^{L}
C18:1 *cis*-11	1.10	1.06	1.03	1.18	0.05	0.63	0.33	0.08	0.45	0.42	0.06^{L}
C18:0	11.9	13.0	12.5	11.7	0.39	0.37	0.72	0.02	0.80	0.55	0.03^{Q}
C18:1 *trans* (total)	2.16	2.25	2.19	2.24	0.09	0.92	0.48	0.84	0.15^{L}	0.05^{L}	0.05^{L,Q}
Yield,[3] g/d											
De novo[4]	341	296	373	282	28.0	0.77	0.01	0.35	0.32	0.04^{L}	0.09^{L}
Mixed[4]	462	437	487	426	27.2	0.83	0.06	0.42	0.15^{Q}	0.08^{L}	0.47
Preformed[4]	850	799	879	772	50.2	0.99	0.07	0.52	0.15^{Q}	0.10^{L}	0.65
C14:1 *cis*-9	11.6	8.8	10.9	11.4	1.22	0.35	0.24	0.10	0.74	<0.01^{L}	0.25
iso-C16:0	3.23	3.25	3.78	2.67	0.33	0.96	0.08	0.07	0.87	<0.01^{L}	0.24
C18:1 *trans*-11	11.4	11.9	13.5	10.4	1.06	0.73	0.18	0.06	0.67	0.07^{L}	0.75
C18:1 *cis*-11	19.5	16.8	18.1	18.1	1.41	0.97	0.36	0.36	0.78	0.02^{L}	0.71
C18:0	211	204	224	178	13.5	0.61	0.05	0.14	0.42	0.01^{L}	0.71
C18:1 *trans* (total)	38.2	35.4	38.9	33.2	3.44	0.83	0.21	0.67	0.89	0.08^{L}	0.86

[1]LS = low starch (22% starch); HS = high starch (28% starch); DGC = dry ground corn; HMC = high moisture corn.

[2]Time = day postpartum. Polynomial interactions are identified with superscripts: L = linear and Q = quadratic.

[3]Approximately 64 individual FA were quantified and used for calculations (summation by source).

[4]De novo FA originate from mammary de novo synthesis (<16 carbons), preformed FA originate from extraction from plasma (>16 carbons), and mixed FA originate from both sources (C16:0 plus C16:1 *cis*-9 and *iso*-C16:0).

and C18:1 *trans*-11, which were higher for LS-DGC and HS-HMC compared with LS-HMC and HS-DGC, with less difference among treatments by the third week PP ($P = 0.06$, quadratic and $P = 0.10$, linear, respectively). Over time, concentration of C18:0 decreased for all treatments, with a greater reduction in concentration by wk 2 PP for LS-DGC and HS-HMC compared with LS-HMC and HS-DGC, with all treatments reaching similar concentration values by the third week ($P = 0.03$, quadratic). Treatments did not affect total concentration of C18:1 *trans* FA, but its concentration increased for all treatments and decreased for LS-HMC after the second week PP ($P = 0.05$, quadratic).

Milk fat yield was decreased by HMC compared with DGC (190 g/d) and linearly increased over time for DGC and decreased for HMC (Albornoz and Allen, 2018). Accordingly, compared with DGC, HMC decreased yields of de novo FA (137 g/d; $P = 0.01$) and tended to decrease yields of mixed and preformed FA (86 and 158 g/d; $P = 0.06$ and $P = 0.07$, respectively), with yields of all sources being greater for DGC compared with HMC after the first week PP ($P = 0.09$, linear, $P = 0.08$, linear, and $P = 0.10$, linear, respectively; Table 4; Supplemental Figure S2; https://doi.org/10.3168/jds.2018-15634). Similarly, yields of individual FA and total C18:1 *trans* FA increased for DGC and decreased for HMC after the first week PP (all $P < 0.08$, linear). However, SC and SF interacted to decrease yield of C14:1 *cis*-9 for LS-HMC and HS-DGC (8.8 and 10.9 g/d) and increase for LS-DGC and HS-HMC (11.6 and 11.4 g/d, respectively; $P = 0.10$). Overall, treatments also interacted to affect yields of *iso*-C16:0, C18:1 *trans*-11, and C18:0, with HMC decreasing their yields for HS compared with DGC (2.67 vs. 3.78 g/d, 10.4 vs. 13.5 g/d, and 178 vs. 224 g/d) and little difference between HMC and DGC for LS (3.25 vs.3.23 g/d, 11.9 vs. 11.4 g/d, and 204 vs. 211 g/d; $P = 0.07$, $P = 0.06$, and $P = 0.14$, respectively). Additional milk FA concentrations and yields are listed as supplemental material in Supplemental Tables S1 and S2 (https://doi.org/10.3168/jds.2018-15634), respectively.

