Author(s): Guinguina A., Yan T., Bayat A.R., Lund P. & Huhtanen P.

Title: The effects of energy metabolism variables on feed efficiency in respiration chamber studies with lactating dairy cows

Year: 2020

Version: Preprint version

Please cite the original version:

Guinguina A., Yan T., Bayat A.R., Lund P., Huhtanen P. (2020). The effects of energy metabolism variables on feed efficiency in respiration chamber studies with lactating dairy cows. Journal of Dairy Science 103(9): 7983-7997. https://doi.org/10.3168/jds.2020-18259.

J. Dairy Sci. 103
https://doi.org/10.3168/jds.2020-18259

The effects of energy metabolism variables on feed efficiency in respiration chamber studies with lactating dairy cows

A. Guinguina,[1] T. Yan,[2] A. R. Bayat,[3] P. Lund,[4] and P. Huhtanen[1]*
[1]Department of Agricultural Research for Northern Sweden, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden
[2]Agri-Food and Biosciences Institute, Hillsborough, Co. Down BT26 6DR, United Kingdom
[3]Production Systems, Natural Resources Institute Finland (LUKE), 31600 Jokioinen, Finland
[4]Department of Animal Science, Aarhus University, AU Foulum, PO Box 50, 8830 Tjele, Denmark

ABSTRACT

The objective of the present study was to investigate factors related to variation in feed efficiency (FE) among cows. Data included 841 cow/period observations from 31 energy metabolism studies assembled across 3 research stations. The cows were categorized into low-, medium-, and high-FE groups according to residual feed intake (RFI), residual energy-corrected milk (RECM), and feed conversion efficiency (FCE). Mixed model regression was conducted to identify differences among the efficiency groups in animal and energy metabolism traits. Partial regression coefficients of both RFI and RECM agreed with published energy requirements more closely than cofficients derived from production experiments. Within RFI groups, efficient (Low-RFI) cows ate less, had a higher digestibility, produced less methane (CH_4) and heat, and had a higher efficiency of metabolizable energy (ME) utilization for milk production. High-RECM (most efficient) cows produced 6.0 kg/d more of energy-corrected milk (ECM) than their Low-RECM (least efficient) contemporaries at the same feed intake. They had a higher digestibility, produced less CH_4 and heat, and had a higher efficiency of ME utilization for milk production. The contributions of improved digestibility, reduced CH_4, and reduced urinary energy losses to increased ME intake at the same feed intake were 84, 12, and 4%, respectively. For both RFI and RECM analysis, increased metabolizability contributed to approximately 35% improved FE, with the remaining 65% attributed to the greater efficiency of utilization of ME. The analysis within RECM groups suggested that the difference in ME utilization was mainly due to the higher maintenance requirement of Low-RECM cows compared with Medium- and High-RECM cows, whereas the difference between Medium- and High-RECM cows resulted mainly from the higher efficiency of ME utilization for milk production in High-RECM cows. The main difference within FCE (ECM/DMI) categories was a greater (8.2 kg/d) ECM yield at the expense of mobilization in High-FCE cows compared with Low-FCE cows. Methane intensity (CH_4/ECM) was lower for efficient cows than for inefficient cows. The results indicated that RFI and RECM are different traits. We concluded that there is considerable variation in FE among cows that is not related to dilution of maintenance requirement or nutrient partitioning. Improving FE is a sustainable approach to reduce CH_4 production per unit of product, and at the same time improve the economics of milk production.
Key words: dairy cow, energy metabolism, feed efficiency, residual feed intake, residual production

INTRODUCTION

The productivity of dairy cattle has risen considerably due to advances in nutrition, genetics, and management. Feed efficiency (**FE**) is an important trait under practical conditions, as it has a major influence on profitability and environmental efficiency in the dairy industry. VandeHaar and St-Pierre (2006) estimated that FE of dairy cows in North America has doubled in the past 50 yr, largely as a consequence of selecting and managing cows for increased productivity. With increased milk production, a greater proportion of feed energy is used for milk instead of cow maintenance, resulting in the dilution of maintenance. However, in intensive production systems, further improvements in FE from increased productivity are marginal. Breeding for increased production has been associated with larger body size, leading to an increased ME requirement per unit of metabolic BW (Agnew and Yan, 2000; Hansen, 2000), partly offsetting the benefits of FE from improved productivity. In addition, nutrient digestibility decreases at high intakes (NRC, 2001; Huhtanen et al., 2009). The digestibility depression may outweigh the dilution of maintenance, and the efficiency may

Received January 26, 2020.
Accepted April 1, 2020.
*Corresponding author: pekka.huhtanen@slu.se

decline with increased intake (VandeHaar, 1998). On the other hand, methane (CH_4) losses as a proportion of gross energy (**GE**) decrease at high intakes (Yan et al., 2000; Ramin and Huhtanen, 2013), alleviating the intake effects on dietary ME concentration.

An increase in productivity has limited potential for further improvements for FE, and thus alternative approaches for increasing FE are needed. Feed conversion efficiency (**FCE**), expressed as ECM/DMI, is a traditional measure of FE in growing and lactating animals. The use of FCE as a selection criterion, however, has many limitations. For instance, selection for greater milk output increases the cow's energy requirement more than intake potential, resulting in mobilization of body tissues to support the increased energy demand of lactation (Connor, 2015). Residual feed intake (**RFI**) is a common measure of FE in dairy cattle in recent literature. It is calculated as a difference between DMI or energy intake and predicted intake estimated by regression models from energy sinks (production, maintenance, and body weight change). A negative RFI value means feed intake is less than expected and indicates an efficient animal, whereas a positive value indicates an inefficient animal. Coleman et al. (2010) proposed residual solids production as an alternative approach to estimating FE in lactating cows. This method estimates the difference between actual and predicted production for a given DMI, body size, and BCS. A positive value indicates greater efficiency and therefore, is more easily understood by producers than negative RFI values that indicate high efficiency.

Berry and Crowley (2013) cautioned that in some cases RFI may not represent true FE, which partly can be due to biases in estimating partial regression coefficients in the model. Furthermore, relationships between DMI and energy sink variables (milk energy; metabolic BW, **MBW**; and BW change, **ΔBW**) can be highly heterogeneous across different trials (Davis et al., 2014). Often, the partial regression coefficients of RFI models are biologically meaningless and different from expected values. This can be attributed to short measurement periods and inaccuracies in estimating energy balance from ΔBW. The mechanisms associated with variation in FE among cows are poorly understood. The variation in true FE (not related to dilution of maintenance requirement or partitioning nutrients between milk production and body tissues) can be related to converting dietary GE to ME, and subsequently converting ME to net energy (**NE**). The former includes variation in fecal, CH_4, and urinary energy (**UE**) losses, and the latter includes heat production (**HP**) associated with body maintenance and HP from milk synthesis. Therefore, analysis of data from respiration calorimetry studies could be useful in elucidating the mechanisms behind variation in FE among dairy cows. The objective of the present study was to quantify the effects of different energy losses on different FE traits. The cows were categorized into low-, medium-, and high-FE groups on the basis of 3 different efficiency traits. The results of factors influencing energy losses, variance components, and correlations are presented in our companion paper (Guinguina et al., 2020).

MATERIALS AND METHODS

Data

A database containing energy balance data for 841 dairy cow observations was established from calorimetry studies conducted at Agri-Food and Biosciences Institute–AFBI (Hillsborough, UK), The Danish Cattle Research Centre (AU Foulum, Denmark), and Natural Resources Institute Finland–LUKE (Jokioinen, Finland). The list of studies used in the current study is given (Supplemental data file; https://doi.org/10.3168/jds.2020-18259). The range of calorimetric data included in the database is summarized in Table 1. Further details of conducted experiments, calculations, outlier detection, diet composition, and energy metabolism traits were reported in our companion paper (Guinguina et al., 2020).

Calculations and Statistical Analysis

Feed efficiency in this study was evaluated as RFI, residual ECM production (**RECM**), and FCE. The MIXED procedure (SAS Institute Inc., Cary, NC) was used to predict DMI for each cow by fitting the following regression model:

$$\text{Predicted DMI} = b_0 + b_1 \times \text{ECM} + b_2 \times \text{MBW} + b_3 \times \text{EB}_p + b_4 \times \text{EB}_n + \text{Exp} + \text{Diet(Exp)} + \text{Period(Exp)}, \quad [1]$$

where b_0 is the intercept, b_1 is the partial regression coefficient of ECM yield (kg/d), b_2 is the partial regression coefficient of MBW (kg), b_3 is the partial regression coefficient of positive energy balance (**EB_p**, MJ/d), b_4 is the partial regression coefficient of negative energy balance (**EB_n**, MJ/d), and Exp, Diet(Exp), and Period(Exp) are random effects of experiment, diet within experiment, and period within experiment, respectively. Residual feed intake was calculated as the difference between actual DMI and predicted DMI. Because RFI represents a difference between actual and

Table 1. Description of the data used in the study (n = 841)

Item	Mean	SD	Minimum	Maximum
Animal data				
DMI, kg/d	18.0	4.0	7.5	30.9
Forage proportion	0.56	0.175	0.25	1.00
ECM yield, kg/d	25.6	8.4	6.2	52
BW, kg	570	84.9	379	847
Energy measurements, MJ/d				
Gross energy	335	79.0	137	582
Digestible energy	247	54.4	104	427
Urinary energy	11.9	4.54	2	28
Methane energy	21.6	4.35	11	35
Metabolizable energy	214	48.6	84	379
Heat production	128	21.2	75	185
Milk energy	80.4	26.4	19	163
Energy balance	5.1	20.2	−49	50

predicted DMI, a low or negative RFI indicates high efficiency.

