Dietary Energy Source in Dairy Cows in Early Lactation: Energy Partitioning and Milk Composition

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ABSTRACT

Metabolic problems related to negative energy balance suggest a role for the balance in supply of lipogenic and glucogenic nutrients. To test the effect of lipogenic and glucogenic nutrients on energy partitioning, energy balance and nitrogen balance of 16 lactating dairy cows were determined by indirect calorimetry in climate respiration chambers from wk 2 to 9 postpartum. Cows were fed a diet high in lipogenic nutrients or a diet high in glucogenic nutrients from wk 3 prepartum until wk 9 postpartum. Diets were isocaloric (net energy basis) and equal in intestinal digestible protein. There was no effect of diet on metabolizable energy intake and heat production. Cows fed the lipogenic diet partitioned more energy to milk than cows fed the glucogenic diet [$1,175 \pm 18$ vs. $1,073 \pm 12$ kJ/(kg^{0.75}·d)] and had a higher milk fat yield (1.89 ± 0.02 vs. 1.67 ± 0.03 kg/d). The increase in milk fat production was caused by an increase in C16:0, C18:0, and C18:1 in milk fat. No difference was found in energy retained as body protein, but energy mobilized from body fat tended to be higher in cows fed the lipogenic diet than in cows fed the glucogenic diet [190 ± 23 vs. 113 ± 26 kJ/(kg^{0.75}·d)]. Overall, results demonstrate that energy partitioning between milk and body tissue can be altered by feeding isocaloric diets differing in lipogenic and glucogenic nutrient content.

Key words: energy balance, milk fat composition, lipogenic nutrient, glucogenic nutrient

INTRODUCTION

Late gestation and early lactation can be considered as the most critical period for high-producing dairy cows. This period is often characterized by metabolic disorders such as fatty liver, ketosis (Grummer, 1993),

and ruminal acidosis (Owens et al., 1998), and reduced fertility (Butler, 2003). Metabolic and reproductive disorders in dairy cows in early lactation have been allocated to a negative energy status, resulting from a genetic potential for high milk production accompanied by a delay in feed intake peripartum (Veerkamp et al., 2003).

Several reviews have indicated dietary energy sources to be an important factor in the prevention and severity of negative energy balance (NEB) and related metabolic disorders (e.g., Grummer and Carroll, 1988; Gong, 2002). The characteristics of NEB-related metabolic problems suggest a role for the balance in availability of lipogenic and glucogenic nutrients (Adler, 1970; van Knegsel et al., 2005). In ruminants, lipogenic nutrients originate either from fiber that stimulates the ruminal production of acetate and butyrate or from dietary fat, or are derived from body reserves. Glucogenic nutrients originate from starch escaped from rumen degradation or gluconeogenesis. In descending order of importance, propionic acid, glucogenic AA and lactic acid are the main contributors to gluconeogenesis in ruminants (Brockman, 2005). The contribution of intestinally digested starch toward glucose is highly variable, depending on factors including dietary source of rumen-resistant starch, technological treatment, and intake level (Mills et al., 1999).

Over 40 yr ago, it was suggested that milk-fat-depressing diets lower the priority for milk fat production relative to fat deposition in body reserves (Van Soest, 1963). This implies that lipogenic nutrients, which increase milk fat yield (Jerred et al., 1990), increase the partitioning of ME into milk (Baldwin et al., 1985) and consequently decrease the partitioning of ME into body reserves. However, the effect of lipogenic nutrients on milk fat also depends on the degree and type of saturation of dietary fat. Polyunsaturated fatty acids and specific intermediates of their biohydrogenation in the rumen, notably C18:2 *trans*-10, *cis*-12, depress milk fat (Bauman et al., 2006) in contrast to saturated fat sources (Baumgard et al., 2001; Schroeder et al., 2003).