DISCUSSION

Feeding the highly fermentable starch source HMC depressed DMI compared with DGC, and to a greater extent when included in the HS diet. Intakes of both NDF and starch followed DMI as well as diet composition for the SC treatment, whereas CP intake followed the same trend as DMI. Hypophagic effects of highly fermentable starch sources are likely related to the increased supply of propionate to the liver, which are greater for cows in a lipolytic state, and are consistent with the hepatic oxidation theory (Allen, 2000).

The HS treatment increased total-tract digestibilities of DM, OM, and gross energy, but decreased NDF digestibility, with a greater decrease for HS-HMC compared with HS-DGC. In contrast, Oba and Allen (2003c) reported no effects of treatment on total-tract NDF digestibility when cows past peak lactation received HS (32%) or LS (21%) diets containing either HMC or DGC. Lower NDF intake by cows in the early PP period compared with early to mid-lactation likely reduces rumen digesta mass and the buffering capacity of the rumen contents (Allen and Piantoni, 2014). Lower NDF intake and higher ruminal starch fermentability for HS-HMC compared with HS-DGC likely diminished ruminal buffering capacity and increased acid production, reducing ruminal pH and NDF digestibility.

Total-tract starch digestibility was similar for LS and HS treatments but greater for HMC compared with DGC. In contrast, in the study by Oba and Allen (2003c), total-tract starch digestibility was affected differently; SF had no effect, whereas HS increased total-tract starch digestibility compared with LS. However, in that study SC was adjusted by inclusion of fNDF, whereas in the present study fNDF was constant across treatments. Interactions among carbohydrate sources in the rumen likely alter ruminal starch digestibility and ultimately affect total-tract starch digestibility.

Intakes of DE, ME, and NE_L followed the same trends as DMI. Rabelo et al. (2003) reported that cows receiving an HS diet (47.2% NFC) increased DM and energy intake compared with cows receiving an LS diet (41.1% NFC) during the first 20 d PP. The starch source in that experiment was dry ground corn and the effect of SC on energy intake was similar to the DGC treatment but not the HMC treatment in the present experiment. Increasing SC from 22 to 28% did not increase intakes of DM or energy in our experiment despite the increase in DM digestibility with the HS compared with the LS treatment. Greater BW loss by HS-HMC, particularly during the second week PP, was likely from a combination of decreased DMI and depletion of body reserves as assessed by BCS and BFT measurements, and resulted in lower energy required for maintenance compared with the other treatments. These findings emphasize the importance of the contribution of DMI compared with DM digestibility to maximize energy intake during the early PP period.

The HMC treatments reduced yields of milk, 3.5% FCM, and ECM (Albornoz and Allen, 2018), resulting in lower milk energy output compared with DGC, particularly during the second and third week PP, which improved energy balance similarly over time. Although HMC decreased DMI compared with DGC, it did not affect energy balance because it also decreased milk energy output. In addition, the increase in BW loss by HMC, likely from decreased gut fill as well as greater mobilization of body reserves, reduced energy required for maintenance compared with DGC. This effect was more pronounced when included in HS, contributing to a reduction in differences in energy balance between SF treatments. This finding suggests that estimation of energy required for maintenance using the NRC (2001) equation may not reflect the actual shift in energy required to maintain BW by cows during the early PP period. Also, the above-mentioned equation was developed using nonpregnant, nonlactating dairy cows, which likely have different maintenance requirements compared with cows during the early PP period that may require additional energy adjustment for other bodily functions (e.g., recovery of reproductive tract, activated immune system, and growth of gut and splanchnic tissue). Over the whole treatment period, the HS treatment improved energy balance compared with LS overall consistent with the study by McCarthy et al. (2015a), who reported that an HS (25.5%) diet improved energy balance 5.1 Mcal/d compared with an LS (20.9%) diet during the early PP period but had no effect on DMI, yields of milk, or 3.5% FCM and caused no change in BW or BCS. These and our results suggest that when SC is increased, energy balance is likely improved, but when feed intake is depressed by highly fermentable starch, decreased milk energy output is the primary mechanism involved in conserving energy.

