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Potential of novel feed efficiency traits for dairy cows based on respiration gas exchanges measured by respiration chambers or GreenFeed

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ABSTRACT

Residual feed intake (RFI), calculated as a difference between observed and predicted intake, is a commonly used estimate of feed efficiency (FE). Determination of FE in practical dairy herds is challenging, as it requires accurate estimation of feed intake of individual cows. Alternatively, FE could be estimated as a difference between observed and predicted metabolic losses derived from gas exchanges. The objectives were to compare respiration chambers (RC) and the GreenFeed (GF) system in estimating FE based on the gas data, and to compare FE estimated from measured feed intake or gas data. The study was conducted using 32 Nordic Red dairy cows (DIM 159 ± 63, BW 634 ± 60 kg, and milk yield 28.9 ± 6.7 kg/d) fed a grass silage-based diet (CP 152 g/kg DM, NDF 395 g/kg DM). The study included two 14-d periods with the GF system with a 1-wk period in RC chambers (3-d measurements) between the GF periods. Residual CO_2 production (RCO_2), residual O_2 consumption (RO_2) and residual heat production (RHP) were estimated as observed minus predicted values derived from energy requirements. Root means squared errors of DMI prediction were smaller for models based on CO_2 or O_2 and ECM yield compared with ECM + BW model both with RC and GF data with minor differences between the methods. The relationship between GF and RC was slightly better for RO_2 ($R^2 = 0.68$) and RHP ($R^2 = 0.67$) compared with RCO_2 ($R^2 = 0.59$). Seventy-five percent of the top 50% (12/16) cows in GF were ranked among the top 50% in RC. Repeatability values of different FE traits were similar or higher for the data based on gas data measured by GF compared with the corresponding values based on measured feed intake. Residual CO_2 production explained 57% of variation in residual ME intake (RMEI). Gross FE expressed as ECM/CO_2 explained 82% of gross FE expressed as ECM/DMI. When the cows were divided into low, medium, and high RCO_2 groups, the differences in various FE traits were consistent with those based on measured feed intake. The difference in RMEI between the Low- and High-RCO_2 cows was 15 MJ/d. Low-RCO_2 cows produced 13% less methane per kilogram ECM, had higher diet digestibility, and produced less heat than high-RCO_2 cows. It is concluded that estimating FE from gas data measured by the GF system has a potential to rank the cows according to FE in farm conditions without requiring measuring feed intake.

Key words: residual gas exchanges, residual heat production, measurement techniques, feed efficiency

INTRODUCTION

Improving efficiency of animal production has been a goal to meet global food demands, to reduce environmental impact of animal production, and to maintain producer profitability. Within the dairy cattle sector, enormous gains in production efficiency have been made due to advances in nutrition, genetics, and management. As feed cost is the greatest single component of total milk production costs, improving feed conversion efficiency (**FCE**) is a desirable target for genetic improvement of dairy cattle. Until now, FCE has improved with increased milk production, as a smaller proportion of feed energy is used for cow maintenance (i.e., dilution of maintenance energy to a greater volume of milk). However, the potential for diluting the maintenance cost is diminishing in intensive systems with increased production level. This potential is further decreased by associated increases in BW with selection for higher yield. Also, maintenance cost per kilogram of metabolic weight (**MBW**) has increased (Yan et al., 1997; NRC, 2021), probably reflecting relative increase in metabolically active visceral tissues. In addition, reduced diet digestibility with increased feed intake (e.g., NRC, 2001) limits the potential of improving FCE by selecting for higher production levels.

Feed efficiency (**FE**) in dairy cows is expressed as residual feed intake (**RFI**), which is estimated as the difference between observed intake and intake predicted by

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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-25. Nonstandard abbreviations are available in the Notes.

