Feed conversion efficiency in dairy cows: Repeatability, variation in digestion and metabolism of energy and nitrogen, and ruminal methanogens

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ABSTRACT

The objective was to study repeatability and sources of variation in feed conversion efficiency [FCE, milk kg/kg dry matter intake (DMI)] of lactating cows in mid to late lactation. Trials 1 and 2 used 16 cows (106 to 368 d in milk) grouped in 8 pairs of 1 high- and 1 low-FCE cow less than 16 d in milk apart. Trial 1 determined the repeatability of FCE during a 12-wk period. Trial 2 quantified the digestive and metabolic partitioning of energy and N with a 3-d total fecal and urine collection and measurement of CH₄ and CO₂ emission. Trial 3 studied selected ruminal methanogens in 2 pairs of cows fitted with rumen cannulas. Cows received a single diet including 28% corn silage, 27% alfalfa silage, 17% crude protein, and 28% neutral detergent fiber (dry matter basis). In trial 1, mean FCE remained repeatedly different and averaged 1.83 and 1.03 for high- and low-FCE cows, respectively. In trial 2, high-FCE cows consumed 21% more DMI, produced 98% more fat- and protein-corrected milk, excreted 42% less manure per kilogram of fat- and protein-corrected milk, but emitted the same daily amount of CH₄ and CO₂ compared with low-FCE cows. Percentage of gross energy intake lost in feces was higher (28.6 vs. 25.9%), but urinary (2.76 vs. 3.40%) and CH₄ (5.23 vs. 6.99%) losses were lower in high- than low-FCE cows. Furthermore, high-FCE cows partitioned 15% more of gross energy intake toward net energy for maintenance, body gain, and lactation (37.5 vs. 32.6%) than low-FCE cows. Lower metabolic efficiency and greater heat loss in low-FCE cows might have been associated in part with greater energy demand for immune function related to subclinical mastitis, as somatic cell count was 3.8 fold greater in low- than high-FCE cows. As a percentage of N intake, high-FCE cows tended to have greater fecal N (32.4 vs. 30.3%) and had lower urinary N (32.2 vs. 41.7%) and greater milk N (30.3 vs. 19.1%) than low-FCE cows. In

trial 3, *Methanobrevibacter* spp. strain AbM4 was less prevalent in ruminal content of high-FCE cows, which emitted less CH₄ per unit of DMI and per unit of neutral detergent fiber digested than low-FCE cows. Thus lower digestive efficiency was more than compensated by greater metabolic efficiencies in high- compared with low-FCE cows. There was not a single factor, but rather a series of mechanisms involved in the observed differences in efficiency of energy utilization of the lactating cows in this study.

Key words: feed efficiency, energy metabolism, nitrogen utilization, manure, dairy cattle

INTRODUCTION

Worldwide meat and milk demand is projected to increase, especially in emerging economies where livestock systems are generally considered inefficient but have multiple socio-economic functions (Herrero et al., 2013). For the dairy sector, the challenge of providing dairy products to a more affluent and increasing population (FAO, 2009) depends in part on increasing the efficiency of nutrient utilization by lactating dairy cows with limited effect on global cycles of C (Asner and Archer, 2010) and N (Galloway et al., 2010). Feed conversion efficiency (**FCE**; kg of milk/kg of DMI; Berry and Crowley, 2013) and N use efficiency [**NUE**; milk N g/100 g of N intake (**NI**)] are common measures of efficiency of dietary energy and N utilization in lactating dairy cows. In contrast to NUE, which has remained typically low (around 25%) and highly variable (10 to 40%; Calsamiglia et al., 2010), considerable improvement in FCE has been achieved through dilution of maintenance (Bauman et al., 1985) associated with genetic selection for higher milk production (USDA, 2013). However, marginal increases in FCE decrease with increasing milk production and future selection for higher milk production alone will no longer lead to substantial increases in FCE, in part because of the loss of digestible energy associated with high rate of passage in cows with high DMI and milk production (NRC, 2001). Thus, alternative approaches need to be explored to

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further improve FCE. Ruminal methanogens appeared to vary in cattle with different feed efficiency (Zhou et al., 2009). However, altering the proportion of gross energy intake (**GEI**) available for milk production can be achieved theoretically by reducing the energy in any of the following pools: feces, urine, enteric CH_4 , maintenance, body gain, or heat. Thus, quantifying variability at each step of energy and N utilization may serve as a guide for future efforts to improve FCE and NUE. For example, if some of the variability is proven heritable, progeny testing or genomic selection could be used to improve FCE (Yan et al., 2010; Woodward et al., 2011). Hence, the objectives of the current study were to determine the repeatability of FCE over time in mid to late lactation (trial 1), to quantify variations in digestive and metabolic partitioning of energy and N (trial 2), and to study selected ruminal methanogens (trial 3) in lactating dairy cows with contrasting FCE.

MATERIALS AND METHODS

The lactating dairy cows used in our study, which was conducted at the US Dairy Forage Research Center, Prairie du Sac, Wisconsin (43°19' N, 89°44' W), were cared for and handled according to protocols approved by the University of Wisconsin-Madison College of Agricultural and Life Sciences Institutional Animal Care and Use Committee. The study was composed of 3 trials. Trial 1 investigated the FCE repeatability of 16 cows during a 12-wk period (February 27 to May 21, 2011). In trial 2, cows of trial 1 were adapted to chambers ($n = 4$) before a 3-d total fecal and urine collection, and CH_4 and CO_2 emission measurements were conducted in blocks of 2 pairs of cows staggered on wk 6, 8, 10, and 12 because of chamber availability. In trial 3, rumen samples were collected during wk 10 from 4 cows that were fitted with a rumen cannula (before their first lactation). All cows were housed in tiestalls and received bST (Posilac, Elanco Animal Health, Greenfield, IN) on the same day every 2 wk during the cow selection process and the trials.