Over time, HS diets increased glucose and insulin concentrations, with LS diets reaching similar values as HS treatments by the third week PP (Albornoz and Allen, 2018). Similarly, at the time of the GTT (second week PP), HS increased baseline (pre-glucose infusion) plasma insulin concentration compared with LS. In accordance with our findings for DMI, Bradford and Allen (2007) reported that hypophagic effects from HMC were exacerbated for cows with higher mean plasma insulin concentration, possibly because downregulated gluconeogenesis stimulated hepatic oxidation of fuels sooner. Whereas higher insulin concentration is expected to decrease lipolysis and increase lipogenesis in adipose tissue (Bauman, 2000), the opposite was observed for HS-HMC, which increased mobilization of body reserves. In addition, increased mean insulin concentration is expected to clear fuels from the blood faster, but at the time of the GTT, baseline (pre-glucose infusion) plasma glucose concentration increased for HMC compared with DGC when included in an HS diet and decreased for HMC compared with DGC when included in an LS diet. Reasons for this finding are not clear, but the opposite interaction was detected for BHB concentration (Albornoz and Allen, 2018), indicating

differences in metabolism of fuels between treatments. Following the glucose infusion, HMC had higher rate of increase in glucose concentration compared with DGC, which could be related to a reduced capacity for glucose uptake by tissues in cows that received HMC. Cows during the early PP period have reduced insulin sensitivity (Bell, 1995), and further research to elucidate how SC and SF affect insulin response to glucose and glucose precursors is needed.

Treatments had opposite effects on proportions of milk de novo and preformed FA, but yields of both FA sources as well as mixed FA decreased with greater SF, following the same trend as milk fat yield (Albornoz and Allen, 2018). Higher SF can affect FA biohydrogenation pathways in the rumen and increase synthesis of certain C18:1 isomers considered risk factors for milk fat depression (Mohammed et al., 2010). Whereas abomasal infusion of CLA *trans*-10,*cis*-12 causes milk fat depression, it also has been reported to increase abundance of genes related to FA synthesis in adipose tissue (Harvatine et al., 2009b). These effects could increase energy retention and improve energy balance. However, evidence for this possibility is not present in our experiment; treatments did not affect concentration or yield of CLA *trans*-10,*cis*-12. Whereas the HS-HMC treatment decreased concentration and yield of C18:1 *trans*-11, a marker of normal biohydrogenation pathways (Harvatine et al., 2009a), the same shift in concentration was observed for LS-DGC. Further, the HS-HMC treatment decreased milk fat yield but not milk fat concentration compared with the other treatments (Albornoz and Allen, 2018), and cows receiving this treatment as well as those receiving the LS-DGC treatment increased loss of BW and BCS in a similar manner. This evidence indicates that milk fat depression via products of altered FA biohydrogenation pathway likely did not occur in our study and cannot explain the treatment differences observed for change in body reserves.

CONCLUSIONS

Feeding the highly fermentable starch source HMC decreased DM and energy intake during the early PP period. Negative effects from HMC compared with DGC were increased when included in an HS diet, despite HS diets increasing DM digestibility. However, over time, the decrease in milk energy output by HMC diminished differences in energy balance between starch sources. Whereas the HS-HMC decreased digestibility of NDF compared with HS-DGC possibly a result of decreased rumen pH, no relationship was found between the reduction in milk FA yield or individual milk FA associated with diet-induced milk fat depression.

ACKNOWLEDGMENTS

We acknowledge financial support for this project by USDA National Research Initiative Competitive Grant no. 2014-67015-21708 to M. S. A., as well as funding from the Fulbright Argentina Program and the Office for International Students and Scholars at Michigan State University to R. I. A. We also thank D. G. Main, R. Longuski, K. Kennedy, L. Gualdron-Duarte, G. Maldini, R. Yair, D. de Souza, and R. West (all from Michigan State University), as well as the staff from the Michigan State University Dairy Cattle Teaching and Research Center (East Lansing) for their assistance with this experiment.

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