linear regression from energy sinks (ECM yield, MBW, and ΔBW; Connor, 2015). The lack of accurate and cost-effective on-farm methods of measuring DMI has limited introducing efficiency traits in breeding indexes of dairy cows. Because between-cow variability in RFI is small compared with daily DMI intake, accurate determination of DMI or energy intake is challenging in commercial farms (feed sampling and analysis, diet selection). Lassen et al. (2023) suggested using a 3-dimensional (**3D**) camera for measuring feed intake in commercial farms. The method is based on estimation of volume of feed eaten by individual cows. Whether the method is accurate enough for ranking of the cows for RFI or other efficiency traits needs to be validated. Using energy losses instead of input variables (DMI and energy intake) could be another alternative for estimation of FE traits. Oxygen consumption, CO_2 production, and heat production (**HP**) are related to energy losses in metabolism that explained most of variation in RFI in respiration chamber (**RC**) studies (Guinguina et al., 2020). Therefore, residual CO_2 production (**RCO_2**), residual O_2 consumption (**RO_2**) or residual HP (**RHP**) estimated similarly as RFI could be used as efficiency indicators. Using data from RC studies, Huhtanen et al. (2021) found that CO_2 production predicted accurately and precisely HP calculated according to Brouwer (1965), and that RCO_2 predicted RFI with root mean squared error (**RMSE**) of 0.42 kg. Several methods have been developed for measuring gas exchanges in farm conditions with focus in methane emissions (Garnsworthy et al., 2012; Lassen et al., 2012; Huhtanen et al., 2015). The methods based on gas fluxes, such as the GreenFeed (**GF**) emission monitoring system (C-Lock Inc., Rapid City, SD), also measure CO_2 production and O_2 consumption allowing to calculate HP. In production studies (e.g., Ramin et al., 2020; Guinguina et al., 2021) using the GF system as an indirect calorimeter resulted in biologically relevant estimates of energy balance and efficiency of ME utilization for milk production with small residual error.

The objectives of this study were (1) to compare RC and GF system in estimating FE traits and (2) to compare FE traits based on measured feed intake and gas data in dairy cows fed grass silage-based diet. We hypothesized that the FE traits based on gas data collected by the GF system would rank the cows similarly compared with gas measurement by the RC system or those based on measured feed intake.

MATERIALS AND METHODS

Details of experimental design, animals, sampling, and feed analysis, and measurements of intake, milk production, and gas exchanges in RC and GF are described in the companion paper (Bayat et al., 2025). Briefly, 32 Nordic Red dairy cows (26 primiparous and 6 multiparous, DIM 159 ± 63, BW 634 ± 60 kg, and milk yield 28.9 ± 6.7 kg/d) fed grass silage-based diet (average forage to concentrate ratio 51:49, CP 152 g/kg DM, NDF 395 g/kg DM). The study included two 14-d measurement periods with the GF system in a loose-house barn with a 1-wk period in RC chambers (3-d measurements) between the GF periods. The cows visited the GF units on average 3.6 ± 0.78 (range 1.7–5.8) times/d during the 28-d measurement period. The GF records outside the range of mean ± 2.5 × SD of all measurements over 4 wk for each cow were identified as outliers and removed (3,115 datapoints; i.e., 6.9% were removed). The GF units and the chambers were located in the same barn.

During the GF measurements, the cows were kept in a freestall barn fitted with transponder collars allowing for identification at the feeding bins, milking parlor, and weigh scales. Grass silage was offered ad libitum (at least 5% refusals) 4 times daily by an automatic feeding wagon (TR Feeding Robot, Pellon Group Ltd., Ylihärmä, Finland) to individual bins system (RIC; Insentec B.V., Marknesse, the Netherlands). Pelleted concentrates consisted of cereal grains, molassed sugar-beet pulp and rapeseed meal were given 5 times daily from automatic concentrate feeders. The cows were milked twice daily at milking parlor during the GF measurements. In milking parlor, the cows received 0.3 kg concentrate. During the RC measurements the cows received grass silage and concentrates manually 4 times daily. The concentrates were given 1 h before silage and the cows were milked inside the chambers.

Carbon dioxide, O_2, and CH_4 exchanges were measured during wk 1, 2, 4, and 5 of the experiment using 2 GF units (C-Lock Inc., Rapid City, SD). The details of the system are described by Hammond et al. (2015) and Huhtanen et al. (2015). The cows were allowed to visit the GF system 5 times a day. During each visit, they received maximum 8 drops of 50 g basal concentrate at 40 s intervals to attract them to the units. During experimental wk 3 for every block, the cows entered the RC (n = 4; 21.5 m^3) for gas measurements, and total fecal and urinary collection (4 d) with the first day being considered as acclimatization as described in detail by Bayat et al. (2022). Feed and milk sampling and analysis are described in the companion paper (Bayat et al., 2025).