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Table 1. Ingredient and chemical composition of glucogenic and lipogenic concentrates

Item	Concentrate	
	Glucogenic	Lipogenic
Ingredient (g/kg)		
Rapeseed meal	127.2	98.5
Lupins	—	166.2
Corn	265.6	—
Corn gluten feed	—	63.3
Milocorn	250.0	—
Palm kernel, expeller	31.6	125.0
Sugarbeet pulp	—	294.5
Peas	131.5	—
Soybean meal, formaldehyde treated	124.0	—
Rapeseed meal, formaldehyde treated	—	148.3
Megalac ¹	—	25.0
Molasses-cane	40.0	40.0
Palm oil	—	25.0
Calcium carbonate	13.6	—
Magnesium oxide	0.7	—
Sodium chloride	8.3	6.6
Mineral-vitamin mixture ²	7.5	7.5
Chemical composition		
DM (g/kg)	873.2	895.8
CP (g/kg of DM)	201.8	212.7
Crude fat	31.0	85.9
NDF	152.2	350.6
Starch	448.0	3.8
Ash	60.9	98.5
DVE ³	137	134
OEB ⁴	13	22
NE _L ⁵ (MJ/kg)	6.69	6.69

¹Ca salts of palm fatty acids (Volac, Hertfordshire, UK).

²Contained per kilogram of mix: 115 g of Ca (CaCO₃); 385 mg of Mg (MgO); 1.67 mg of Cu (CuSO₄·5H₂O); 1.34 mg of Mn (MnO₂); 2.67 mg of Zn (ZnSO₄·7H₂O); 0.04 mg of Co (CoSO₄·7H₂O); 0.13 mg of I (KI); 0.03 mg of Se (Na₂SeO₃); 667,000 IU of vitamin A; 160,000 IU of cholecalciferol (Premix 2031, PreMervo, Utrecht, the Netherlands).

³Intestinal digestible protein (Tamminga et al., 1994).

⁴Degraded protein balance (Tamminga et al., 1994).

⁵Net energy for lactation calculated with VEM system (Van Es, 1975).

On the other hand, glucogenic nutrients decrease milk fat content (e.g., Grum et al., 1996; Ruppert et al., 2003) and increase plasma insulin (Miyoshi et al., 2001). These observations suggest that glucogenic nutrients stimulate body fat deposition and the partitioning of ME into body tissue. This indicates possibilities to improve the energy balance of dairy cows in early lactation by increasing the availability of glucogenic nutrients at the expense of lipogenic nutrients.

In addition, not only milk fat yield, but also milk fatty acid composition is affected by lactation stage (Palmquist et al., 1993; Garnsworthy et al., 2006) and diet composition (Chilliard and Ferlay, 2004). Both dietary fat addition and body fat mobilization increase the bioavailability of C18 fatty acids (Ward et al., 2002). Furthermore, the early lactation period is usually characterized by a higher concentrate intake compared with

Table 2. Ingredient and chemical composition of glucogenic and lipogenic diets¹

Item	Diet	
	Glucogenic	Lipogenic
Ingredient (g/kg)		
Corn silage ²	388.3	388.4
Grass silage ³	388.3	388.4
Chopped alfalfa hay ⁴	29.1	29.1
Concentrate	194.3	194.3
Chemical composition		
DM (g/kg)	472	482
CP (g/kg of DM)	162	169
Crude fat	34	54
NDF	324	396
ADF	214	260
Starch	267	95
Ash	78	84
DVE ⁵	88	86
OEB ⁶	14	18
NE _L ⁷ (MJ/kg of DM)	6.67	6.59

¹Based on 40:60 concentrate to forage ratio (DM basis).

²Corn silage, g/kg: 316 DM, 291 OM, 24 CP, 9 crude fat, 134 NDF, 101 starch and sugars, 16 DVE, -10 OEB (Blgg, Oosterbeek, the Netherlands).

³Grass silage, g/kg: 326 DM, 290 OM, 64 CP, 13 crude fat, 170 NDF, 8 sugars, 21 DVE, 21 OEB (Blgg).