Cow Selection and Diet Composition

Feed conversion efficiency was measured on a group of 140 cows with DIM ranging from 106 to 368 in a 14-d period before the start of the study (Asher et al., 2014). The 8 cows with the highest and the 8 cows with the lowest FCE were selected and paired based on parity (4 first and 4 second lactation pairs), and the additional selection constraint was that cows within a pair be less than 16 DIM apart from each other. This protocol resulted in a high-FCE group ($n = 8$) and a

low-FCE group ($n = 8$) with DMI of (LSM $\pm$ SD) 24.0 ± 2.2 and 21.2 ± 3.0 kg/d, milk production of 44.9 ± 6.5 and 24.3 ± 5.4 kg/d, and FCE of 1.87 ± 0.22 and 1.14 ± 0.20 , respectively.

The same ration was offered throughout the entire study starting 4 wk before the selection period. It included (DM basis) 28.2% corn silage, 26.7% alfalfa silage, 23.2% high-moisture corn, 7.1% distillers dried grains, 3.6% soybean meal, 8.8% roasted soybeans, and 2.4% vitamin and mineral premix, which contained monensin (373 mg/kg of DM). From wk 4 to 12, feed ingredients were sampled once a week, stored at -20°C , and dried at 60°C (in a forced-air oven) for 48 h. Weekly samples were composited in a single sample using equal weight either before grinding (nonforage samples) or after grinding (forage samples) through a 1-mm Wiley mill screen (Arthur H. Thomas Co., Philadelphia, PA). Ground samples were analyzed for total N content (Leco FP-2000 N Analyzer, Leco Instruments Inc., St. Joseph, MI), analytical DM at 100°C for 24 h, ash content (AOAC, 1996; method 942.05), and NDF content using α -amylase (Ankom Technology, Macedon, NY) with sodium sulfite and corrected for ash concentration according to Van Soest et al. (1991), adapted for Ankom200 Fiber Analyzer (Ankom Technology, Fairport, NY). Ether extract (**EE**) was determined using the Soxtec System Application Note AN390 with acid hydrolysis followed by AOAC method 920.39 (AOAC, 1996) using petroleum ether, which determines the total level of fat including fat that is present as fecal soaps (Johnson and McClure, 1973). Total C was determined by combustion assay (Elementar VarioMax CN analyzer; Elementar Vario, Hanau, Germany), and gross energy (**GE**) was measured using Parr 6400 adiabatic bomb calorimeter (Parr Instrument Company, Moline, IL). Nonfiber carbohydrate was calculated according to NRC (2001). Dietary chemical composition was calculated based on chemical analysis of feed samples and dietary feed ingredient composition.

Feed Conversion Efficiency (Trial 1)

DMI. The amount of TMR offered daily at 0800 h was adjusted to allow for 10% refusals from the previous day, and adjustments of diet ingredient mixes were made 3 times per week for change in forage DM content. Amounts offered and refused were recorded daily. Samples of TMR and next morning refusals were collected in 3 consecutive days each week of the study. Weekly samples were stored at -20°C and dried at 60°C (in a forced-air oven) for 48 h. Dry matter intake was calculated on a 100°C basis using the analytical composition of each ingredient offered (see above) and 100°C DM of refusals. Cows had free access to water.

Milk Production and Composition. Daily milk production was calculated as the sum of the milk production recorded at the afternoon milking (1700 h) and next morning milking (0600 h). Milk samples were collected at 4 consecutive milkings in wk 1 to 12 (trial 1) and an additional 4 consecutive milkings in wk 8 to 12 (trial 2, see below). Samples were analyzed for fat, true protein, lactose, and MUN using infrared prediction (AgSource Milk Analysis Laboratory, Menomonie, WI) with a Foss FT6000 (Foss North America Inc., Eden Prairie, MN), and SCC was determined by Fossomatic 500 FC (Foss Food Technology Corp., Hillerød, Denmark). Milk component yields were calculated as the sum of the evening and morning milk production multiplied by their respective milk component concentrations. Daily output of milk NE_L (Mcal/d) was based on milk component yields and NRC (2001) prediction equation. For each week, FCE was calculated as milk production (kg/d) divided by DMI (kg/d) and feed efficiency for lactation (FE_L , Mcal/kg) was calculated as milk NE_L (Mcal/d) divided by DMI (kg/d).

Digestive and Metabolic Partitioning of Energy and N (Trial 2)

Chamber Adaptation. In addition to measurements described previously, a 3-d fecal, urinary, CO_2 , and CH_4 measurement was conducted on 2 pairs of cows in 4 blocks from wk 6 to 12. Cows were acclimated to an air flow-controlled chamber for 10 d before measurements. Chambers were built originally as a modified tiestall barn to accommodate 4 cows each (Powell et al., 2007), but were proven to be suitable for individual cow measurements (Arndt, 2014). To minimize the risk of isolation stress, 2 mirrors were installed next to one another sideways of the cow between adjacent chambers providing a total reflection area of 122×244 cm. Mirrors reduced isolation stress in heifers (Piller et al., 1999) and in horses (Kay and Hall, 2009).

Collection of Feces and Urine. Feces were collected daily for 3 consecutive days starting after the evening milking of d 18. Stainless steel pans ($1.23 \times 0.38 \times 0.076$ m) were placed in the gutter behind each cow. The actual collection period lasted approximately 22 h due to milking interruptions. Once a day fecal materials were collected into a large container and total weight was recorded before thorough mixing and sampling. Samples (500 g) were stored at $-20^\circ C$. Upon thawing, samples were dried at $60^\circ C$ (in a forced-air oven) for 72 h, ground to pass a 1-mm Wiley mill screen (Arthur H. Thomas Co.), composited by daily excretion weight (on $60^\circ C$ DM basis), and analyzed at $100^\circ C$ for DM, total N, ash, NDF, EE, total C, and GE

using the procedures described previously. Urine was collected with indwelling Foley catheters (24 French, 75-mL balloon lubricious catheter, C. R. Bard Inc., Covington, GA) on the same 3 d as the fecal collection. Catheters emptied into large carboys with 500 to 700 mL of 50% H_2SO_4 for acidification (final pH < 4). Each day urine was weighed and 2-mL aliquots were diluted immediately with 10 mL of 0.072 N H_2SO_4 and stored at $-20^\circ C$ for later analysis of total N. Apparent digestibility of DM, OM, CP, NDF, and EE were determined using daily intake and fecal excretion data. However, a factor of 1.099 was used to adjust the measured mass of feces and urine to an estimated 24-h excretion.