FE Calculations

Residual ME intake (**RMEI**) was calculated as the difference between observed and expected ME intake

(**MEI**) according to Luke (2024) requirements omitting BW change (**BWC**):

$$\text{RMEI (MJ/d)} = \text{MEI (MJ/d)} - (0.515 \times \text{MBW} + 5.15 \times \text{ECM}), \quad [1]$$

where 0.515 and 5.15 are ME requirements for maintenance (MJ/kg MBW) and ECM production (MJ/kg), respectively. The effects of BWC were not considered because of large errors in BWC during short measurement periods, and the effects would be similar between different traits of FE. The ME concentration for silage was calculated as 16 × D-value (digestible OM, kg/kg) and for concentrate using analyzed chemical composition (Bayat et al., 2025) and digestibility coefficients from feed tables (Luke, 2024).

The RCO_2 was calculated as the difference between observed and expected CO_2 production ignoring the effect of BWC. Expected CO_2 production was calculated from HP based on ME requirements (Luke, 2024): ECM production 2.01 MJ/kg ECM (5.15 MJ ME/kg ECM – 3.14 MJ/kg ECM) and maintenance (0.515 MJ/kg MBW). Maintenance CO_2 production was calculated assuming that respiratory quotient (**RQ**) is 1.0 (Yan et al., 1997). Heat production based on Luke (2024) requirements was calculated for a 600-kg cow producing 0, 10, 20, 30 and 40 kg ECM/d. The following relationship between ECM and RQ was estimated from the current RC data:

$$\text{RQ} = 1.005 \pm 0.0274 + 0.00237 \pm 0.000834 \times \text{ECM } (P = 0.008). \quad [2]$$

Heat production per liter of O_2 was estimated using the coefficients of Brouwer (1965):

$$\text{HP}/O_2 \text{ (MJ/L } O_2) = 0.01618 + \text{RQ} \times 0.00502. \quad [3]$$

The total O_2 consumption at different production levels was estimated as HP (MJ/d)/(HP/O_2). Carbon dioxide production was then estimated as CO_2 (L/d) = O_2 (L/d) × RQ.

Carbon dioxide production for maintenance and ECM production, estimated from the intercept and slope of regression CO_2 production on ECM, were 48 g/kg MBW and 209 g/kg ECM, respectively. The corresponding values for O_2 consumption were 40 g/kg MBW and 129 g/kg ECM, respectively.

Residual CO_2 was calculated as:

$$RCO_2 \text{ (kg/d)} = 0.001 \times [CO_2 \text{ production (g/d)} - \text{ECM (kg/d)} \times 209 \text{ (g/kg)} - \text{MBW (kg)} \times 48 \text{ g/kg)}]. \quad [4]$$

Residual O_2 consumption was calculated as:

$$RO_2 \text{ (kg/d)} = 0.001 \times [O_2 \text{ consumption (g/d)} - \text{ECM (kg/d)} \times 129 \text{ (g/kg)} - \text{MBW (kg)} \times (40 \text{ g/kg})]. \quad [5]$$

Residual HP was calculated as the difference between observed and expected HP based on Luke (2024) requirements. Heat production was calculated using the Brouwer (1965) equation. Because urinary N excretion was not determined, its contribution was estimated to be 1.2 MJ/d assuming 200 g/d of urinary N output. Relative to the total HP (in the current study about 130 MJ/d) between-cow variation in urinary N has only negligible effects on HP.

Residual CH_4 production (**RCH_4**) was estimated as:

$$RCH_4 \text{ (g/d)} = \text{Observed } CH_4 \text{ (g/d)} - [a \times \text{DMI (kg/d)} + b \times \text{BW (kg)}]. \quad [6]$$

Feed conversion efficiency (**FCE**) was expressed as ECM/MEI (g/MJ), ECM/CO_2 (kg/kg), and ECM/O_2. Indexes of FCE (**FCEI**) were calculated considering dilution of maintenance energy to the greater production level as follows:

$$\text{FCEI}_{\text{ME}} = \text{ECM/MEI} - \text{ECM/ME requirement}, \quad [7]$$

$$\text{FCEI}_{CO2} = \text{ECM}/CO_2 - \text{ECM}/(0.048 \times \text{MBW} + 0.209 \times \text{ECM}). \quad [8]$$

Positive values indicated that the cow produced more than expected from requirements. The purpose of these indexes is to exclude the dilution effect with increased production and avoid problems related to using ratios.