⁴Chopped alfalfa hay, g/kg: 891 DM, 840 OM, 187 CP, 28 crude fat, 338 NDF, 42 starch and sugars (Blgg).

⁵Intestinal digestible protein (Tamminga et al., 1994).

⁶Degraded protein balance (Tamminga et al., 1994).

⁷Net energy for lactation calculated with VEM system (Van Es, 1975).

the mid and late lactation or dry period, which results in a lower ruminal acetate:propionate ratio (Bannink et al., 2006). Accordingly, the availability of precursors for de novo lipogenesis is reduced (Bauman and Griinari, 2003), resulting in a decrease in medium- and short-chain fatty acids in milk fat. Thus, dietary fat, body fat, and the reduced acetate:propionate ratio may increase the proportion of long-chain fatty acids in milk fat. Hence, a relationship between dietary energy source and an NEB with milk fat composition can be expected. However, very few comparisons on the effect of the interaction between body fat mobilization and diet composition on milk fat composition have been made (Smith et al., 1978).

The objective of this study was to compare on an isocaloric basis the effects of a mainly glucogenic or a mainly lipogenic diet on energy partitioning and milk fat composition in early-lactation dairy cows in a NEB. The companion paper (van Knegsel et al., 2007) focuses on the effects of dietary energy source on blood metabolites and metabolic hormones and their relationship with the determined energy balance by indirect calorimetry.

Table 3. Fatty acid composition of the glucogenic and lipogenic concentrate¹

Fatty acid (g/kg of DM)	Concentrate	
	Glucogenic	Lipogenic
≤10:0	0.14	0.55
12:0	0.97	3.86
14:0	0.37	1.37
16:0	3.18	12.16
16:1	0.10	0.06
18:0	0.50	1.71
18:1	8.07	29.24
18:2	11.31	11.86
18:3	0.89	0.97
≥20:0	0.34	1.67
Total	25.89	63.44

¹Calculated according to Centraal Veevoederbureau (CentraalVeevoederbureau, 2005).

MATERIALS AND METHODS

Experimental Design

The Institutional Animal Care and Use Committee of Wageningen University approved the experimental protocol. Energy balance of 16 lactating dairy cows was determined as energy retention in body mass (**ER**) using climate respiration chambers (Verstegen et al., 1987) over 8 successive balance periods (1 wk) from wk 2 to 9 postpartum (**pp**). The animals were divided into 4 groups. Within each group, 1 pair of animals was assigned to each of 2 experimental diets 3 wk prepartum. Experimental diets were either mainly lipogenic or mainly glucogenic.

Animals and Housing

Sixteen Holstein-Friesian dairy cows, 4 cows per group, with comparable milk production (>9,500 kg of fat- and protein-corrected milk per 305 d), were selected

from a group of 44 cows that were inseminated at synchronized ovulation (the Crestar+ method, Intervet, Boxmeer, the Netherlands). Ovulation was synchronized to obtain natural calving cows with at most 4 d variation in calving date. Selection of the 16 experimental cows was based on calving date. Postcalving, parity of the selected cows ranged from 2 to 4. Within 1 wk pp, 4 cows were transported and housed (2 cows per chamber) in 2 identical, large, open-circuit, indirect climate respiration chambers (Verstegen et al., 1987). Per group dietary treatment was assigned alternately to 1 of the 2 chambers. The cows were housed in the chamber in a tie stall. Chamber temperature was maintained at 16°C and relative humidity was set at 70%. Air velocity was <0.2 m/s. Cows were exposed to 16 h of light (0600 to 2200 h) and 8 h of darkness. Body condition was scored (1 to 5 scale) every 3 wk from wk 3 prepartum until wk 9 pp. Body weight was recorded at the start and end of each 1-wk balance period. Cows were milked twice daily (0600 and 1700 h) in the climate respiration chamber with a mobile milking system.