Instead of milk solids production (fat + protein) used by Coleman et al. (2010), we used ECM (1 kg of ECM = 3.14 MJ; Sjaunja et al., 1990) as a measure of milk production. We used GE instead of DMI in predicting ECM yield to account for the possible effects of fat supplementation on energy metabolism. Using GE instead of determined ME intake in predicting ECM yield accounts for energy losses in the conversion of GE to ME (fecal, CH_4, and UE losses). The following model was used to predict ECM yield:

$$\text{Predicted ECM} = b_0 + b_1 \times \text{GE intake} + b_2 \times \text{MBW} + b_3 \times EB_p + b_4 \times EB_n + \text{Exp} + \text{Diet(Exp)} + \text{Period(Exp)}, \quad [2]$$

where b_0 is the intercept, b_1 is the partial regression coefficient of GE intake (MJ/d), b_2 is the partial regression coefficient of MBW (kg), b_3 is the partial regression coefficient of EB_p (MJ/d), b_4 is the partial regression coefficient of EB_n (MJ/d), and Exp, Diet(Exp), and Period(Exp) are random effects of experiment, diet within experiment, and period within experiment, respectively. Residual ECM yield was calculated as the difference between actual and predicted ECM yield. Because RECM represents a difference between actual and predicted ECM yield, a high or positive RECM indicates high efficiency.

Feed conversion efficiency was calculated as FCE = ECM (kg)/DMI (kg) without taking into account the effects of BW change that is not usually recorded in short-term respiration chamber studies.

The efficiency of ME utilization for milk production (k_l) was calculated as

$$k_l = E_{l(0)}/(\text{ME intake} - \text{ME requirement for maintenance}),$$

all expressed as MJ/d, where $E_{l(0)}$ is milk energy corrected for zero energy balance calculated as milk energy + (1/0.95) × EB_p or milk energy + 0.84 × EB_n (AFRC, 1993).Cows were categorized into 3 groups of approximately equal sizes (n = 278–284) by RFI value and classified as high RFI (**High-RFI**; RFI >0.72), medium RFI (**Medium-RFI**; RFI −0.39 to 0.72) or low RFI (**Low-RFI**; RFI < −0.39). Similarly, they were grouped by RECM value and classified as high RECM (**High-RECM**; RECM >1.2), medium RECM (**Medium-RECM**; RECM −1.32 to 1.2) or low RECM (**Low-RECM**; RECM < −1.32). Cows with FCE below 1.28 were categorized to group low FCE (**Low-FCE**), cows with FCE 1.28 to 1.51 were categorized to group medium FCE (**Medium-FCE**) and cows with FCE above 1.51 were categorized to high-FCE (**High-FCE**). The effects of RFI, RECM, and FCE groups on intake, production, and energy metabolism variables were determined using the MIXED Procedure of SAS according to a model that included the fixed effect of RFI, RECM, or FCE group and random effects of Exp, Diet(Exp), and Period(Exp). Further pairwise comparisons of least squares means among the efficiency groups were performed using the PDIFF option in the LSMEANS statement. Mixed model regression analysis with random effects of Exp, Diet(Exp), and Period(Exp) was used to evaluate quantitative relationships between variables.

RESULTS

The following equations were derived from the data for RFI and RECM:

Table 2. Production and energy metabolism characteristics of low (n = 279), medium (n = 282), and high (n = 280) residual feed intake (RFI) in respiration chamber studies (total n = 841)

	RFI				
Item	Low	Medium	High	SEM	*P*-value
Animal data					
RFI, kg/d	−1.20	0.16	1.41		
DMI, kg/d	15.9	17.6	18.5	0.52	<0.001
ECM yield, kg/d	23.7	24.0	23.9	1.19	0.72
RECM,[1] kg/d	2.20	−0.21	−2.39	0.33	<0.001
ECM/DMI	1.47	1.34	1.28	0.033	<0.001
BW, kg	562	580	569	9.7	0.01
Energy measurements, MJ/d					
Gross energy (GE)	294	325	340	10.6	<0.001
Fecal energy	72.4	84.5	92.8	3.70	<0.001
Digestible energy (DE)	222	241	247	7.5	<0.001
Methane energy (CH_4E)	19.3	21.4	22.6	0.52	<0.001
Urinary energy (UE)	10.4	11.7	12.2	0.59	<0.001
ME	192	208	213	6.8	<0.001
Milk energy	74.3	75.5	75.2	3.73	0.72
Heat production	114	127	135	2.7	<0.001
Energy balance	5.1	6.8	3.3	2.01	0.09
Energy utilization efficiency, kJ/MJ					
DE/GE	753	742	729	5.0	<0.001
ME/GE	651	638	625	4.4	<0.001
ME/DE	864	861	858	3.1	0.002
CH_4E/GE	67.0	67.1	67.3	1.58	0.95
UE/GE	36.1	36.4	36.1	1.62	0.88
k_l[2]	0.694	0.642	0.598	0.0107	<0.001
CH_4E, g/kg of ECM	15.9	17.1	17.9	0.63	<0.001

[1]RECM = residual ECM yield.

[2]Efficiency of ME use for lactation, calculated as milk energy adjusted to zero energy balance/(ME intake – ME for maintenance).

$$\text{RFI} = \text{DMI} - (1.06 \pm 0.45 + 0.347 \pm 0.0081 \times \text{ECM} + 0.0645 \pm 0.00383 \times \text{MBW} + 0.0704 \pm 0.00330 \times \text{EB}_\text{p} - 0.0581 \pm 0.00412 \times \text{EB}_\text{n}),\ \text{residual variance} = 0.79, \quad [3]$$

where RFI, DMI, and ECM are expressed in kg/d; MBW as kg; and EB_p and EB_n as MJ/d. Excluding the intercept, the contributions of ECM, MBW, EB_p and EB_n on predicted intake were 53, 44, 5, and −2%, respectively;

$$\text{RECM} = \text{ECM} - (0.11 \pm 1.058 + 0.108 \pm 0.0023 \times \text{GE intake} + 0.0816 \pm 0.0083 \times \text{MBW} + 0.149 \pm 0.0083 \times \text{EB}_\text{p} - 0.140 \pm 0.0097 \times \text{EB}_\text{n}),\ \text{residual variance} = 4.45, \quad [4]$$

where RECM and ECM are as kg/d, MBW as kg, and GE intake, EB_p, and EB_n as MJ/d.

Means and standard error of the mean of different animal and energy metabolism variables for RFI groups are presented in Table 2. The difference in RFI between Low- and High-RFI cows was 2.6 kg/d ($P < 0.001$), but ECM yield was similar among RFI groups. However, RECM was 4.6 kg/d ($P < 0.001$) greater for Low- than for High-RFI cows and Medium-RFI cows were intermediate. Feed conversion efficiency in terms of ECM/DMI followed the same pattern. Medium-RFI cows were 11 kg heavier than Low- and High-RFI cows. Energy losses in feces, CH_4, and urine increased ($P < 0.001$) with increasing RFI. As a result of reduced energy losses (21 MJ/d) with higher efficieccy (Low-RFI), the difference in ME intake (25 MJ/d) between Low- and High-RFI groups was about 45% of the difference in GE intake (46 MJ/d). Greater (25 MJ/d; $P < 0.001$) ME intake of High-RFI cows was counterbalanced by a greater HP (21 MJ/d; $P < 0.001$), resulting in no differences in energy balance. Lower ($P < 0.001$) HP in Low- compared with High-RFI cows was associated with improved ($P < 0.001$) efficiency of ME utilization for milk production.

Gross energy digestibility (digestible energy/GE) was 24 g/kg higher ($P < 0.001$) for Low- than for High-RFI cows. Methane and UE, as proportions of GE intake, were not different between the efficiency groups, but their combined effect resulted in a 6 kJ/MJ higher ($P = 0.002$) ME/digestible energy ratio for Low- than High-RFI cows. Metabolizability of GE (ME/GE) was

Table 3. Production and energy metabolism characteristics of low (n = 279), medium (n = 278), and high (n = 284) residual ECM production (RECM) in respiration chamber studies (total n = 841)

Item	RECM			SEM	*P*-value
	Low	Medium	High		
Animal data					
RECM, kg/d	−2.81	−0.14	3.17		
DMI, kg/d	17.1	17.2	17.3	0.55	0.88
RFI,[1] kg/d	0.96	0.04	−0.97	0.132	<0.001
ECM yield, kg/d	21.2	23.3	27.0	1.08	<0.001
ECM/DMI	1.23	1.34	1.55	0.025	<0.001
BW, kg	571	571	567	9.7	0.78
Energy measurements, MJ/d					
Gross energy (GE)	317	317	318	10.9	0.98
Fecal energy	86.5	81.3	78.7	3.90	<0.001
Digestible energy (DE)	231	236	239	7.5	0.04
Methane energy (CH_4E)	21.6	20.7	20.3	0.55	<0.001
Urinary energy (UE)	11.5	11.4	11.1	0.60	0.22
ME	197	204	208	6.7	0.005
Milk energy	66.6	73.2	84.8	3.39	<0.001
Heat production	128	124	119	3.0	<0.001
Energy balance	2.7	7.0	5.4	1.94	0.03
Energy measurements, kJ/MJ					
DE/GE	730	745	753	5.0	<0.001
ME/GE	624	642	652	4.2	<0.001
ME/DE	854	862	867	2.9	<0.001
CH_4E/GE	69.4	66.5	65.6	1.52	<0.001
UE/GE	36.8	36.5	35.5	1.61	0.16
k_l[2]	0.600	0.653	0.695	0.0106	<0.001
CH_4, g/kg of ECM	19.3	16.9	14.6	0.51	<0.001

[1]RFI = residual feed intake.