Statistical Analysis

Statistical analyses were performed using the Mixed model regression analysis of SAS (version 9.4; SAS Institute Inc., Cary, NC). Repeatability values (**Rep**) between the 2 GF periods were calculated as Rep = σ^2Cow / (σ^2Cow + σ^2Residual), where σ^2Cow and σ^2Residual are cow within block and residual variances, respectively. Deviating observations were investigated from leverage and influence by the diagnostics DFFITS_i and $\text{DFBETAS}_{j,i}$, where i = 1, 2, …, 32 and j,i denotes the jth regression coefficient in the regression equation (= 0 or 1) estimated without observation i, where i = 1, 2, …, 32, respectively (Belsley et al., 1980). Cutoff values suggest-

Table 1. Descriptive data of feed intake, milk production and gas variables during GreenFeed periods (n = 32)[1]

Item	Mean	SD	Minimum	Maximum	Repeatability
DMI, kg/d	21.6	2.82	17.1	29.2	0.86
Milk yield, kg/d	27.8	6.35	15.0	41.5	0.97
ECM yield, kg/d	32.0	5.86	20.2	46.1	0.96
Milk composition, g/kg					
Fat	50.3	5.10	41.7	66.7	0.91
Protein	40.6	4.02	33.1	47.4	0.97
Gas exchanges, g/d					
O_2	8,882	904	7,126	11,612	0.92
CO_2	12,890	1,285	10,171	16,655	0.90
CH_4	467	63.3	375	631	0.86
CH_4, g/kg DMI	21.7	1.63	18.4	26.1	0.80
CH_4/CO_2, g/kg	36.2	2.32	31.4	43.1	0.85
RQ[2]	1.06	0.028	0.98	1.13	0.71

[1] Adopted from Bayat et al. (2025).

[2] RQ = respiratory quotient (CO_2/O_2 on volume basis).

ing that an observation warrants examination were set at $|\text{DFFITS}_i| > 2\sqrt{(p/n)}$ and $|\text{DFBETASj,i}| > 2/\sqrt{n}$, where P = parameters estimated in the model and n = total number of observations. For the comparison of the measurements with 2 techniques (RC and GF), the following model was used: RC = GF + Chamber + Block + error. Chamber was included in the model to account differences between the chambers. Random effect of the chamber was included in the model to account for the differences between the 4 chambers. Mixed model regression analysis was used for DMI predictions with block and chamber (only RC data) as random factors. The cows were classified into 3 groups (low [n = 10], medium [n = 12], and high [n = 10]) by RCO_2 values and parity. Two of 6 multiparous cows were included in each group based on their RCO_2 values. The differences between RCO_2 groups were analyzed by the MIXED procedure of SAS with block as a random factor. Linear and quadratic contrasts were used to compare the groups. The differences in gas-based FE traits determined by the GF system between the top and bottom 20% cows were also estimated.

RESULTS

Repeatability of Production and Gas Data

Mean DMI, milk production, and gas exchanges including SD, minimum, and maximum values are reported in Table 1. Variability of production parameters was high reflecting differences in the stage of lactation DIM (96–305) in the middle of the experiment and parity. The cows were in mid to late lactation as indicated by the range in DIM. Repeatability values for milk production variables were high indicating stability of intake and production of mid-lactation cows. Repeatability values of the gas data were also high with the highest value being observed for the O_2 consumption and the lowest for the CH_4 production. Repeatability of O_2 consumption and CO_2 production were numerically higher than that of DMI.

Intake Predictions

The ECM + BW model resulted in smaller RMSE with GF than with RC, probably reflecting greater random variability during the short chamber periods (Table 2). The models based on O_2 consumption or CO_2 production, and ECM yield resulted in smaller RMSE and corrected Akaike information criterion values compared with the models based on ECM and BW in both GF and RC. The effect of BW was not significant (models not shown) when added to bivariate O_2 + ECM or CO_2 + ECM models. Repeatability of DMI predictions of models based on ECM yield and CO_2 production was high (0.95) for the GF data. Regression coefficients of ECM were more consistent in bivariate models with BW, O_2 and CO_2 for the GF data (0.30–0.34) than for the RC data (0.11–0.30).