Diets

Cows were fed 1 kg/d of the experimental concentrates 3 wk prepartum followed by 2 kg/d in the last week prepartum. Roughage did not differ between diets and was supplied ad libitum; it consisted of grass silage, corn silage, and wheat straw in a 45:45:10 ratio (DM basis). Postpartum, wheat straw was replaced by 1.5 kg/d of chopped alfalfa hay. Concentrate supply was increased stepwise by 0.5 kg/d until concentrate intake reached 10.0 kg/d with a concentrate to forage ratio of 40:60 (DM basis). Ingredient and chemical compositions of both concentrates and diets are presented in Table 1 and 2. Calculated fatty acid composition of the concentrates is presented in Table 3. Diets were fed as

Table 4. Dry matter intake, milk production, and milk composition of dairy cows fed a mainly glucogenic or mainly lipogenic diet during wk 2 to 9 of lactation

Variable	Diet		SEM	P-value ¹		
	Glucogenic	Lipogenic		Diet (D)	Week (W)	D × W
DMI (kg/d)	20.8	20.7	0.5	0.94	<0.01	NS
Milk yield (kg/d)	39.8	39.8	0.7	0.88	<0.01	NS
Milk lactose						
%	4.44	4.56	0.05	0.08	0.16	NS
kg/d	1.76	1.82	0.04	0.32	<0.01	NS
Milk fat						
%	4.27	4.81	0.15	0.02	<0.01	NS
kg/d	1.68	1.90	0.06	0.03	0.02	0.05
Milk protein						
%	3.11	3.13	0.06	0.64	<0.01	NS
kg/d	1.23	1.24	0.03	0.66	0.11	0.02

¹Diet × week interaction was excluded from the model if not significant ($P > 0.05$).

Figure 1. A) Milk protein content; B) milk fat content; and C) milk lactose content of dairy cows fed a mainly glucogenic or mainly lipogenic diet from wk 2 to 9 of lactation. Values represent means during 8 balance periods of 1 wk. Overall SEM: milk protein, 0.03; milk fat, 0.07; milk lactose, 0.01.

TMR, were isocaloric according to the Dutch NE_L system (Van Es, 1975), and were equal in intestinal digestible protein and degraded protein balance (DVE/OEB system; Tamminga et al., 1994). Diets were fed twice a day in equal proportions before milking.

Energy and Nitrogen Balance

Feces with urine were collected quantitatively per chamber, pooled per balance period, sampled for energy and nitrogen analysis, and stored at -20°C until analysis. Feed intake was monitored per cow per balance period and feed samples were collected per day and pooled per balance period, sampled for energy and nitrogen analysis, and stored at 4°C until analysis. Milk was sampled each milking (3 g/kg of milk), pooled per cow per balance period, and stored at 4°C during the balance period and at -20°C after each balance period. Gross energy (GE) values of feed, energy in feces with urine, and energy in milk were measured using bomb calorimetry (IKA-C700, Janke & Kunkel, Heitersheim, Germany) and N content by Kjeldahl analysis. Intake of ME per chamber was calculated from the GE content of the feed, feces with urine, and produced methane. Heat production (HP) was determined indirectly at 9-min intervals by measuring the exchange of oxygen, carbon dioxide, and methane as described earlier (Versteegen et al., 1987). Energy retention in body mass was calculated by subtracting the HP and energy in milk from the ME. The total N retention (NR; g/d) was estimated from N in feed, feces, urine, milk, dust, and water that condensed on the heat exchanger, and in acidified liquid samples through which outflowing air from the chambers was led to trap aerial ammonia. Energy retention as body protein (ER_p) was derived from the protein gain ($N \times 6.25$; except N in milk $\times 6.38$) multiplied by 23.6 kJ/g (energetic value of body protein; ARC, 1980). Energy retention as fat (ER_f) was calculated from the difference between ER and ER_p . Energy retention data are expressed per $\text{kg}^{0.75}$, where the mean BW per cow per balance period was used to calculate the metabolic BW.