[2]Efficiency of ME use for lactation, calculated as milk energy adjusted to zero energy balance/(ME intake – ME for maintenance).

4.0% ($P < 0.001$) greater for Low- vs. High-RFI group. Methane intensity (g of CH_4/kg of ECM) was 11% lower ($P < 0.001$) for Low-RFI cows compared with High-RFI cows.

High-RECM cows produced 6.0 kg of ECM /d more ($P < 0.001$) than Low-RECM cows at the same DMI (Table 3). Feed conversion efficiency (ECM/DMI) was 26% higher ($P < 0.001$) for High- compared with Low-RECM cows. Gross energy losses as feces ($P < 0.001$) and as CH_4 emission were lower ($P < 0.001$) for High-RECM (efficient cows) when compared with their Low-RECM counterparts. The High-RECM cows had a higher ($P < 0.02$) ME intake and produced less ($P < 0.001$) heat than Low-RECM cows. The contributions of improved digestibility, and reduced CH_4 and urinary losses to greater ME intake of High- compared with Low-RECM group were 83, 12, and 4%, respectively. Methane yield was higher in Low-RECM cows compared with other groups. Diet digestibility and metabolizability were 23 and 28 kJ/MJ higher ($P < 0.001$) in High- compared with Low-RECM cows. The cows in the High-RECM group had a higher ($P < 0.001$) efficiency of ME utilization (k_l) than cows in Medium- and Low-RECM groups. The contribution of increased ME intake to RECM, calculated using the difference in ME intake and observed k_l-value, of the Medium-RECM group was 2.2 kg/d; that is, about 37% of the observed difference between High- and Low-RECM groups. Consequently, 63% of the difference in RECM was attributed to the higher k_l of High-RECM cows. When RECM was estimated using observed ME intake, the difference in RECM between High-RECM and Low-RECM groups was 4.1 kg/d. Methane production per kg of ECM was reduced ($P < 0.001$) with improved efficiency, at 24% lower in High- compared with Low-RECM cows.

The following linear regressions of milk energy-corrected for zero energy balance (MJ/d) on ME intake (MJ/d), both scaled to MBW, were estimated for different RECM groups:

$$\text{Low-RECM: milk energy} = -0.510 \pm 0.0279 + 0.658 \pm 0.0152 \times \text{ME intake}, \quad [5]$$

$$\text{Medium-RECM: milk energy} = -0.432 \pm 0.0297 + 0.645 \pm 0.0157 \times \text{ME intake}, \quad [6]$$

Table 4. Production and energy metabolism characteristics of low (n = 279), medium (n = 282), and high (n = 280) feed conversion efficiency (ECM/DMI) cows in respiration chamber studies (total n = 841)

Item	Feed conversion efficiency			SEM	*P*-value
	Low	Medium	High		
Animal data					
ECM/DMI	1.15	1.39	1.66		
RECM,[1] kg/d	−1.74	0.12	2.55	0.316	<0.001
RFI[2]	0.38	0.07	−0.59	0.173	<0.001
DMI, kg/d	17.2	17.4	17.0	0.55	0.16
ECM yield, kg/d	20.2	24.2	28.4	0.91	<0.001
BW, kg	582	567	555	10.2	<0.001
Energy measurements, MJ/d					
Gross energy (GE)	316	321	314	10.9	0.19
Fecal energy	81.8	83.0	81.6	3.87	0.47
Digestible energy (DE)	235	238	233	7.6	0.22
Methane energy (CH_4E)	20.7	21.2	20.8	0.55	0.22
Urinary energy (UE)	11.4	11.4	11.2	0.60	0.72
ME	203	205	201	6.8	0.26
Milk energy	64.0	76.0	89.2	2.86	<0.001
Heat production	124	125	123	3.0	0.40
Energy balance	15.6	5.2	−10.6	2.25	<0.001
Energy measurements, kJ/MJ					
DE/GE	743	743	741	5.1	0.56
ME/GE	640	640	638	4.5	0.55
ME/DE	862	861	860	3.1	0.70
CH_4E/GE	66.8	67.1	67.6	1.58	0.61
UE/GE	36.4	36.1	36.3	1.61	0.86
k_l[3]	0.654	0.647	0.646	0.0131	0.42
CH_4, g/kg of ECM	19.6	16.3	14.0	0.45	<0.001

[1]RECM = residual ECM yield.

[2]RFI = residual feed intake.

[3]Efficiency of ME use for lactation, calculated as milk energy adjusted to zero energy balance/(ME intake – ME for maintenance).

$$\text{High-RECM: milk energy} = -0.434 \pm 0.0279 + 0.674 \pm 0.0142 \times \text{ME intake}. \quad [7]$$

The intercept (maintenance energy requirement) tended to be greater ($P = 0.06$) for Low- than for Medium- and High-RECM cows. Numerically, k_l (slope) was greater for High- compared with Medium-RECM cows.

Table 4 summarizes the production and energy metabolism characteristics of the Low-, Medium-, and High-FCE groups. High-FCE cows produced 44% more ($P < 0.001$) ECM per kg of DMI than Low-FCE cows. The difference was mainly due to differences in partitioning nutrients between milk production and body energy retention, and partly due to lower BW of High-compared with Low-FCE cows. No differences between the groups were observed in converting GE to ME or the utilization of ME. Methane intensity was 28.6% (5.6 g/kg of ECM; $P < 0.001$) greater for low- than for high-FE cows with the difference entirely attributed to greater ECM yield of the latter group.

The following relationship was estimated between the 2 efficiency traits:

$$\text{RECM (kg/d)} = 0.10 \pm 0.271 - 1.85 \pm 0.049 \times \text{RFI (kg/d; residual variance 1.54)}.$$

The residuals of regressions of RECM on RFI were positively related to DMI and ECM yield (Figure 1). Methane yield was negatively related to the residuals (Figure 2). The effects of other variables (BW, digestibility, energy balance, and k_l) on the residual were small.

DISCUSSION

Several measures of FE and their respective advantages and disadvantages have been presented in the literature (Archer et al., 1999; Connor, 2015). Traditionally, efficiency is expressed as a ratio between product and feed intake in the form of mass or energy value of milk per unit (mass or energy) of intake. A major shortcoming of this definition is that it does not fully account for body tissue mobilization patterns, especially during early lactation (Berry et al., 2006). Residual feed intake has been applied successfully in