BW and BCS. Cow BW was measured weekly on 3 consecutive days after evening milking and BW gain was calculated as the slope of the of BW versus days using an Excel spreadsheet (Microsoft Corp., Redmond, WA). Body condition score (Wildman et al., 1982) was recorded once in wk 12.

Emission of CH_4 and CO_2 . Concentration of CH_4 and CO_2 entering and exiting the chambers were measured using a photo-acoustic multigas monitor (Innova model 1412; Airtech Instruments, Ballerup, Denmark). Chambers were opened and data were not recorded during milking and feeding times (approximately 0430 to 0800 and 1630 to 1800 h). In addition, the first hour of data after closing the chambers was excluded from analysis because of the time necessary for equilibration of gases in the chamber. Thus, concentration measurements were available for approximately 17 h/d. A C balance approach was used to determine fluxes of CH_4 and CO_2 . First, emitted C was calculated using the following equation:

$$\text{Emitted C (g/d)} = CI - (FC + UC + MC + BGC),$$

where CI is C intake, FC is fecal C, UC is urine C, MC is milk C, and BGC is body gain C (all terms expressed as g/d). In the equation, FC was measured directly and UC was estimated with C content of urinary constituents as reported in Bristow et al. (1992), leading to an average of 9.51 g of C/L of urine. Milk C were based on C content of milk protein (53%; Rouwenhorst et al., 1991), milk fat [74.5%; calculated with FA data composition from Bitman (1976) and C carbon content of FA], and milk lactose (42%). The BGC was based on empty body chemical composition at various BCS (NRC, 2001), assuming C contents of 53% for body protein (Rouwenhorst et al. 1991) and 75.9% for body fat [calculated based on FA composition of gain from Bitman (1976) and the C content of the FA]. It was then assumed that emitted C comprised CO_2 and CH_4 only, in effect assuming that emission of other C-containing

gases was negligible and that CH₄-C (74.9% of CH₄) and CO₂-C (27.3% of CO₂) were emitted in proportion to measured concentrations.

Energy and N Partitioning Calculations. The equation used to describe energy partitioning was

$$\text{GEI} = \text{FE} + \text{UE} + \text{CH}_4\text{E} + \text{NE}_\text{M} + \text{milk NE}_\text{L} \\ + \text{NE}_\text{G} + \text{NMH},$$

where FE is fecal energy, UE is urine energy, CH₄E is CH₄ energy, and NMH is nonmaintenance heat production (all terms expressed as Mcal/d). Gross energy intake and daily fecal energy excretion were obtained by multiplying DMI and fecal DM excretion with their respective energy concentrations measured with a bomb calorimeter, as described above. Urine energy concentration was estimated from urine N according to Street et al. (1964) and methane energy concentration was assumed to be 13.26 Mcal/kg (Ramin and Huhtanen, 2013). The NRC (2001) equations were used to predict NE_M using BW, milk NE_L using milk production and composition, and NE_G using empty body chemical composition determined at the BCS recorded for each cow and BW gain. Energy for pregnancy was not accounted for because cows were less than 190 d pregnant. Digestible energy was calculated as GEI minus fecal energy; ME was calculated as digestible energy minus the sum of urine energy and methane energy. Heat production was estimated as ME – (NE_L + NE_G), and nonmaintenance heat production was estimated after rearranging the terms of the above equation.

The equation used to describe N partitioning was

$$\text{NI} = \text{FN} + \text{UN} + \text{N}_\text{L} + \text{N}_\text{G},$$

where FN is fecal N, UN is urine N, N_L is milk N, and N_G is N in body gain (all terms expressed as g/d). Except for N_G, all N outputs were measured as described previously. Individual cow N_G was calculated using empty body chemical composition at the measured BCS (NRC, 2001), assuming a N content of 16% for body protein. The effect of neglecting hair and scurf N (a negligible N pool; Tine et al., 2001) and the cumulative error associated with each terms of the equation was determined with N recovery calculated as $[100 \times (\text{FN} + \text{UN} + \text{N}_\text{L} + \text{N}_\text{G})/\text{NI}]$, where all terms were as defined in the equation above.

Ruminal Methanogens (Trial 3)

On wk 10, the 2 pairs of rumen-cannulated cows on the study were used for trial 3. Rumen samples were

collected for DNA isolation to conduct quantitative (real-time) PCR. Sampling was conducted at 0700 h (1 h prefeeding) on the 3 d of emission measurements. Liquid and solid content were isolated in separate vessels after squeezing ruminal samples through 4 layers of cheesecloth. Both fluid and solid content were frozen immediately at –20°C and later stored at –80°C until DNA isolation. Procedures for DNA extraction, PCR reactions, and calculation of relative population sizes based on 16S rRNA gene copy numbers have been described previously (Stevenson and Weimer, 2007). Quantitative (real-time) PCR, including relative quantification against total methanogen DNA, was conducted as described in Stevenson and Weimer (2007), with the primer set for total methanogens, *Methanosphaera stadtmanae*, and *Methanobrevibacter* spp. strain AbM4 as described by Zhou et al. (2009). Annealing and extension stage within each cycle was carried out at 58°C for 60 s for total methanogens, at 56°C for 90 s for *Ms. stadtmanae*, and at 50°C for 90 s for *Methanobrevibacter* spp. strain AbM4. Ruminal pH and temperature measurements were conducted every 5 min during the same 3 d using rumen bolus pH probes and receivers (Kahne Ltd., Auckland, New Zealand), as outlined in Xiaoxiao (2009). Boluses were calibrated to pH 4 and 7 at 39°C every morning during milking and before feeding.

Statistical Analysis

All data were analyzed using the MIXED procedure of SAS (SAS Institute, 2004). In all models described below, μ referred to the overall mean, FCE (high-FCE cows vs. low-FCE cows) was the treatment, pair was treated as a random variable, and residual errors were assumed independent and normally distributed. Significance was declared for $P \leq 0.05$ and tendencies for $0.05 < P \leq 0.10$.