Comparison of Efficiency Traits Between RC and GF

The relationship between RCO_2 determined in RC and GF is shown in Figure 1. The relationships were similar when RCO_2 was estimated separately for the data of the 2 GF periods. The differences between RCO_2 based on RC and GF data were not related ($P > 0.31$) to DIM, parity, BW, ECM, or BWC determined by regression during the whole 5-wk experimental period. When the cows were ranked according to RCO_2 based on the GF data, 12 of the top 50% cows (n = 16) were ranked among the top 50% according to RC.

The relationship between RC and GF was better for RO_2 compared with RCO_2 (Figure 2). As for RCO_2, the relationships between the 2 systems were similar between the 2 GF periods. Animal variables were not related ($P >$ 0.28) to the difference between the methods estimating

Table 2. Prediction of DMI from animal or gas exchange variables (X variables are expressed as kg/d except CH_4, g/d)

		Intercept		X_1[1]		X_2				
X_1	X_2	Estimate	SE	Estimate	SE	Estimate	SE	*P*-value	Adj. RMSE	AICc[2]
GreenFeed										
ECM	BW	0.8	1.78	0.345	0.0323	0.015	0.0033	<0.001	0.90	99.8
CO_2		0.6	2.73	1.63	0.210				1.27	121.4
O_2		1.9	2.60	2.22	0.288				1.18	121.2
CH_4		4.0	2.03	0.038	0.0043				1.47	128
CO_2	ECM	0.7	1.54	0.88	0.157	0.299	0.0342	<0.001	0.81	89.3
O_2	ECM	1.2	1.52	1.15	0.218	0.317	0.0359	<0.001	0.78	89.8
CH_4	ECM	3.8	1.19	0.018	0.0036	0.288	0.0375	<0.001	0.86	97.2
Respiration chamber										
ECM	BW	3.9	2.88	0.298	0.050	0.012	0.0054	0.03	1.28	128.5
CO_2		−3.2	1.65	1.87	0.121				0.63	95.6
O_2		−0.1	2.29	2.42	0.249				0.85	117.2
CH_4		−1.6	2.21	0.051	0.0048				0.89	120.4
CO_2	ECM	−2.2	1.74	1.59	0.203	0.079	0.0460	0.10	0.66	97.4
O_2	ECM	1.3	2.15	1.54	0.337	0.198	0.0520	0.001	0.92	112.9
CH_4	ECM	1.5	1.57	0.031	0.0049	0.177	0.0398	<0.001	0.95	110.7

[1] All $P < 0.001$.

[2] Akaike information criterion.

RO_2. Twelve of the top 50% ranked cows according RO_2 determined by the GF were ranked among the top 50% according to RO_2 based on the RC data, with the remaining 4 cows ranked to places 17 to 20. The relationship between the systems in RHP was similar to that observed for RO_2 (Figure 3). (Figure 4)

Relationship of FE Traits in Barn Conditions

The relationships between RCO_2 and RMEI are presented in Figure 5. Three outliers were deleted from the data. In terms of R^2, the relationship was better during period 2, mainly reflecting greater ranges in both RCO_2 and RMEI. The intercept was positive ($P < 0.01$) for both periods. The relationships as regards to R^2 and RMSE were similar between RCO_2 or RHP with RMEI to those observed with RCO_2 (data not shown). The relationship in gross FE expressed as ECM/DMI or ECM/CO_2 is presented in Figure 6 and was characterized with a high R^2 of 0.82.

The mean values of different efficiency variables with their SD and repeatability are presented in Table 3. Repeatability values of FCE based on the GF data were higher than those based on intake measurements. Repeatability values for RMEI and residuals based on the GF data were high (0.87–0.92) with RCO_2 being marginally lower.

When the cows were grouped according to RCO_2, the low-RCO_2 cows had a numerically lower DMI, higher ECM yield and smaller BW that resulted in 1.77 kg/d

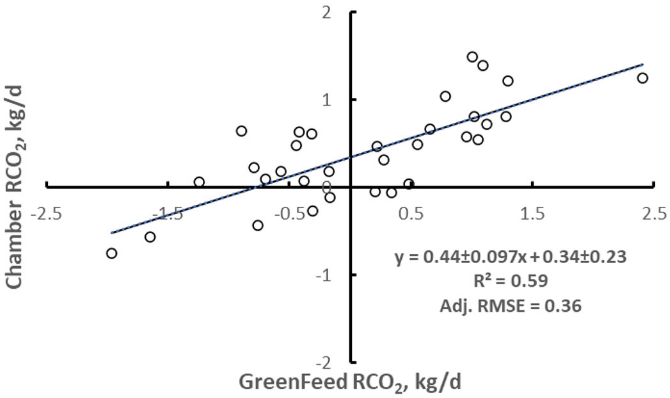

Figure 1. Relationship between RCO_2 determined in respiration chambers and GreenFeed.