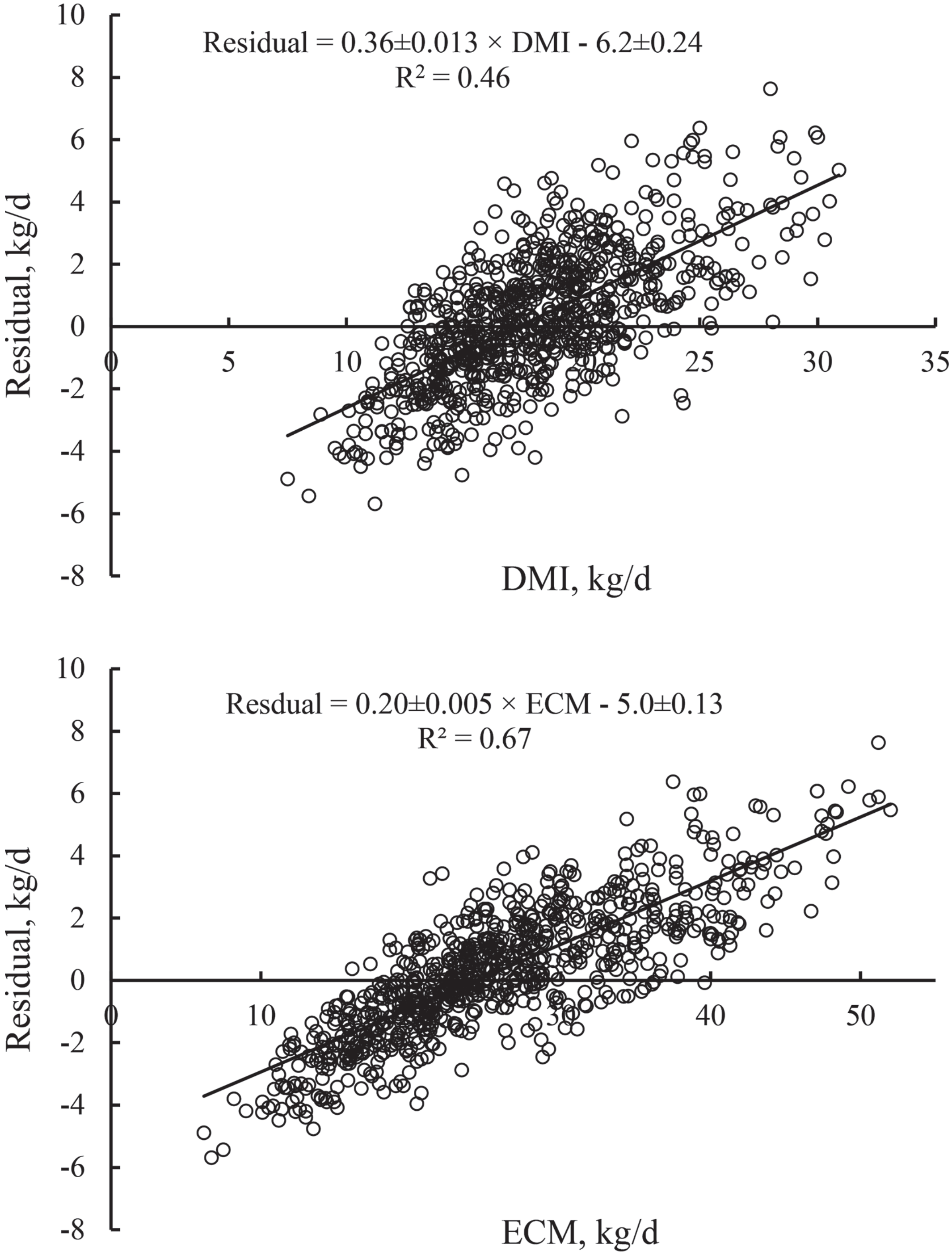

Figure 1. The effects of DMI and ECM yield on the residuals of regressions of residual ECM on residual feed intake (n = 841).

growing animals (Koch et al., 1963; Berry and Crowley, 2013), and is now used in lactating cow populations (Pryce et al., 2014; Li et al., 2017). Residual ECM production is an alternative approach to assessing FE in dairy cows. Residual feed intake correlates positively with feed intake, but not with milk yield, MBW, or ΔBW, suggesting that efficient (i.e., low RFI) cows eat less. In contrast, efficient cows with high RECM have higher milk yields at similar feed intake and MBW than low RECM cows. While the RFI approach focuses

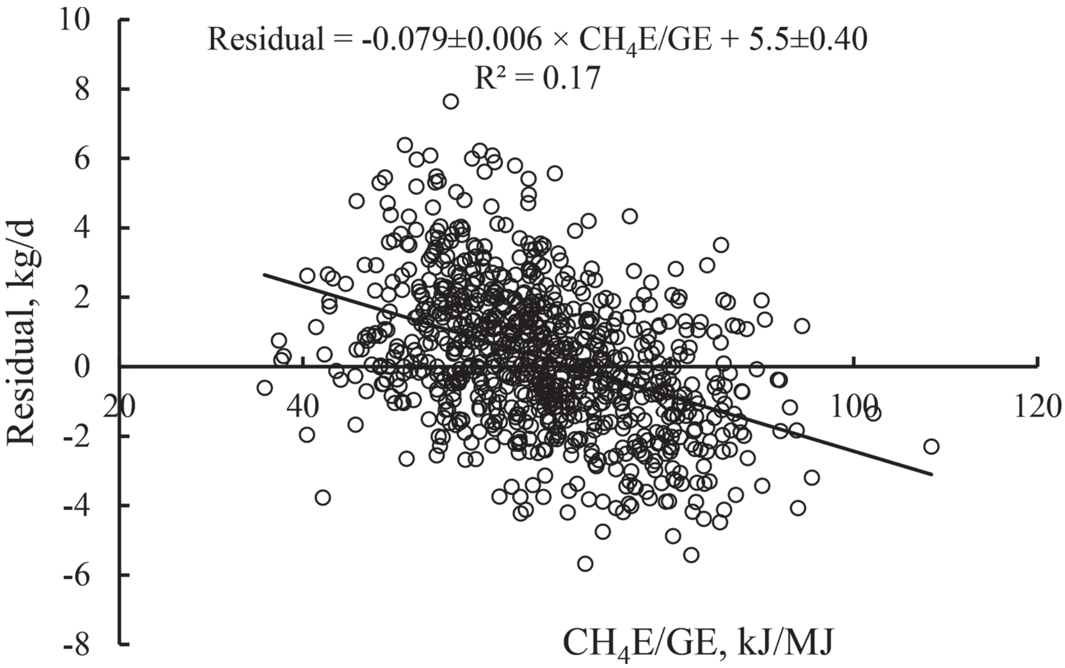

Figure 2. The effects of methane yield on the residuals of regressions of residual ECM on residual feed intake (n = 841). CH_4E = methane energy; GE = gross energy.

on production cost, dividing it over a range of energy sinks, the RECM approach changes focus from cost to income (Løvendahl et al., 2018). Residual feed intake or RECM on their own, however, do not measure production efficiency. This is because large animals that eat more than small animals, but have the same ECM yield, may have the same RFI or RECM, but clearly different production efficiency (ECM/DMI) or milk income over feed cost. Economically, RECM as a measure of efficiency is more favorable than RFI; assuming that relative price of ECM is 2-fold compared with DMI, the difference in milk income over feed cost between the most and the least efficient groups would be about 4 times greater for RECM than for RFI. According to our knowledge, this was the first time that RFI or RECM were estimated from respiration chamber data. Partial regression coefficients of DMI or ECM on energy sinks agreed reasonably well with energy requirements based on respiration chamber studies (e.g., NRC, 2001).

Residual analysis of the model predicting RECM from RFI (Figure 1) indicated that these 2 variables are not the same traits; at a given RFI, the cows with higher DMI or ECM yield had a higher RECM. In other studies (Coleman et al., 2010; Hurley et al., 2016; Løvendahl et al., 2018), the correlation coefficient between RFI and RECM ranged from −0.53 to −0.68, suggesting that RFI and RECM are not the same traits.

Residual Feed Intake Model

The observed variation in RFI (standard deviation, **SD** = 16.2 MJ of ME) was similar to the variation Connor et al. (2019) reported for full lactation RFI in Holstein cows (SD = 16.4 MJ of ME). For DMI prediction, the partial regression coefficient for ECM (0.347; Eq. 3) was slightly lower than that reported by NRC (2001). Using the mean ME concentration of 11.8 MJ/kg of DM and a value of 0.64 for k_l would give a value of 0.417 kg DM/kg of ECM. The average coefficient of DMI on ECM for cows in 50 to 150 DIM was 0.37 (range of 0.29–0.47) from 12 research stations in different countries (Templeman et al., 2015). In the studies of Li et al. (2017) and Løvendahl et al. (2018), the coefficients of DMI on ECM were markedly lower, ranging from below 0.05 to 0.25 at different stages of lactation. The minimum coefficient of ECM would be 0.17 assuming no losses of dietary GE in digestion and metabolism. In the study of Mehtiö et al. (2018), the overall partial regression coefficient of ME intake on ECM (2.67 MJ/kg of ECM) was lower than the energy content of ECM (3.14 MJ/kg). They also reported almost 3-fold differences in their coefficient of ECM at different stages of lactation. In the present data, DIM was negatively associated with k_l, but quantitatively the effect was small (0.017 units, a 2.7% change, per

100 d). The variation in k_l during lactation contradicts with the constant k_l estimated using the AFRC (1993) requirements at different stages of lactation (Yan et al., 2006).

In the present study, the regression coefficient of DMI on MBW (0.0645; Eq. 3) is markedly greater than the corresponding coefficients (0.044 and 0.055) calculated using maintenance requirements of NRC (2001) and feed into milk (**FiM**; Thomas, 2004), respectively. However, it agrees with the value 0.0624 estimated from the current data using the regression approach (Guinguina et al., 2020) using the average dietary ME concentration (11.8 MJ/kg of DM). In the study of Tempelman et al. (2015), the partial regression coefficient of DMI on MBW averaged 0.092 (range from 0.06–0.16), which, for a 600 kg cow, corresponds to 11 kg of DMI to meet the maintenance requirements. Mehtiö et al. (2018) reported a value of 0.81 MJ of ME/kg of MBW (0.0686 kg of DM when ME = 11.8 MJ/kg of DM) ranging from 0.48 to 1.09 at different stages of lactation.

Contrary to other studies investigating RFI, we used determined EB as an energy sink instead of ΔBW. The coefficient of DMI on positive energy balance (0.0704 kg/MJ; Eq. 3) corresponds to 1.36 and 1.57 kg of DM per kg of ΔBW, calculated using the energy values of ΔBW in the FiM (Thomas, 2004) and in the NRC (2001) systems (19.3 and 22.3 MJ/kg respectively; BCS = 3.0). Using these ΔBW energy values for the efficiency of ME utilization for body tissue gain (0.65 and 0.75 in FiM and NRC, respectively), the expected coefficient of DMI on ΔBW were 2.50 kg/kg for both systems. Random errors in estimating EB could, at least partly, explain the discrepancy between observed and expected values. In respiration chamber studies, EB is calculated as a difference between GE intake and all energy sinks, and therefore all measurement errors are accumulated in EB. The coefficient was numerically greater for positive than negative energy balance, which is consistent with the greater ME requirement for body gain than the energy supply from mobilization. The ratio of these coefficients was consistent with the NRC (2001) coefficients.