Trial 1. Data from wk 9 to 12 were missing for one pair of cows and milk analysis data for another pair were excluded from the analysis in wk 12. In the former case 1 cow had peritonitis and in the latter case the milk sample was deemed unreliable because automatic sampler's inability to collect a representative milk sample when milk production is less than approximately 5 kg per milking. Milk production performance, DMI, FCE, and FE_L were evaluated as a split plot in time with FCE and pair in the main plot and week ($n = 12$) in the subplot using repeated measurements, the ar(1) co-variance matrix function, and the following model:

$$Y_{ijk} = \mu + G_i + P_j + W_k + G_i \times W_k + e_{ijk},$$

Table 1. Repeatability of feed conversion efficiency and feed efficiency for lactation of cows with high and low feed conversion efficiency (trial 1)

Item	FCE group ¹			P-value		
	High	Low	SEM	FCE	wk	FCE × wk
DMI (kg/d)	23.7	20.6	0.89	0.03	<0.01	0.73
Milk (kg/d)	43.1	21.2	2.09	<0.01	<0.01	0.09
Milk NE _L (Mcal/d)	30.3	15.9	1.69	<0.01	0.02	0.39
Efficiency ²						
FCE (milk kg/kg of DMI)	1.82	1.03	NA ³	<0.01	<0.01	0.10
FE _L (milk Mcal/kg of DMI)	1.28	0.77	0.07	<0.01	<0.01	0.27

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (FCE, milk kg/kg of DMI) before the start of the study.

²FE_L = feed efficiency for lactation.

³Statistical inferences based on rank analysis. NA = not applicable.

where Y_{ijk} = measured responses, G_i is FCE group ($i = 1$ to 2), P_j is pair ($j = 1$ to 8), W_k is week ($k = 1$ to 12), $G_i \times W_k$ is the FCE by week interaction term, and e_{ijk} is the residual error. Data for FCE, milk fat percent, milk protein percent, milk lactose percent, MUN, SCC, and lactose yield were not normally distributed and were analyzed using ranks.

Trial 2. Data were analyzed as a randomized complete block ($n = 4$) and paired t -tests. The effect of FCE on measured responses (Y_{ijk}) was determined with the following model:

$$Y_{ijk} = \mu + G_i + B_k + G_i \times B_k + P_{j(k)} + e_{ijk},$$

where G_i is FCE group ($i = 1$ to 2), B_k is block ($k = 1$ to 4), $G_i \times B_k$ is the FCE by block interaction term, $P_{j(k)}$ is pair j ($j = 1$ to 8) within block k , and e_{ijk} is the residual error. Data for milk NE_L, NE_{MLG}, SCC, and milk C were not normally distributed but were analyzed using natural logarithm. The $G_i \times B_k$ term was retained in the model only when $P \leq 0.25$.

Trial 3. Response variables were analyzed using a paired t -test and the model $Y_{ijk} = \mu + G_i + P_j + e_{ijk}$, where all terms were as previously described.

RESULTS AND DISCUSSION

Diet Composition

Chemical composition of the diet was 47.3% DM, and (DM basis) 92.5% OM, 17.2% CP, 28.1% NDF, 41.3% NFC, 5.9% EE, and 45.8% C. Dietary GE content was 4.68 Mcal/kg of DM and monensin content was 8.95 mg/kg of DM.

FCE (Trial 1)

In trial 1, FCE and FE_L was (LSM $\pm$ SD) 1.43 ± 0.48 and 1.03 ± 0.32 , respectively. Vallimont et al. (2011) re-

ported comparable values (1.61 and 0.98, respectively) calculated from 305-d lactation data collected in commercial farms. Spurlock et al. (2012) reported FCE >1.8 for the first 150 DIM. As expected, the contribution of body reserve to milk production inflates FCE when cows are in negative energy balance in early lactation compared with FCE collected later in lactation. In our trial, high-FCE cows had 15% greater DMI and 103% greater milk production, which resulted in 78% greater FCE compared with low-FCE cows (Table 1). All cows were after lactation peak and, thus, milk production and DMI declined throughout the trial. Although the decline in DMI did not differ between the 2 groups, a tendency for a faster decline in milk production was noted in the low- compared with high-FCE cows, which was probably the reason for the tendency for FCE to decline faster in low- compared with high-FCE cows (Figure 1).

Digestive and Metabolic Partitioning of Energy and N (Trial 2)

Cow Performance, Milk Composition, and Efficiencies. The 2 groups of cows did not differ for BW (665 ± 84 kg), but BW gain tended to be 0.29 kg/d lower and BCS was 0.9 units lower in high- than low-FCE cows (Table 2). In addition, DMI and milk production was 4.1 and 22.5 kg/d higher in high- than low-FCE cows. Percent fat in milk did not differ ($3.85 \pm 0.55\%$), but milk protein percent was 0.33 percentage units lower (3.01 vs. 3.34%) and SCC was 381,000 cells/mL lower (107,000 vs. 488,000 cells/mL), whereas lactose percent tended to be 0.38 percentage units greater (4.98 vs. 4.66%) in high- compared with low-FCE cows. Others have shown that selection for higher milk production resulted in greater susceptibility to disease and in particular mastitis (Kitchen, 1981; Shook, 1989; Aldist et al., 1995). Although in some studies high

Figure 1. Repeatability of feed conversion efficiency (FCE) for mid- to late-lactation cows grouped as high FCE (black boxes, FCE = 1.87 ± 0.22 , LSM $\pm$ SD) and low FCE (white boxes, FCE = 1.14 ± 0.20) at the start of the trial; vertical bars are SEM; the *P*-value for the interaction between FCE group and week was 0.10 (data from trial 1).

SCC has been negatively correlated with lactose percent (Harmon, 1994) and milk protein percent (Auldist et al., 1995), the observed lower milk protein content in cows with low SCC in our study could have been due to a dilution effect. Guidelines of Dairy Records Management Systems (DRMS, 2011) were used to convert SCC to SCS and estimate milk losses to further explore the effect of the difference in SCC on FCE. Expected milk loss was 0.77 and 2.22 kg/d ($P = 0.02$) for high- and low-FCE cows, respectively. This difference explained 6.4% of the observed difference in milk production between the 2 groups of cows and highlighted the possible contribution of immune response to the FCE.