Milk Yield and Composition

Milk yield was recorded daily. Milk samples for fat, protein, and lactose analysis (ISO 9622, Melkcontrolestation, Zutphen, the Netherlands) were collected 4 times per balance period (2 morning and 2 evening milkings). An individual morning sample per balance period was stored at -20°C until analysis for milk fatty acid composition.

For milk fatty acid analysis, the stored individual milk samples were heated to 50°C and directly centrifuged (20 min at $1,600 \times g$) at 4°C . The upper layer (fat and cream) was collected and filtered on folded filter paper. The fat-and-cream mixture was collected from the filter and stored overnight at -20°C . The mixture was heated for 10 min at 50°C . The oily substance was centrifuged at room temperature (5 min at $1,130 \times g$), and the fat fraction was transferred to a tube containing

Table 5. Gross energy intake, ME intake, methane production, heat production, and energy retention in body mass of dairy cows fed a mainly glucogenic or lipogenic diet during wk 2 to 9 of lactation¹

Variable	Diet		SEM	<i>P</i> -value ²	
	Glucogenic	Lipogenic		Diet	Week
	kJ/(kg ^{0.75} ·d)				
Gross energy intake (GE)	3,415	3,492	122	0.67	<0.01
Metabolizable energy intake (ME)	2,079	2,124	74	0.68	<0.01
ME:GE ratio (%)	60.7	60.8	0.6	0.90	<0.01
Methane production	179	178	9	0.96	<0.01
Heat production	1,096	1,124	30	0.54	<0.01
Energy in milk	1,075	1,173	23	0.01	<0.01
Energy retention in body mass (ER) ³	−94	−172	28	0.12	<0.01
Energy retention as body protein (ER _p)	19	18	7	0.89	<0.01
Energy retention as body fat (ER _f)	−113	−190	24	0.09	<0.01

¹Values are least squares means.²Diet × week interaction was not significant ($P > 0.05$) for any of the variables.³ER = GE – (energy in feces + urine) – methane production – heat production – energy in milk [all in kJ/(kg^{0.75}·d)].

a small amount of anhydrous sodium sulfate. The milk fats were stored at -20°C until analysis. Before analysis, samples were heated to 50°C . A portion of 50 μL was taken, weighed, and added to 5 mL of hexane, containing 0.02% C23 (Alltech, Breda, the Netherlands) as an internal standard. The glycerol-bound fatty acids were transesterified to methyl esters by vortexing 1 min with 200 μL of sodium methanolate in methanol (30%). The solution was neutralized with 1 g of sodium hydrogen sulfate and dried with anhydrous sodium sulfate. Fatty acid methyl esters (**FAME**) were injected into a gas chromatograph (Carlo Erba HRGC Mega 2, Fisons, Milan, Italy), equipped with a flame-ionization detector (detector temperature of 260°C). The carrier gas was helium, and the inlet pressure 330 kPa. Samples were injected by split injection (split ratio 1:20), injection temperature was 260°C . Separation of FAME was performed with a Supelco column (100 m $\times$ 0.25 mm $\times$ 0.2 μm ; SP 2560, Sigma-Aldrich, Zwijndrecht, the Netherlands). The oven temperature was programmed from 140°C for 4 min, followed by an increase of $4^{\circ}\text{C}/\text{min}$ to 240°C , and held for 30 min. The FAME concentrations were determined by using the Chrom Card program (Thermo Finnigan, Milan, Italy) using the Supelco FAME mix (Sigma-Aldrich) as a standard.

Statistical Analysis

In groups 2 and 3, 3 cows in total were excluded from the experiment because of left displaced abomasum (1 cow fed a lipogenic diet, 2 cows fed a glucogenic diet). Therefore, values are based on 13 cows (glucogenic diet: $n = 6$; lipogenic diet: $n = 7$) for analysis of milk yield, energy in milk, and milk fat, protein, and lactose (model 1) or 6 climate respiration chambers ($n = 3$ per dietary treatment per lactation week) for analysis of GE, ME,