In RFI studies, the coefficients of DMI on ΔBW have been unrealistically low (Tempelman et al., 2015; Li et al., 2017; Løvendahl et al., 2018), vary between studies (Templeman et al., 2015) and at different stages of lactation (Li et al., 2017; Løvendahl et al., 2018; Mehtiö et al., 2018). This can reflect that ΔBW is a poor proxy of EB. Random variation in ΔBW measurements is large, especially when experimental periods are short. Even if ΔBW was measured accurately, it may not reflect changes in EB correctly. The energy content of ΔBW could be highly variable. In early lactation, the cows can be in negative energy balance at zero ΔBW, when high energy fat tissues are mobilized and low energy visceral tissues are growing (Gibb et al., 1992). The energy concentration of mobilized and gained tissues is also related to BCS, and is higher for cows with high BCS (NRC, 2001). It could improve accuracy to include BCS in RFI and RECM models because BCS affects both maintenance requirement per kg of MBW and the energy value of ΔBW. Even when based on whole lactation data, the partial regression coefficients obtained in models for predicting ME intake were not biologically meaningful based on NRC (2001) values for the energy requirements (Connor et al., 2019). Their coefficients for MBW were too high and too low for ECM, meaning that the model overestimated the variability in energy intake assigned to MBW and underestimated variability assigned to ECM.

Overall, we can conclude that our partial regression coefficients of DMI on energy sinks were more consistent with energy requirements in different systems (e.g., NRC, 2001) than the coefficients estimated from feeding experiments in research stations (Li et al., 2017; Løvendahl et al., 2018; Connor et al., 2019). Inconsistent coefficients, especially in early lactation, can be related to the poor relationship between DMI and ECM yield due to the mobilization of body tissues, and to poor predictions of true EB from ΔBW.

Residual ECM Model

Partial regression coefficients of ECM yield on GE intake, MBW, EBp, and EBn were consistent with energy requirements in the FiM (Thomas, 2004) and NRC (2001) systems. Using the average GE concentration (18.4 MJ/kg of DM), the calculated increase in ECM yield was 2.0 kg/kg of DMI, approximately 85% of expected ECM per DMI according to the energy systems stated above. The effect of MBW as an energy sink corresponded to 10 kg of ECM for a 600 kg cow. According to the NRC (2001) system, the maintenance requirement of a 600 kg cow is equivalent to requirements of 12 to 13 kg of ECM. The partial regression coefficients of ECM on EB_p and on EB_n were about 55% of the coefficients presented by NRC (2001). When determined ME intake was used in the RECM model (results not shown), the partial regression coefficients were closer to those based on energy requirement: ME intake = 90%, maintenance requirement = 12.5 kg of ECM, and EB_p and EB_n approximately 60% of requirements (NRC, 2001). Closer agreement with the ME model is likely because it takes into account the metabolizability of the diet (ME/GE), but the model based on GE intake analysis allowed us to evaluate the effects of fecal, CH_4 and UE losses on the efficiency variables. Partial regression coefficients of ECM on intake and other energy sinks are seldom reported. Løvendahl et al. (2018) reported values ranging from 0.4 to 1.0 kg of DM per 1 kg of ECM at different stages of lactation; these values were markedly lower than expected according to energy systems.

Factors Influencing Residual Feed Intake and Residual ECM Yield

The major components affecting FE were as follows: (1) factors that alter the dilution of maintenance, i.e., the proportion of NE that is captured in milk instead of used for maintenance and (2) factors that alter the conversion of GE to NE; that is, energy losses in digestion and metabolism of nutrients. As a measure of FE, RFI is independent of production level, BW, and ΔBW (or energy balance in the present study), whereas RECM is independent of intake, BW, and ΔBW. However, selection for RFI and RECM may be difficult because they require accurate measures of individual feed intake, which is seldom recorded on commercial farms. As such, indirect selection using related component traits may be helpful in understanding the expected effect of genetic selection for FE on these traits.

Digestibility. In the present study, diet digestibility was positively related to improved FE, expressed as either RFI or RECM (Tables 2 and 3). Increased fecal energy losses (20.4 MJ/d) accounted for 44% of the greater (46 MJ/d) GE intake of High-RFI cows compared with Low-RFI cows. Reduced DMI and improved digestibility contributed to 42 and 58% of the lower fecal energy losses, respectively, in Low- compared with High-RFI cows. We calculated that the difference in digestibility between Low- and High-RECM cows accounted for 30% (1.8 kg of ECM) of the difference in RECM. Our findings are consistent with other studies that demonstrated negative relationships between diet digestibility and RFI, although these were not always significant. Based on limited data for beef cattle, the contribution of the variation in digestive efficiency to the differences in RFI among cows was 10 to 20% (Herd and Arthur, 2009; VandeHaar et al., 2016). In a study involving young bulls and heifers phenotypically ranked as low or high for RFI, Richardson et al. (1996) found that the differences in DM digestibility accounted for 14% of the difference in RFI between the 2 groups of cattle. In lactating Holstein cows (n = 109) fed 2 diets, Potts et al. (2017) reported that variation in digestibility could account for up to 31% of the variation in RFI. Ben Meir et al. (2018) reported 2.1% percentage units, and Fischer et al. (2018) 3% percentage units, higher DM digestibility for high efficient cows compared with low efficient cows. In growing beef cattle, RFI correlated negatively with DM digestibility (Johnson et al., 2019). The differences in DM digestibility were 3.8 and 3.0% percentage units in favor of groups with low RFI in 2 studies (Johnson et al., 2019).

In the present study, digestibility estimated by linear regression among RFI groups was reduced by 8.8 g/kg of DMI (results not shown), agreeing with the value (7.2) reported by Cantalapiedra-Hijar et al. (2018) from a meta-analysis of RFI studies. Cantalapiedra-Hijar et al. (2018) suggested that that overall higher digestibility in low RFI cattle might be the consequence of lower DMI. However, in the present study digestibility was not significantly influenced by DMI (Guinguina et al., 2020). The difference in digestibility between the RFI groups was much greater than the value of 2.6 g/kg of DMI reported by Huhtanen et al. (2009) from a meta-analysis examining the effects of intake and diet composition on digestibility. Overall, the differences in digestibility between RFI groups found in the study by Huhtanen et al. (2009) were greater than could be predicted from DMI effects, resulting from increased digesta passage rate for high-RFI group. This suggests that RFI groups are more divergent in digestibility than could be expected from differences in digesta passage rate. The differences in digestibility between efficiency groups might also be associated with the longer rumination time per kilogram of DM in high-efficient cows (Ben Meir et al., 2018). Eating rate has been found to be slower in low-RFI cows than in high-RFI cows (Connor et al., 2013; Ben Meir et al., 2018; Fischer et al., 2018), but this may not necessarily cause digestibility differences.

Methane. Considering the concerns that enteric CH_4 production from ruminants is contributing to climate change, improving FE could help mitigate CH_4 production, while sustaining current levels of milk production (Potts et al., 2015). Most studies conducted in beef cattle have reported a positive relationship between RFI and CH_4 production (Nkrumah et al., 2006; Hegarty et al., 2007; Alemu et al., 2017). When the cows were grouped according to RFI, CH_4 production was 3.4 MJ/d lower in Low- than in High-RFI cows, which equals 7% of the difference in GE intake between the groups. The lack of differences in CH_4 yield (kJ of CH_4E/MJ of GE) between RFI groups was unexpected because CH_4 yield is normally negatively associated with intake (Blaxter and Clapperton, 1965; Yan et al., 2000; Ramin and Huhtanen, 2013) and positively associated with digestibility (Blaxter and Clapperton, 1965; Ramin and Huhtanen, 2013). Positive relationship between digestibility and CH_4 production (Løvendahl et al., 2018), which was also observed in the present study (Guinguina et al., 2020), and lower DMI should increase CH_4 yield in Low-RFI cows. The model based on treatment means data (Ramin and Huhtanen, 2013) predicted 5 kJ/MJ higher CH_4 yield for low-RFI cows than for high-RFI cows, but there were no differences in CH_4 yield between RFI groups in our study.

When the cows were grouped according to RECM, the lower (1.3 MJ/d) CH_4 production contributed to 12% of the greater ME intake of High- compared with Low-RECM cows at the same DMI. Methane yield was the highest in the Low-RECM cows, despite having the lowest digestibility. However, within each RECM group, there was a positive ($P < 0.001$) association between digestibility and CH_4 yield ranging from 0.06 to 0.09 kJ/MJ of GE per kJ/MJ difference in GE digestibility. Predicted (Ramin and Huhtanen, 2013) CH_4 yield was 1.5 kJ/MJ greater for High- than for Low-RECM cows but in contrast, the observed difference was −3.8 kJ/MJ in the current study. Our findings do not fully agree with Freetly et al. (2015), who suggested that if the efficiency improves as a result of increased metabolic efficiency, the CH_4 yield would not decrease. However, if the improved efficiency is due to an increase in digestibility, CH_4 production may increase. In an earlier study (Yan et al., 2010), efficiency variables were negatively related to CH_4 yield when the statistical model included study effect, but not diet nor period effects.