The yield of all milk components and milk NE_L differed between FCE groups, most likely because of the difference in milk production. Feed conversion efficiency, FE_L, and feed efficiency for lactation, maintenance, and body gain were 76, 66, and 17% higher in high- than in low-FCE cows (Table 2). These data suggested that differences in milk production was the main contributor to differences in FCE, but the tendency for lower BW gain of the high-FCE cows may have contributed to their higher efficiency compared with low-FCE cows. These results are in agreement with Vallimont et al. (2011), who concluded that larger cows and cows with higher BCS are genetically inclined toward lower feed efficiency and selection for high milk production and lower BW will increase efficiency.

Intake and Digestibility of Nutrients. Table 3 summarized intake and digestibility data. As it was true for DMI, intake of OM, CP, NDF, NFC, and EE were

Table 2. Performance and efficiencies of cows with high and low feed conversion efficiency (trial 2)

Item	FCE group ¹		SEM	<i>P</i> -value
	High	Low		
BW (kg)	633	696	30	0.18
BW gain (kg/d)	0.40	0.69	0.13	0.08
BCS	2.84	3.74	0.18	0.01
DMI (kg/d)	23.6	19.5	0.96	0.01
Milk (kg/d)	41.9	19.4	1.82	<0.01
FPCM ² (kg/d)	39.0	19.7	1.90	<0.01
Milk component content				
Fat (%)	3.62	4.08	0.18	0.12
Protein (%)	3.01	3.34	0.06	0.01
Lactose (%)	4.98	4.60	0.13	0.06
MUN (mg/dL)	10.32	10.68	0.30	0.43
SCC ³ (10 ³ cell/mL)	107	488	2.00	0.03
Milk component yield				
Fat (kg/d)	1.52	0.81	0.10	<0.01
Protein (kg/d)	1.26	0.65	0.05	<0.01
Lactose (kg/d)	2.08	0.85	1.08	<0.01
MUN (g/d)	4.32	2.03	0.24	<0.01
Energy				
Milk NE _L (Mcal/kg)	0.70	0.75	0.02	0.11
Milk NE _L (Mcal/d)	29.5	14.8	1.44	<0.01
NE _{LMG} ⁴ (Mcal/d)	41.5	29.8	1.07	<0.01
Efficiency				
FCE ⁵ (milk kg/kg of DMI)	1.78	1.01	0.08	<0.01
FE _L ⁶ (milk Mcal/kg of DMI)	1.26	0.76	0.06	<0.01
FE _{LMG} ⁷ (Mcal/kg of DMI)	1.79	1.53	0.07	0.01

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

²FPCM = fat- and protein-corrected milk = milk (kg/d) $\times$ [0.1226 $\times$ fat (%) + 0.0776 $\times$ true protein (%) + 0.2534] (IDF, 2010).

³Mean and *P*-value from SCC derived from data analysis using natural log-transformation.

⁴NE_{LMG} = milk NE_L + NE_M + NE_G.

⁵FCE = feed conversion efficiency, milk kg/kg DMI.

⁶FE_L = feed efficiency for lactation.

⁷FE_{LMG} = feed efficiency for lactation, maintenance, and body gain.

greater for high- than for low-FCE cows. However, apparent digestibility of OM, EE, and TDN at productive level (Table 3) were 2.6, 2.5, and 2.6 percentage units lower, and apparent digestibility of CP tended to be 2.1 percentage units lower for high- than for low-FCE cows. Interestingly, the dietary fraction with the highest variability (SEM) in digestibility among cows was NDF (Table 3). Results are consistent with decreased digestibility of dietary feed fractions with greater DMI (NRC, 2001; Tine et al., 2001). Despite lower apparent digestibility, the digested amounts of DM, OM, CP, NFC, EE, and TDN at productive level were higher in high- than in low-FCE cows. The higher fractional rate of passage associated with higher DMI for high-compared with low-FCE cows may have contributed to equalizing the amount of NDF digested in both groups of cows (Table 3).

Methane and Carbon Dioxide Emissions. Emissions data reported in Table 4 were within the

Table 3. Intake and digestibility of nutrients in cows with high and low feed conversion efficiency (trial 2)

Item	FCE group ¹		SEM	P-value
	High	Low		
Intake (kg/d)				
DM	23.6	19.5	0.96	0.01
OM	21.8	18.0	0.89	0.01
CP	4.1	3.4	0.16	0.01
NDF	6.6	5.4	0.28	0.01
NFC	9.8	8.1	0.39	0.01
EE ²	1.4	1.2	0.06	0.01
Apparent digestibility (%)				
DM	68.0	70.6	0.73	0.07
OM	69.5	72.1	0.67	0.05
CP	67.7	69.8	0.62	0.08
NDF	46.0	49.7	1.40	0.14
NFC	86.6	88.5	0.78	0.13
EE	64.3	66.9	1.26	0.04
TDN _P ³	68.2	70.7	0.62	0.04
Apparently digested (kg/d)				
DM	16.0	13.8	0.69	0.04
OM	15.1	13.0	0.65	0.04
CP	2.8	2.4	0.12	0.04
NDF	3.0	2.7	0.18	0.22
NFC	8.5	7.2	0.37	0.03
EE	0.9	0.8	0.04	0.02
TDN _P	16.1	13.8	0.69	0.03

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

²EE = ether extract.

³TDN_P = TDN at production level = DOMI + DFAI $\times$ 1.25, where DOMI and DFAI are apparently digestible OM intake (kg/d) and apparently digested FA intake (kg/d), respectively (Broderick et al., 2010).

range of those reported in nutritional studies (Aguerre et al., 2011; Hassanat et al., 2013; Arndt et al., 2015). Emitted C did not differ between high- and low-FCE cows (4.30 and 4.60 kg/d, respectively; $P = 0.26$, data not shown). Similarly, emissions of CH₄-C (0.33 and 0.37 kg/d; $P = 0.26$, data not shown) and CO₂-C (3.97 vs. 4.23 kg/d, $P = 0.47$, data not shown) did not differ between high- and low-FCE cows. Consequently, daily emissions of CH₄ and CO₂ did not differ between the 2 groups of cows (Table 4). However, emissions expressed per unit of DMI, NDF intake, and amount of NDF digested were 26, 20, and 62% lower for high- compared with low-FCE cows, suggesting that the similar daily CH₄ emission observed between groups may have been the result of a reduced methanogenesis per unit of NDF digested for high- compared with low-FCE cows.