methane production, HP, ER, ER_p, and ER_f (model 2). Although multiple measurements per animal cannot be regarded as independent units of observation, repeated-measures ANOVA (Littell et al., 2006; SAS, version 9.1) was performed. Cow (model 1) or chamber (model 2) was included as the repeated subject. Diet (glucogenic or lipogenic), week (wk 2 to 9 pp), and their interaction were included in the model as fixed effects. In case of lack of significance ($P > 0.05$), the diet $\times$ week interaction was excluded from the model. A first-order autoregressive structure [AR(1)] was the best fit and was used to account for within-cow variation (model 1) or within-chamber variation (model 2). Model assumptions were evaluated by examining the distribution of residuals. Values are presented as least squares means with their SEM.

RESULTS

Animal Performance

Body weight (595 ± 14 kg) and BCS (2.7 ± 0.1) at entry of the climate respiration chambers at 1 wk pp were not different between dietary treatments. At the end of the experiment (wk 9 pp), BW (548 ± 13 kg) and BCS (2.3 ± 0.1) did not differ between dietary treatments. Dry matter intake and milk yield did not differ between diets (Table 4), but both increased linearly with time pp ($P < 0.05$). Dry matter intake increased from 16.5 kg/d (± 0.6 kg/d) in wk 2 to 22.7 kg/d (± 0.2 kg/d) in wk 9 pp. Milk yield increased from 34.2 kg/d (± 0.7 kg) in wk 2 to 41.5 kg/d (± 0.7 kg/d) in wk 9 pp. Milk fat content and daily milk fat yield were higher ($P < 0.05$) in cows fed the lipogenic diet compared with cows fed the glucogenic diet. Protein content, protein yield, lactose content, and lactose yield did not differ between

Figure 2. A) Metabolizable energy intake (ME); B) energy in milk (NE_{milk}); C) energy retention as body mass (ER); D) energy retention as protein (ER_p); and E) energy retention as fat (ER_f) of dairy cows fed a mainly glucogenic or mainly lipogenic diet from wk 2 to 9 of lactation. Values represent means [kJ/(kg^{0.75}·d)] for 3 climate respiration chambers with 2 cows each during 8 balance periods of 1 wk. Overall SEM: ME = 74; NE_{milk} = 23; ER = 28; ER_p = 7; ER_f = 24.

dietary treatments. Milk fat, milk protein, and milk lactose content were affected by time pp ($P < 0.01$; Figure 1). Daily milk fat yield and milk protein yield were affected by the diet $\times$ week interaction ($P < 0.05$), but effects of these interactions were small.

Energy Partitioning

Gross energy intake, ME intake, methane production, and heat production were not different between diets (Table 5). Intake of ME increased ($P < 0.01$) from

Table 6. Milk fatty acid composition of dairy cows fed a mainly glucogenic or lipogenic diet during wk 2 to 9 of lactation¹

Fatty acid	Diet		SEM	P-value ²	
	Glucogenic	Lipogenic		Diet	Week
	— g/100 g of fatty acids —				
4:0	6.36	6.19	0.33	0.71	0.03
6:0	2.61	2.23	0.10	0.02	<0.01
8:0	1.26	1.01	0.07	0.03	0.01
10:0	2.53	1.93	0.17	0.03	<0.01
11:0	0.24	0.16	0.02	<0.01	<0.01
12:0	2.69	2.44	0.16	0.29	<0.01
13:0	0.09	0.07	0.01	<0.01	<0.01
Total short-chain	15.80	14.00	0.66	0.07	<0.01
14:0	9.81	8.48	0.36	0.02	<0.01
14:1	0.67	0.49	0.04	0.01	<0.01
15:0	0.67	0.65	0.04	0.64	0.03
16:0	29.17	31.47	0.71	0.03	<0.01
16:1	0.98	1.30	0.20	0.26	0.07
Total medium-chain	41.34	42.38	0.97	0.44	<0.01
17:0	0.91	0.71	0.12	0.25	<0.01
17:1	0.25	0.19	0.02	0.02	<0.01
18:0	12.62	14.16	0.40	0.02	<0.01
18:1	25.74	25.41	1.05	0.82	<0.01
18:2	2.25	2.05	0.18	0.42	0.08
18:3	0.55	0.45	0.02	<0.01	0.72
20:0	0.42	0.34	0.13	0.64	0.01
20:1	0.07	0.06	0.01	0.32	0.84
20:4	0.02	0.03	0.01	0.38	<0.01
22:0	0.02	0.03	0.01	0.19	0.24
CLA	0.34	0.37	0.04	0.55	0.02
Total long-chain	42.85	43.42	1.28	0.66	<0.01