Different relationships between digestibility and CH_4 yield on individual cow and efficiency group basis is difficult to explain. One reason could be a rumen fermentation pattern that favors metabolic efficiency and low CH_4 production. However, Olijhoek et al. (2018) did not observe differences in rumen fermentation patterns between low- and high-RFI cows. Similarly, no differences in rumen fluid VFA were observed between RFI groups in feedlot cattle (Lam et al., 2018). According to a review by Kenny et al. (2018), the differences between RFI groups in rumen VFA patterns were inconsistent between low- and high-RFI beef cattle. In addition, variation in rumen fermentation pattern between cows fed the same diet was small (Cabezas-Garcia et al., 2017), and therefore unlikely to explain the unexpected effects of efficiency groups on CH_4 yield. Zhou et al. (2009) demonstrated a probable association between the "methanogenic biome" and FE in cattle. They (Zhou et al., 2009) suspected that *Methanobrevibacter* ssp. might use acetate as a substrate for CH_4 production, possibly leading to greater energy loss. However, it could be questioned if a difference in the methanogenic population was a causative factor for differences in FE. Even if the CH_4 energy loss between Low- and Medium-RECM (0.9 MJ/d) was due to greater utilization of acetate for methanogenesis in Low-RECM cows, the quantitative effect on ME supply is insufficient to account for any major part of the differences in RECM between the efficiency groups. Overall, the contributions of reduced CH_4 production to improved efficiency was only 7% (RFI) or 5% (RECM), indicating that if differences in the methanogenic population were the causative factor, the mechanism was not energy-sparing from methanogenesis. Because of the relatively small contribution to ME supply, the possible effects of methanogenic populations on the efficiency should, therefore, be mediated via body metabolism.

Methane intensity (g of CH_4/kg of ECM) clearly improved with increased efficiency, as the differences between low and high-efficiency groups were greater for RECM than for RFI (4.8 vs. 2.0 g/kg). Based on Akaike's information criteria and residual variance, RECM and ECM were better predictors of CH_4 intensity than total CH_4 production or CH_4 yield. Changes in CH_4 intensity were mainly due to reduced DMI (RFI model) or increased production (RECM model), with only minor effects assigned to changes in CH_4 yield. Our results suggest that selecting efficient animals is the most sustainable and efficient way to reduce CH_4 production per unit of product, and does not require any measurements of CH_4 production, which is challenging under commercial conditions.

The Efficiency of ME Utilization. The efficiency of ME utilization had a greater influence than the metabolizability of the diet (ME/GE) on both FE variables (i.e., RFI and RECM). The greater ME intake (20.5 MJ/d) of High- compared with Low-RFI cows was counterbalanced by an equivalent loss as heat. As heat is produced only from ME and body energy mobilization, it can be calculated that the difference in HP accounts for 1.7 kg of DM using the average dietary ME concentration (20.5 MJ of ME/11.8 MJ of ME/kg of DM = 1.7 kg of DM). Therefore, 65% of the difference in RFI between low- and high-efficiency cows could be attributed to a more efficient metabolic processes, i.e., converting ME to milk energy. Similarly, when using RECM as an efficiency trait improved metabolic efficiency accounted for 64% of the higher efficiency of High- compared with Low-RECM cows. Herd and Arthur (2009) estimated that the contribution to RFI of various biological processes in cattle was 37% tissue metabolism, 9% heat increment of feeding, 10% activity, and 5% body composition. In total, the processes that are related to differences in the metabolism of absorbed nutrients contributed 61% to the variation in RFI (Herd and Arthur, 2009).

We calculated k_l using the classical approach by regressing milk energy-corrected for zero energy balance against ME intake per MBW. With this approach, almost all variation in the efficiency is attributed to metabolic efficiency of converting ME above maintenance to milk, whereas maintenance requirement is only influenced by ME/GE (q-value) that varies marginally between cows fed the same diet. However, when milk energy at zero energy balance was regressed against ME intake separately for each RECM group, the difference between Low- vs. Medium- and High-RECM cows was in the intercept (i.e., maintenance requirement), whereas the difference between Medium- and High-RECM cows was mainly due to the higher slope (i.e., k_l) of High-RECM cows. According to McNamara (2015), the efficiency of energy utilization in the mammary gland is rather constant and the variation in maintenance requirement is the main cause of differences in the efficiency. Baldwin et al. (1985) stated that resting energy expenditures could vary over a 2- to 3-fold range in animals of equal weight. The coefficient of variation of fasting HP of 14 dairy cows was 10.4% (mean = 0.42 MJ/kg of MBW) when measured 31 d after lactation ceased (Holter, 1976). One SD unit lower in maintenance requirement for a 600-kg cow would reduce NE requirement by 5.3 MJ, equivalent to 1.7 kg of ECM. In the study of Yan et al. (1997), the coefficient of variation of fasting HP of 12 cows in 2 studies was on average 8.1%. Earlier, van Es (1961) found that the ME requirement for maintenance varied by 8 to 10% between cows of similar size. The results from fasting HP studies suggest that the variation in the maintenance requirement can have a large effect on between-cow variation in FE, attributable to the tissue metabolism component.

Differences in activity and feeding behavior could contribute to variation in the efficiency of dairy cows. However, in the studies of Connor et al. (2013) and Ben Meir et al. (2018), RFI was not related to the activity estimated by a pedometer. This is not surprising considering a low (140 steps/h; SD ~30) overall activity rate of dairy cows in barn conditions (Ben Meir et al., 2018) and the low energy expenditures of walking relative to total energy requirements. According to the NRC (2001), ME requirement for 1 km of walking for a 600-kg cow is about 1.6 MJ of ME, equal to the requirement of 0.3 kg of ECM (5% of the difference between Low- and High-RECM). Differences between high- and low-efficient cows in feeding behavior have been inconsistent. Eating time was positively correlated with RFI in the study of Xi et al. (2016) and negatively in the study of Fischer et al. (2018). In contrast, studies of Conner et al. (2013) and Ben Geir et al. (2018) showed eating time was similar for low- and high-RFI cows. Eating rate (Conner et al., 2013; Ben Geir et al., 2018; Fischer et al., 2018) was slower for low- compared with high-RFI cows, and efficient cows spent more time for rumination per kg of DMI (Ben Meir et al., 2018; Fischer et al., 2018). Considering the differences in HP between low and high-efficiency cows (21 MJ/d for High-RFI vs. Low-RFI; 9 MJ/d for High-RECM vs. Low-RECM), it is unlikely that differences in feeding behavior have any major contribution to the differences in FE.

Xi et al. (2016) found a positive phenotypic correlation between SCC and RFI, suggesting that increased SCC might partly explain variation in the efficiency of feed conversion among cows. In agreement, increased SCC was associated with decreases in ECM yield and DMI, but as the relative decrease was greater for ECM yield, FE expressed as ECM/DMI decreased (Potter et al., 2018). Hou et al. (2012) found that more efficient cows exhibited differences in genes associated with immunity and the inflammatory response, which could affect their ability to elicit a response to an immune challenge. The effect of SCC on FE is likely related to increased energy expenditure associated with inflammation.

Energy Balance. Increasing negative energy balance is a major concern when using FE expressed as an input/output ratio. In the current analysis, differences in partitioning nutrients between milk production and body energy resources explained most of the differences in ECM/DMI between FE groups without any differences in metabolizability of GE or in k_l. However, both RFI and RECM indicated differences in the efficiency between FE groups. Overestimation of k_l for cows with positive EB could be one reason for this discrepancy. We used the AFRC (1993) value (0.60) for the efficiency of ME utilization for energy gain. This value is lower than the NRC (2001) value (0.75) based on Moe et al. (1971), and especially the values (0.84–0.86) reported in a more recent study (Kebreab et al., 2003). Using the efficiency values for energy retention and mobilization estimated from the current data, the k_l-values for Low-, Medium- and High-FCE groups were 0.624, 0.640, and 0.664 ($P < 0.001$), respectively. This indicated that there were true differences in the efficiency of ME utilization between the FE groups. The differences in k_l between RFI and RECM groups were similar whether $E_{l(0)}$ was calculated using coefficients of AFRC (1993) or those derived from the current data.

The results of the current study indicate that there are large differences in the efficiency of feed conversion among cows that are not related to dilution of maintenance requirement or repartitioning of nutrients between milk production and body tissues. It also showed that between-cow differences in converting dietary GE to ME and the efficiency of ME utilization had a strong influence on efficiency traits. The current study was based on respiration chamber data that most likely give a more accurate estimate of energy balance than estimates from ΔBW, especially if the measurement periods are short. However, Xi et al. (2016) and Fischer et al. (2018) found no differences in plasma nonesterified fatty acid concentrations between low- and high-RFI cows, indicating that higher efficiency was not due to differences in mobilization. In the present study, the residuals were not related to energy balance when RECM was predicted from RFI, suggesting that energy balance influences these 2 efficiency traits in the same way. Coleman et al., (2010), found no correlation between RFI and fertility, but reported a positive correlation between residual milk solids production, and fertility, suggesting that the mechanisms are different. It is possible that efficient cows have more resources available for other functions, such as reproduction.