Energy Partitioning. In this trial, daily GEI, digestible energy, urine energy, methane energy, and ME averaged 102.2, 74.2, 3.1, 6.2, and 64.9 Mcal/d, respectively. These values were in agreement with the respective values of 104.5, 72.8, 3.8, 5.8, and 63.2 Mcal/d reported by Tine et al. (2001) for cows consuming 23.4 kg/d fed a 60% corn silage-based diet (DM basis) and

producing 32.2 kg/d of 3.5% FCM. High-FCE cows of the current trial consumed 20% more GE (Table 5), digested 16% more energy, and excreted 33% more fecal energy than low-FCE cows. Daily losses as methane energy and urine energy did not differ between the 2 groups, leading to a 20% greater ME supply for high-compared with low-FCE cows (70.6 vs. 59.1 Mcal/d, respectively). Daily expenditure for NE_M did not differ between the 2 groups, but expenditure as milk NE_L was greater and expenditure as NE_G was lower for high-compared with low-FCE cows. Also, in our trial, heat production averaged 39.4 ± 4.91 Mcal/d, which was comparable to the 35.3 Mcal/d reported in Tine et al. (2001) for cows at similar production levels, but higher than the 26.8 and 30.7 Mcal/d reported in Belyea and Adams (1990) and Reynolds et al. (2001), respectively, for lower-producing cows. Greater DMI (23.6 vs. 19.5 kg/d; Table 2), TDN at productive level digested (16.1 vs. 13.8 kg/d; Table 3), and net energy expenditure in the form of milk and body gain (31.5 vs. 18.4 Mcal/d; Table 5) should have led to greater heat production for high- compared with low-FCE cows. Thus, the absence of difference in heat production between high- and low-FCE cows was unexpected. Although heat production was estimated by difference and thus the error was cumulative, these data suggested that differences in FCE could have been associated with differences in efficiency of chewing activity, rumen fermentation, or conversion of ME to net energy.

As a percentage of GEI, high-FCE cows had 10.4% [$100 \times (28.6 - 25.9)/25.9$; Table 5] greater fecal energy

Table 4. Methane and carbon dioxide emissions of cows with high and low feed conversion efficiency (trial 2)

Item	FCE group ¹		SEM	P-value
	High	Low		
CH ₄ (g/d)	439	494	32.08	0.26
CH ₄ /DMI (g/kg)	18.6	25.1	0.84	<0.01
CH ₄ /NDFI ² (g/kg)	66.9	91.3	2.88	<0.01
CH ₄ /NDFD ³ (g/kg)	147	184	4.92	<0.01
CH ₄ /milk (g/kg)	10.6	30.4	3.59	<0.01
CH ₄ /milk NE _L (g/Mcal)	15.2	39.6	4.89	0.01
CH ₄ /NE _{LMG} ⁴ (g/Mcal)	10.7	16.5	0.90	<0.01
CO ₂ (g/d)	14,553	15,494	879	0.47
CO ₂ /DMI (g/kg)	618	789	24.9	<0.01
CO ₂ /NDFI (g/kg)	2,225	2,870	81.8	<0.01
CO ₂ /NDFD (g/kg)	4,878	5,766	1.0	<0.01
CO ₂ /milk (g/kg)	353	960	116	0.01
CO ₂ /milk NE _L (g/Mcal)	506	1,252	157	0.01
CO ₂ /NE _{LMG} (g/Mcal)	356	520	32.4	<0.01

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

²NDFI = NDF intake.

³NDFD = NDF digested.

⁴NE_{LMG} = NE_L + NE_M + NE_G.

Table 5. Energy partitioning of high and low feed conversion efficient cows (trial 2)

Item	FCE group ¹ (Mcal/d)				FCE group (% GEI ²)			
	High	Low	SEM	<i>P</i> -value	High	Low	SEM	<i>P</i> -value
GEI	111.5	92.8	4.46	0.01	100	100		
Fecal E ³	31.9	24.0	1.43	<0.01	28.6	25.9	0.70	0.03
DE ⁴	79.6	68.8	3.22	0.04	71.4	74.1	0.70	0.03
Urine E ⁵	3.09	3.17	0.20	0.75	2.76	3.40	0.12	<0.01
CH ₄ E ⁶	5.82	6.55	0.43	0.26	5.23	6.99	0.24	<0.01
ME	70.6	59.1	2.71	0.01	63.5	63.7	0.52	0.76
Milk NE _L	29.2	13.9	1.07	<0.01	26.4	16.2	1.17	<0.01
NE _M	10.1	10.8	0.35	0.18	9.1	11.8	0.35	<0.01
NE _G	2.30	4.49	0.81	0.05	2.02	4.63	0.78	0.02
NE _{LMG} ⁷	41.9	30.2	2.22	<0.01	37.5	32.6	1.45	0.01
Heat ⁸	37.8	40.7	1.55	0.23	34.1	44.1	1.65	<0.01
NMH ⁹	28.8	29.0	1.65	0.95	26.0	31.1	1.33	0.02

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

²GEI = gross energy intake.

³Fecal E = fecal energy.

⁴DE = digestible energy.

⁵Urine E = urine energy.

⁶CH₄ E = ethane energy.

⁷NE_{LMG} = NE_L + NE_M + NE_G.

⁸Heat calculated as ME - (NE_L + NE_G).

⁹NMH = nonmaintenance heat calculated as Heat - NE_M; NMH expressed as a percent of ME was 40.9 and 48.8 for high-FCE and low-FCE cows, respectively (SEM = 2.22, *P* = 0.04).

and 3.6% lower GE digestibility than low-FCE cows. However, the digestibility loss was compensated by an 18.8% reduction in urine energy and a 25.1% reduction in methane energy in high- compared with low-FCE cows, leading to the same percentage of GE converted to ME in both groups (63.5 vs. 63.7%; Table 5). The conversion of DE to ME, however, was 3.3% higher for high- than low-FCE cows (88.8 vs. 86.0%; *P* < 0.01, data not shown), and the conversion of ME to the sum of NE_L, NE_G, and NE_M was 15% higher for high- than low-FCE cows (59.1 vs. 51.1%; *P* = 0.01, data not shown). As a result, the conversion of GEI to the sum of NE_L, NE_G, and NE_M was 5.1 percentage units higher in high- compared with low-FCE cows (37.5 vs. 32.6%, respectively; Table 5), and heat production was 10 percentage units lower in high- than in low-FCE cows (34.1 vs. 44.1%, respectively; Table 5). Net efficiency of use of dietary ME for milk production was 0.61 (high FCE) versus 0.62 (low FCE) when calculated according to INRA (1989). Similarly, when calculated according to AFRC (1990), milk production was 0.64 for both high and low FCE. These values were in agreement with the milk production estimates reported by Yan et al. (1997).