¹Values are least squares means.²Diet × week interaction was not significant ($P > 0.05$) for any of the variables.

wk 2 to 9 pp (Figure 2). The ME:GE ratio was not different between diets, but increased ($P < 0.01$) from wk 2 to 9 pp. Energy in milk was higher ($P < 0.05$) for cows fed the lipogenic diet compared with cows fed the glucogenic diet. Energy retention tended to be lower ($P = 0.12$) for cows fed the lipogenic diet compared with cows fed the glucogenic diet. Specifically, ER_p did not differ between diets, but diets tended ($P = 0.09$) to be different for ER_f . For both diets, ER_p was positive from wk 3 pp. Moreover, ER_f was positive from wk 8 pp for cows fed the glucogenic diet, whereas ER_f was still negative [$-11 \pm 39 \text{ kJ}/(\text{kg}^{0.75} \cdot \text{d})$] in wk 9 pp for cows fed the lipogenic diet.

Milk Fat Composition

Of the short-chain fatty acids in milk fat, C6:0, C8:0, C10:0, C11:0, and C13:0 were higher for cows fed the glucogenic diet compared with cows fed the lipogenic diet ($P < 0.05$; Table 6). Of the medium-chain fatty acids, the concentrations of C14:0 and C14:1 in milk fat were higher for cows fed the glucogenic diet ($P < 0.05$), and C16:0 was higher for cows fed the lipogenic diet ($P < 0.05$). Of the long-chain fatty acids, the concentration of C18:0 was higher and C18:3 was lower ($P < 0.05$) for

cows fed the lipogenic diet compared with cows fed the glucogenic diet. Total production of milk fatty acids was 195 g of fatty acids per day more for cows fed the lipogenic diet compared with cows fed the glucogenic diet. This increase in milk fatty acid production could be explained almost entirely by an increase in secretion of C16:0 (96 g/d), C18:0 (51 g/d), and C18:1 (45 g/d). The daily production of medium-chain fatty acids ($\geq C14$ and $\leq C16$) in milk fat increased linearly with week in lactation (Figure 3). The production of long-chain fatty acids ($> C16$) decreased linearly from wk 2 until wk 9 in lactation.

DISCUSSION

This study agrees with other studies that observed an increase in milk fat percentage after feeding more lipogenic nutrients (e.g., Grum et al., 1996; Moallem et al., 1999). However, those studies not only increased the proportion of lipogenic nutrients, but also the energy density and energy intake by adding lipogenic nutrients to the diet. Consequently, milk yield increased in the treatment group compared with the control diet. Feeding extra glucogenic nutrients, accompanied by an increase in energy intake, resulted in an increase in milk

Figure 3. A) Milk fatty acid production (g/d) of dairy cows fed a mainly glucogenic diet from wk 2 to 9 in lactation; B) milk fatty acid production (g/d) of dairy cows fed a mainly lipogenic diet from wk 2 to 9 in lactation. Values represent means per week. SEM for cows fed the glucogenic diet: <C14 = 58; ≥C14 and ≤C16 = 86; >C16 = 128. SEM for cows fed the lipogenic diet: <C14 = 39; ≥C14 and ≤C16 = 63; >C16 = 100.

yield (Grum et al., 1996; Hurtaud et al., 2000). However, extra glucogenic nutrients often decreased the milk fat percentage and increased the milk protein percentage. In contrast to these studies, the present study was designed to feed isocaloric diets with a contrast in lipogenic and glucogenic nutrient content. As a result, GE and ME intakes were not different between diets. Despite a similar quantity of available ME, cows fed the lipogenic diet partitioned more energy to milk compared with cows fed the mainly glucogenic diet. The increased partitioning of energy to milk resulted in an increase

in milk fat production, but had no effect on total milk yield or milk protein yield.