CONCLUSIONS

Data from respiration chamber studies showed considerable variation in FE among cows when expressed as either RFI or RECM. The partial regression coefficients of energy sinks for predicting DMI or ECM were biologically meaningful. About 65% of the difference between low- and high-efficiency cows, irrespective of efficiency trait (RFI or RECM), was derived from improved utilization of ME, and 35% assigned to greater metabolizability of GE. Improved digestibility and reduced CH_4 production accounted for 83 and 12% of increased ME intake, respectively. Regression analysis within each RECM group suggested that the difference between Low- vs. Medium- and High-RECM groups was mainly due to the higher maintenance requirement in Low-RECM cows, while the difference between Medium- and High-RECM groups resulted mainly from improved k_l. Variation among cows in FCE was mainly due to differences in partitioning energy between milk production and body tissues when milk energy at zero energy balance was estimated using AFRC (1993) coefficients. Methane production per kg of ECM reduced with improved efficiency, with a greater difference between RECM groups than between RFI groups. Increased ECM yield from the same DMI (RECM) or reduced DMI at the same ECM yield (RFI) contributed to most of the differences in CH_4/ECM among the efficiency groups, while differences in CH_4/DMI had only minor (RECM) or no (RFI) effects on CH_4/ECM. Therefore, improving FE is a sustainable way to reduce CH_4 production per unit of product.

ACKNOWLEDGMENTS

This study was funded by the Faculty of Animal Science and Veterinary Medicine of Swedish University of Agricultural Sciences (SLU) with co-funding from Swedish Farmers' Foundation for Agricultural Research (SLF), Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), and the Feed Utilization in Nordic Cattle (FUNC) project (Denmark). The authors thank their colleagues from Agri-Food and Biosciences Institute (Hillsborough, UK), Agri-Food Research in Finland (currently Natural Resources Institute Finland(LUKE), Jokioinen, Finland), and Aarhus University (Aarhus, Denmark), for the experimental data used in the present study. The authors have not stated any conflicts of interest.

REFERENCES

Agnew, R., and T. Yan. 2000. Impact of recent research on energy feeding systems for dairy cattle. Livest. Prod. Sci. 66:197–215.

Agricultural and Food Research Council (AFRC). 1993. Energy and Protein Requirements of Ruminants. CAB International, Wallingford, UK.

Alemu, A. W., D. Vyas, G. Manafiazar, J. A. Basarab, and K. A. Beauchemin. 2017. Enteric methane emissions from low- and high-residual feed intake beef heifers measured using GreenFeed and respiration chamber techniques. J. Anim. Sci. 95:3727–3737. https://doi.org/10.2527/jas2017.1501.

Archer, J., E. Richardson, R. Herd, and P. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: A review. Aust. J. Agric. Res. 50:147–162. https://doi.org/10.1071/A98075.

Baldwin, B. R., N. E. Forsberg, and C. Y. Hu. 1985. Potential for altering energy partition in the lactating cow. J. Dairy Sci. 68:3394–3402. https://doi.org/10.3168/jds.S0022-0302(85)81252-2.

Ben Meir, Y. A., M. Nikbachat, Y. Fortnik, S. Jacoby, H. Levit, G. Adin, M. Cohen Zinder, A. Shabtay, E. Gershon, M. Zachut, S. J. Mabjeesh, I. Halachmi, and J. Miron. 2018. Eating behavior, milk production, rumination, and digestibility characteristics of high- and low-efficiency lactating cows fed a low-roughage diet. J. Dairy Sci. 101:10973–10984. https://doi.org/10.3168/jds.2018-14684.

Berry, D., R. Veerkamp, and P. Dillon. 2006. Phenotypic profiles for body weight, body condition score, energy intake, and energy balance across different parities and concentrate feeding levels. Livest. Sci. 104:1–12. https://doi.org/10.1016/j.livsci.2006.02.012.

Berry, D. P., and J. J. Crowley. 2013. Cell biology sumposium: Genetics of feed efficiency in dairy and beef cattle. J. Anim. Sci. 91:1594–1613. https://doi.org/10.2527/jas.2012-5862.

Blaxter, K. L., and J. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. Br. J. Nutr. 19:511–522. https://doi.org/10.1079/BJN19650046.

Cabezas-Garcia, E. H., S. Krizsan, K. J. Shingfield, and P. Huhtanen. 2017. Between-cow variation in digestion and rumen fermentation variables associated with methane production. J. Dairy Sci. 100:4409–4424. https://doi.org/10.3168/jds.2016-12206.

Cantalapiedra-Hijar, G., M. Abo-Ismail, G. Carstens, L. Guan, R. Hegarty, D. Kenny, M. McGee, G. Plastow, A. Relling, and I. Ortigues-Marty. 2018. Review: Biological determinants of between-animal variation in feed efficiency of growing beef cattle. Animal 12(Supp s2):s321–s335. https://doi.org/10.1017/S1751731118001489.

Coleman, J., D. P. Berry, K. M. Pierce, A. Brennan, and B. Horan. 2010. Dry matter intake and feed efficiency profiles of 3 genotypes of Holstein-Friesian within pasture-based systems of milk production. J. Dairy Sci. 93:4318–4331. https://doi.org/10.3168/jds.2009-2686.

Connor, E. E. 2015. Invited review: Improving feed efficiency in dairy production: Challenges and possibilities. Animal 9:395–408. https://doi.org/10.1017/S1751731114002997.

Connor, E. E., J. L. Hutchison, H. D. Norman, K. M. Olson, C. P. Van Tassell, J. M. Leith, and R. L. Baldwin. 2013. Use of residual feed intake in Holsteins during early lactation shows potential to improve feed efficiency through genetic selection. J. Anim. Sci. 91:3978–3988. https://doi.org/10.2527/jas.2012-5977.

Connor, E. E., J. L. Hutchison, C. P. Van Tassell, and J. B. Cole. 2019. Defining the optimal period length and stage of growth or lactation to estimate residual feed intake in dairy cows. J. Dairy Sci. 102:6131–6143. https://doi.org/10.3168/jds.2018-15407.

Davis, S. R., K. A. Macdonald, G. C. Waghorn, and R. J. Spelman. 2014. Residual feed intake of lactating Holstein-Friesian cows predicted from high-density genotypes and phenotyping of growing heifers. J. Dairy Sci. 97:1436–1445. https://doi.org/10.3168/jds.2013-7205.

Fischer, A., N. C. Friggens, D. P. Berry, and P. Faverdin. 2018. Isolating the cow-specific part of residual energy intake in lactating dairy cows using random regressions. Animal 12:1396–1404. https://doi.org/10.1017/S1751731117003214.

Freetly, H. C., A. Lindholm-Perry, K. Hales, T. Brown-Brandl, M. Kim, P. Myer, and J. Wells. 2015. Methane production and methanogen levels in steers that differ in residual gain. J. Anim. Sci. 93:2375–2381. https://doi.org/10.2527/jas.2014-8721.

Gibb, M. J., W. E. Ivings, M. S. Dhanoa, and J. D. Sutton. 1992. Changes in body components of autumn-calving Holstein-Friesian cows over the first 29 weeks of lactation. J. Anim. Sci. 55:339–360. https://doi.org/10.1017/S0003356100021036.

Guinguina, A., T. Yan, P. Lund, A. R. Bayat, A. L. F. Hellwing, and P. Huhtanen. 2020. Between-cow variation in the components of feed efficiency. J. Dairy Sci. 103:XXXX–XXXX. https://doi.org/10.3168/jds.2020-18257.

Hansen, L. B. 2000. Consequences of selection for milk yield from a geneticist's viewpoint. J. Dairy Sci. 83:1145–1150. https://doi.org/10.3168/jds.S0022-0302(00)74980-0.

Hegarty, R. S., J. Goopy, R. Herd, and B. McCorkell. 2007. Cattle selected for lower residual feed intake have reduced daily methane production. J. Anim. Sci. 85:1479–1486. https://doi.org/10.2527/jas.2006-236.

Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. J. Anim. Sci. 87(Suppl 14):E64–71.

Holter, J. B. 1976. Fasting heat production in lactating versus dry dairy cows. J. Dairy Sci. 59:755–759. https://doi.org/10.3168/jds.S0022-0302(76)84270-1.

Hou, Y., D. M. Bickhart, H. Chung, J. L. Hutchison, H. D. Norman, E. E. Connor, and G. E. Liu. 2012. Analysis of copy number variations in Holstein cows identify potential mechanisms contributing to differences in residual feed intake. Funct. Integr. Genomics 12:717–723. https://doi.org/10.1007/s10142-012-0295-y.

Huhtanen, P., M. Rinne, and J. Nousiainen. 2009. A meta-analysis of feed digestion in dairy cows. 2. The effects of feeding level and diet composition on digestibility. J. Dairy Sci. 92:5031–5042. https://doi.org/10.3168/jds.2008-1834.

Hurley, A. M., N. López-Villalobos, S. McParland, E. Kennedy, E. Lewis, M. O'Donovan, J. L. Burke, and D. P. Berry. 2016. Interrelationships among alternative definitions of feed efficiency in grazing lactating dairy cows. J. Dairy Sci. 99:468–479. https://doi.org/10.3168/jds.2015-9928.