Figure 2 was constructed to compare the percentage of GEI available as digestible energy, ME, and the sum of NE_L, NE_G, and NE_M for cows in the current trial with recent literature and to illustrate that the loss of

digestibility in high- compared with low-FCE cows was more than compensated by a combination of at least 3 mechanisms: a reduction in methane energy, a reduction in urine energy, and a greater efficiency of utilization of ME. The suggestion that high-producing dairy cows may have a more efficient intermediary metabolism was proposed by Belyea and Adams (1990), who reported lower heat production per kilogram of metabolic BW in high- than in low-producing cows. Although our study did not investigate genetic differences, none of the results could be attributed to nutritional effects. Recent work has indicated that there might be a genetic component to FCE (calculated as 305-d FCM/305-d DMI; Vallimont et al., 2011). Together, data of Table 4 (CH₄/sum of NE_L, NE_G, and NE_M, g/Mcal) and data of Table 5 strengthened the suggestion of Yan et al. (2010) that lower heat production (i.e., greater efficiency of utilization of ME) was associated also with lower methane energy as a proportion of GEI.

Nitrogen Partitioning. In our study, N recovery was similar for the high- and low-FCE cows (97.9 and 95.5%, respectively). Furthermore, NI, fecal N, urine N, and milk N averaged 597, 188, 219, and 150 g/d, respectively, which corresponded closely to data in Hassanat et al. (2013) and Arndt et al. (2015). As indicated in Table 6, NI was 21% greater, fecal N was 30% greater, milk N was 94% greater, but urine N did not differ and body gain N tended to be lower for high- compared

Figure 2. Energy partitioning of mid- to late-lactation cows grouped based on feed conversion efficiency (FCE; milk kg/kg of DMI) as low FCE (light gray boxes, FCE = 1.14 ± 0.20) and high FCE (dark gray boxes, FCE = 1.87 ± 0.22, LSM ± SD) at the start of the trial. DE = digestible energy; FE = fecal energy; CH₄E = methane energy; UE = urine energy; NE_{LMG} = net energy for milk production, maintenance, and body gain; and NMH = nonmaintenance heat production. Upward-pointing arrows labeled a, b, and c indicate the DE, ME, and NE_{LMG} reported in Tine et al. (2001), Reynolds et al. (2001), and Cammell et al. (2000), respectively (data from trial 2).

with low-FCE cows. Also, apparently metabolized N was 79 g/d higher in high- compared with low-FCE cows (230 vs. 151 g/d, respectively). There was no difference in daily manure N excretions (fecal N + urinary

N), but urinary N-to-fecal N ratio increased from 1.00 in high-FCE cows to 1.39 in low-FCE cows.

As a percentage of NI, high-FCE cows tended to excrete 6.9% more fecal N and apparent N digest-

Table 6. Nitrogen partitioning of high and low feed conversion efficient cows (trial 2)

Item	FCE group ¹ (g/d)				FCE group (% N intake)			
	High	Low	SEM	P-value	High	Low	SEM	P-value
N Intake	653	540	26.2	0.01				
Fecal N	212	163	8.4	<0.01	32.4	30.3	0.6	0.08
ApDN ²	441	377	19.3	0.04	67.6	69.7	0.6	0.08
Urine-N	211	227	15.4	0.42	32.2	41.7	1.5	<0.01
ApMN ³	230	151	13.1	<0.01	35.4	28.0	1.8	<0.01
N _L ⁴	198	102	7.3	<0.01	30.3	19.1	1.0	<0.01
N _G ⁵	10	17	3.2	0.10	1.57	3.06	0.5	0.03
N _{LG} ⁶	208	119	9.3	<0.01	31.9	22.2	1.1	<0.01
Manure N ⁷	423	390	22.5	0.22	65.6	72.0	1.77	<0.01

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

²ApDN = apparently digested n = N intake – fecal N.

³ApMN = apparently metabolized N = apparently digested N – urine N.

⁴N_L = milk N.

⁵N_G = body gain N.

⁶N_{LG} = N_L + N_G.

⁷Manure N = fecal N + urine N.

Figure 3. Nitrogen partitioning of mid- to late-lactation cows grouped based on feed conversion efficiency (FCE, milk kg/kg of DMI) as low FCE (light gray boxes, $FCE = 1.14 \pm 0.20$) and high FCE (dark gray boxes, $FCE = 1.87 \pm 0.22$, $LSM \pm SD$) at the start of the trial. ApDN = apparently digested N; FN = fecal N; ApMN = apparently metabolizable N; UN = urine N; N_L = milk N; N_G = body gain N; and N_u = N unaccounted for. Upward-pointing arrows labeled a, b, and c indicate the ApDN, ApMN, and milk N_L reported in Colmenero and Broderick (2006), Hassanat et al. (2013), and Arndt et al. (2015), respectively (data from trial 2).

ibility tended to be reduced by 3.1% compared with low-FCE cows. Also, NI partitioned toward milk was 59% greater, but N in body gain was 49% lower, and urinary N was 23% lower in high- compared with low-FCE cows. Excess metabolizable N relative to the need for milk protein synthesis in lower-producing low-FCE cows contributed to higher urinary N and reduced NUE compared with high-FCE cows. These relationships have been reported earlier (Kebreab et al., 2002; Dijkstra et al., 2011) and are predicted by the NRC (2001). Figure 3 was constructed to illustrate N partitioning between the 2 groups of cows of the present study, to highlight the pool of N unaccounted for [which may be due to cumulative error, the hair and scurf N, and possibly other possible unidentified N pool (e.g., body urea-N) that remained unmeasured], and to compare our results to recent literature.