In the current study, cows fed the glucogenic diet seemed to lower the priority of milk fat production as indicated by a lower milk energy output, and increased the priority of energy retention in body reserves as indicated by the numerically increased energy balance. This observation is in agreement with the review of Van Soest (1963), who suggested that milk-fat-depressing diets lower the priority of milk production relative to body reserves. In the present experiment, dietary energy source did not alter the body protein balance, but specifically the body fat balance was less negative with feeding a more glucogenic diet. Concerning the period of wk 2 to 9 pp, cows fed the glucogenic diet mobilized 18.6 kg of body fat (1 g of body fat = 39.8 kJ; Wenk et al., 2001) compared with 31.2 kg for cows fed the mainly lipogenic diet. Cows fed the lipogenic diet mobilized 226 g/d more body fat compared with cows of comparable BW, BCS, and milk yield but fed the mainly glucogenic diet (332 vs. 558 g/d of body fat, respectively). The difference in body fat mobilization is in accordance with 220 g/d more milk fat produced for cows fed the lipogenic diet compared with cows fed the glucogenic diet. After subtracting body fat mobilization from milk fat production, cows fed the glucogenic diet produced 1,348 g/d of milk fat from ME intake compared with 1,342 g/d of milk fat for cows fed the lipogenic diet. This suggests the extra milk fat production for cows fed the lipogenic diet originated predominantly from body fat mobilization that was increased by 68% compared with cows fed a mainly glucogenic diet.

Energy retention as protein was positive for both treatment groups from wk 3 pp onward, which is in agreement with Tamminga et al. (1997), who estimated changes in body composition with time after parturition. They reported that body protein mobilization stabilized from wk 2 pp and body protein gain stabilized from wk 4 pp. Total estimated mobilization of body reserves during the first 8 wk of lactation was 41.6 kg and included 30.9 kg of body fat and 2.4 kg of body protein (Tamminga et al., 1997). This corresponds with the current study, where on average the cows mobilized 24.9 kg of body fat and 5.2 kg of body protein (1 g of body protein = 23.6 kJ; ARC, 1980) from wk 2 to wk 9 in lactation.

The results confirm the hypothesis that a mainly lipogenic diet during early lactation increases the secretion of long-chain fatty acids in milk fat compared with a mainly glucogenic diet. Because the lipogenic diet has a higher dietary fat content, and because body fat mobilization is higher compared with cows fed the glucogenic diet, it can be suggested that both sources of long-chain fatty acids (dietary and endogenous) contribute to the

increased secretion of long-chain fatty acids in milk fat of cows fed the lipogenic diet. As well as the diet treatment, negative energy status also seems to have an effect on milk fat composition. A decrease from early to mid lactation in the production of long-chain fatty acids relative to medium-chain fatty acids has been reported earlier (Garnsworthy et al., 2006). This corresponds with the current study showing that with increasing energy balance during wk 2 to 9 pp, the daily production of medium-chain fatty acids ($\geq C14:0$ and $\leq C16:0$) increased and at the same time the production of long-chain fatty acids ($\geq C18:0$) decreased (Figure 3).

CONCLUSIONS

This study confirmed the hypothesis that energy partitioning between milk and body tissue can be altered by feeding isocaloric diets that differ in lipogenic and glucogenic nutrient content. Although ME intake was not different, daily milk fat yield and energy in milk were higher in the lipogenic diet group. Consequently, the higher milk energy resulted in a tendency for less energy to be partitioned into body fat for cows fed the lipogenic diet compared with cows fed the glucogenic diet.

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