Johnson, J. R., G. E. Carstens, W. K. Krueger, P. A. Lancaster, E. G. Brown, L. O. Tedeschi, R. C. Anderson, K. A. Johnson, and A. Brosh. 2019. Associations between residual feed intake and apparent nutrient digestibility, in vitro methane-producing activity, and volatile fatty acid concentrations in growing beef cattle. J. Anim. Sci. 97:3550–3561. https://doi.org/10.1093/jas/skz195.

Kebreab, E., J. France, R. E. Agnew, T. Yan, M. S. Dhanoa, J. Dijkstra, D. E. Beever, and C. K. Reynolds. 2003. Alternatives to linear analysis of energy balance data from lactating dairy cows. J. Dairy Sci. 86:2904–2913. https://doi.org/10.3168/jds.S0022-0302(03)73887-9.

Kenny, D. A., C. Fitzsimons, S. Waters, and M. McGee. 2018. Invited review: Improving feed efficiency of beef cattle-the current state of the art and future challenges. Animal 12:1815–1826. https://doi.org/10.1017/S1751731118000976.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486–494. https://doi.org/10.2527/jas1963.222486x.

Lam, S., J. Munro, M. Zhou, L. Guan, F. Schenkel, M. Steele, S. Miller, and Y. Montanholi. 2018. Associations of rumen parameters with feed efficiency and sampling routine in beef cattle. Animal 12:1442–1450. https://doi.org/10.1017/S1751731117002750.

Li, B., B. Berglund, W. F. Fikse, J. Lassen, M. H. Lidauer, P. Mäntysaari, and P. Løvendahl. 2017. Neglect of lactation stage leads to naive assessment of residual feed intake in dairy cattle. J. Dairy Sci. 100:9076–9084. https://doi.org/10.3168/jds.2017-12775.

Løvendahl, P., G. Difford, B. Li, M. Chagunda, P. Huhtanen, M. Lidauer, J. Lassen, and P. Lund. 2018. Selecting for improved feed efficiency and reduced methane emissions in dairy cattle. Animal 12(Supp s2):s336–s349. https://doi.org/10.1017/S1751731118002276.

McNamara, J. P. 2015. Triennial lactation symposium: Systems biology of regulatory mechanisms of nutrient metabolism in lactation. J. Anim. Sci. 93:5575–5585. https://doi.org/10.2527/jas.2015-9010.

Mehtiö, T., E. Negussie, P. Mäntysaari, E. A. Mäntysaari, and M. H. Lidauer. 2018. Genetic background in partitioning of metabolizable energy efficiency in dairy cows. J. Dairy Sci. 101:4268–4278. https://doi.org/10.3168/jds.2017-13936.

Moe, P. W., H. F. Tyrrell, and W. P. Flatt. 1971. Energetics of body tissue mobilization. J. Dairy Sci. 54:548–553. https://doi.org/10.3168/jds.S0022-0302(71)85886-1.

Nkrumah, J. D., E. Okine, G. Mathison, K. Schmid, C. Li, J. Basarab, M. Price, Z. Wang, and S. Moore. 2006. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. J. Anim. Sci. 84:145–153. https://doi.org/10.2527/2006.841145x.

NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. National Academies Press, Washigton DC.

Olijhoek, D. W., P. Løvendahl, J. Lassen, A. Hellwing, J. Höglund, M. Weisbjerg, S. Noel, F. McLean, O. Højberg, and P. Lund. 2018. Methane production, rumen fermentation, and diet digestibility of Holstein and Jersey dairy cows being divergent in residual feed intake and fed at 2 forage-to-concentrate ratios. J. Dairy Sci. 101:9926–9940. https://doi.org/10.3168/jds.2017-14278.

Potter, T. L., C. Arndt, and A. N. Hristov. 2018. Short communication: Increased somatic cell count is associated with milk loss and reduced feed efficiency in lactating dairy cows. J. Dairy Sci. 101:9510–9515. https://doi.org/10.3168/jds.2017-14062.

Potts, S. B., J. Boerman, A. Lock, M. Allen, and M. VandeHaar. 2015. Residual feed intake is repeatable for lactating Holstein dairy cows fed high and low starch diets. J. Dairy Sci. 98:4735–4747. https://doi.org/10.3168/jds.2014-9019.

Potts, S. B., J. Boerman, A. Lock, M. Allen, and M. VandeHaar. 2017. Relationship between residual feed intake and digestibility for lactating Holstein cows fed high and low starch diets. J. Dairy Sci. 100:265–278. https://doi.org/10.3168/jds.2016-11079.

Pryce, J. E., W. Wales, Y. De Haas, R. Veerkamp, and B. Hayes. 2014. Genomic selection for feed efficiency in dairy cattle. Animal 8:1–10. https://doi.org/10.1017/S1751731113001687.

Ramin, M., and P. Huhtanen. 2013. Development of equations for predicting methane emissions from ruminants. J. Dairy Sci. 96:2476–2493. https://doi.org/10.3168/jds.2012-6095.

Richardson, E., R. Herd, P. Arthur, J. Wright, G. Xu, K. Dibley, and V. Oddy. 1996. Possible physiological indicators for net feed conversion efficiency in beef cattle. Pages 103–106 in Proc. Aust. Soc. Anim. Prod. Pergamon press, Sydney, Australia.

Sjaunja, L. O., L. Baevre, L. Junkkarinen, J. Pedersen, and J. Setälä. 1990. A Nordic proposal for an energy corrected milk (ECM) formula. Pages 156–192 in European Association for Animal Production Publication, Performance Recording of Animals: State of the Art, 1990; 27th Biennial Session of the International Committee for Animal Recording. P. Gaillon and Y. Chabert, ed. Centre for Agricultural Publishing and Documentation, Paris, France.

Tempelman, R. J., D. M. Spurlock, M. Coffey, R. F. Veerkamp, L. E. Armentano, K. A. Weigel, Y. de Haas, C. R. Staples, E. E. Connor, Y. Lu, and M. J. VandeHaar. 2015. Heterogeneity in genetic and nongenetic variation and energy sink relationships for residual feed intake across research stations and countries. J. Dairy Sci. 98:2013–2026. https://doi.org/10.3168/jds.2014.8510.

Thomas, C. 2004. Feed Into Milk: A New Applied Feeding System for Dairy Cows: An Advisory Manual. No. v. 1. Nottingham University Press, Nottingham, UK.

van Es, A. J. H. 1961. Between-animal variation in the amount of energy required for the maintenance of cows. PhD thesis. Wageningen University and Research, the Netherlands.

VandeHaar, M. J., L. Armentano, K. Weigel, D. Spurlock, R. Tempelman, and R. Veerkamp. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. J. Dairy Sci. 99:4941–4954. https://doi.org/10.3168/jds.2015-10352.

VandeHaar, M. J. 1998. Efficiency of nutrient use and relationshipto profitability on dairy farms. J. Dairy Sci. 81:272–282. https://doi.org/10.3168/jds.S0022-0302(98)75576-6.

VandeHaar, M. J., and N. St-Pierre. 2006. Major advances in nutrition: Relevance to the sustainability of the dairy industry. J. Dairy Sci. 89:1280–1291. https://doi.org/10.3168/jds.S0022-0302(06)72196-8.

Xi, Y. M., F. Wu, D. Q. Zhao, Z. Yang, L. Li, Z. Y. Han, and G. L. Wang. 2016. Biological mechanisms related to differences in residual feed intake in dairy cows. Animal 10:1311–1318. https://doi.org/10.1017/S1751731116000343.

Yan, T., R. E. Agnew, F. J. Gordon, and M. G. Porter. 2000. Prediction of methane energy output in dairy and beef cattle offered grass silage-based diets. Livest. Prod. Sci. 64:253–263. https://doi.org/10.1016/S0301-6226(99)00145-1.

Yan, T., F. Gordon, R. Agnew, M. Porter, and D. Patterson. 1997. The metabolisable energy requirement for maintenance and the efficiency of utilisation of metabolisable energy for lactation by dairy cows offered grass silage-based diets. Livest. Prod. Sci. 51:141–150. https://doi.org/10.1016/S0301-6226(97)00065-1.

Yan, T., C. S. Mayne, F. G. Gordon, M. G. Porter, R. E. Agnew, D. C. Patterson, C. P. Ferris, and D. J. Kilpatrick. 2010. Mitigation of enteric methane emissions through improving efficiency of energy utilization and productivity in lactating dairy cows. J. Dairy Sci. 93:2630–2638. https://doi.org/10.3168/jds.2009-2929.

Yan, T., C. S. Mayne, T. W. J. Keady, and R. E. Agnew. 2006. Effects of dairy cow genotype with two planes of nutrition on energy partitioning between milk and body tissue. J. Dairy Sci. 89:1031–1042. https://doi.org/10.3168/jds.S0022-0302(06)72170-1.

Zhou, M., E. Hernandez-Sanabria, and L. L. Guan. 2009. Assessment of the microbial ecology of ruminal methanogens in cattle with different feed efficiencies. Appl. Environ. Microbiol. 75:6524–6533. https://doi.org/10.1128/AEM.02815-08.

ORCIDS

A. Guinguina https://orcid.org/0000-0002-9325-512X
A. R. Bayat https://orcid.org/0000-0002-4894-0662
P. Lund https://orcid.org/0000-0002-9113-4500
P. Huhtanen https://orcid.org/0000-0001-7855-7448