Manure and Manure N Characterization. Fecal excretion, urinary excretion, N in fecal DM, and N in urine averaged 43.4 kg/d, 24.8 kg/d, 2.83 g/100 g, and 0.895 g/100 mL, respectively. These values were in agreement with data reported in Wattiaux and Karg (2004). High-FCE cows produced 40% more feces, 22% more urine, and 33% more manure than low-FCE cows (Table 7). Concentration of N in feces did not differ, but

urinary N concentration was lower in high-FC compared with low-FCE cows. Nutritional studies have indicated that, for the most part, the excess metabolizable N not used for milk production was lost as urinary urea-N. In the current study, there was a nonsignificant ($P = 0.12$) 19% reduction in urinary urea-N excretion, but a significant decrease in the concentration of urinary urea-N in high- compared with low-FCE cows. Ammonia emission from manure ($P = 0.12$), which is a serious concern (Galloway et al., 2010), originates primarily from urine and especially urinary urea-N. Thus, the changes in fecal N and urinary N excretions (Table 6) and urinary N composition (Table 7) suggested that manure N might be less vulnerable to ammonia volatilization in high- compared with low-FCE cows. However, in our study, low-FCE cows were fed excess N.

Ruminal Methanogens (Trial 3)

Ruminal temperature, pH, and time of pH <6.0 averaged 39.2 versus 39.4°C ($P = 0.59$), 6.23 versus 6.36 ($P = 0.23$), and 227 versus 122 min ($P = 0.38$) for high- versus low-FCE cows, respectively. However, Table 8 showed that a 36% lower prevalence of *Methanobrevibacter* spp. strain AbM4 in the ruminal

Table 7. Manure production and characterization of high and low feed conversion efficient cows (trial 2)

Item	FCE group ¹		SEM	P-value
	High	Low		
Feces, as-is (kg/d)	50.7	36.1	2.10	<0.01
Feces DM, as-is (%)	15.0	15.8	1.0	0.09
Feces DM (kg/d)	7.57	5.70	0.32	<0.01
Feces N (% DM)	2.80	2.86	0.04	0.24
Urine (kg/d)	27.2	22.3	1.16	0.01
Urine N (g/100 mL)	0.78	1.01	0.05	0.01
Urine urea-N (g/100 mL)	0.53	0.80	0.05	0.01
Urine urea-N (g/d)	145	180	14.5	0.12
Manure, as-is (kg/d)	77.9	58.5	2.7	<0.01
Manure/milk (kg/kg)	1.87	3.49	0.21	0.01
Manure/FPCM ² (kg/kg)	2.01	3.48	0.20	0.01
Manure/DMI (kg/kg)	3.29	3.01	0.06	0.03

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg DMI) before the start of the study.

²FPCM = fat- and protein-corrected milk = milk (kg/d) $\times$ [0.1226 $\times$ fat (%) + 0.0776 $\times$ true protein (%) + 0.2534] (IDF, 2010).

solids of high-FCE cows compared with low-FCE cows. Zhou et al. (2009) reported greater prevalence of 16S rRNA genes of *Ms. stadtmanae* and *Methanobrevibacter* spp. strain AbM4 in inefficient steers compared with efficient steers as determined by residual feed intake. Zhou et al. (2009) suspected that *Methanobrevibacter* spp. strain AbM4 might use acetate as a substrate for CH₄ production, possibly leading to greater CH₄ energy loss in low-feed efficiency beef cattle (Nkrumah et al., 2006; Hegarty et al., 2007). Our data indicated that in dairy cattle also higher prevalence of *Methanobrevibacter* spp. strain AbM4 (Table 8) was associated with higher emission of CH₄ per unit of DMI or digested NDF (Table 4), which in turn may have contributed to the observed difference in FCE. These potentially acetoclastic methanogens, however, represented only a small percentage of the rumen methanogen population and the observed effects may have been the results of other factors (e.g., differential passage rate) in effects precluding us from establishing an unequivocal causal relationship.

CONCLUSIONS

The current study demonstrated that FCE was a repeatable trait in mid to late lactation. High-FCE cows had greater production performance compared with low-FCE cows; thus, part of their greater FCE was caused by dilution of maintenance for both energy and N. In spite of losses in digestive efficiency, greater DMI led to greater supplies of digestible energy and apparently digested N in high- compared with low-FCE. However, ME expressed as a percentage of GEI did not differ between groups because high-FCE cows partitioned a lower proportion of GEI to methane energy and urinary energy compared with low-FCE cows. The reduced loss of urinary energy reflected a lower loss of urinary N, whereas the reduced loss of methane energy was associated with lower prevalence of *Methanobrevibacter* spp. strain AbM4 in ruminal solids of high- compared with low-FCE cows. Similar daily methane emission, in spite of differences in DMI, may have been the result of a reduced methanogenesis per unit of NDF digested in high- compared with low-FCE cows. Furthermore, efficiency of conversion of ME to milk and body gain was higher in high- than low-FCE cows. No difference in ruminal temperature suggested no difference in fermentative heat, but, all together, less methane energy, less urine energy, less metabolic heat, and less energy spent for immune response may have contributed to the observed differences in FCE. The low N use efficiency observed in our study for the low-FCE cows was most likely associated with excess N intake relative to mammary gland requirements. Data were insufficient to explore possible differences that might be associated with the kidney's role in urea-N conservation, or the liver's role as a major site of N transformation.

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Table 8. Comparison of copy numbers (percentage of total methanogens) of targeted methanogen 16S rRNA genes in high and low feed conversion efficient cows (trial 3)

Item	FCE group ¹		SEM	P-Value
	High	Low		
Liquid phase of rumen contents				
<i>Methanosphaera stadtmanae</i>	1.05	0.59	0.07	0.13
<i>Methanobrevibacter</i> spp. strain AbM4	1.29	1.36	0.08	0.54
Solid phase of rumen contents				
<i>Ms. stadtmanae</i>	1.39	1.08	0.20	0.32
<i>Methanobrevibacter</i> sp. strain AbM4	1.14	1.79	0.17	0.01

¹FCE group = cows with high (1.87 ± 0.22) and low (1.14 ± 0.20) feed conversion efficiency (milk kg/kg of DMI) before the start of the study.

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