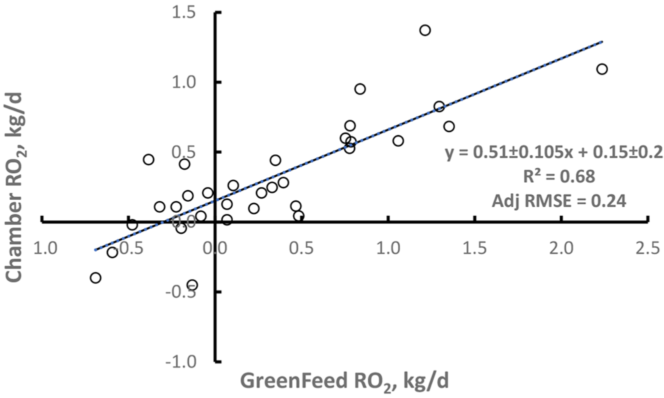

Figure 2. Relationship between RO_2 determined in respiration chambers and GreenFeed.

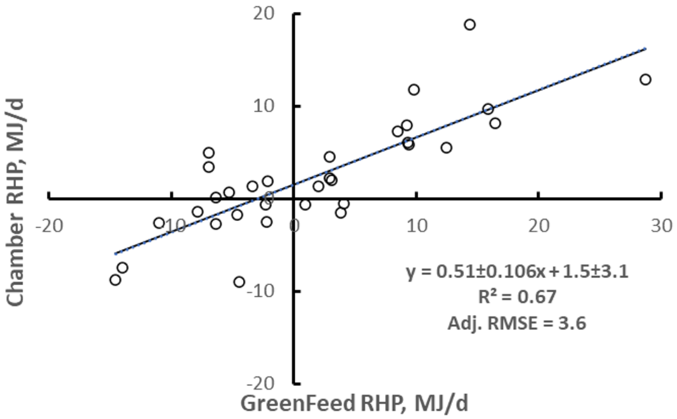

Figure 3. Relationship between RHP determined in respiration chambers and GreenFeed.

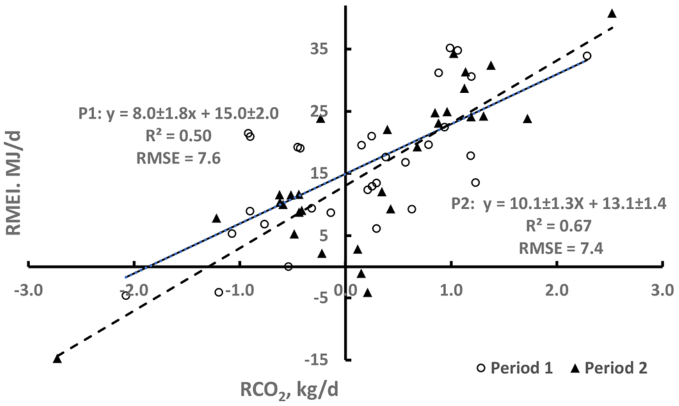

Figure 5. Relationship between RCO_2 determined by the GreenFeed system and RMEI during the 2 periods (P1 = period 1, P2 = period 2) in the barn conditions.

difference in RCO_2 compared with the high-RCO_2 cows (Table 4). The difference between the top and bottom 20% cows was 2.37 kg/d. The medium-RCO_2 cows had slightly higher BWC compared with the other groups, probably reflecting later stage of lactation. Residual O_2 consumption reflected similar pattern to RCO_2 (Table 5). Pearson correlation between RO_2 and RCO_2 was 0.94. The low-RCO_2 cows had higher OMD (P = 0.03) and lower HP (P = 0.01) than the high-RCO_2 cows. Residual MEI increased in parallel to RCO_2 (P = 0.004). Feed conversion efficiency expressed as ECM yield per MJ ME intake or kg CO_2 production was negatively related to RCO_2. Similar patterns were observed when FCE was expressed as an index (i.e., as the difference between observed and expected FCE based on requirements). Total and residual CH_4 emissions were lower ($P \leq 0.03$) for the low-RCO_2 cows compared with the high-RCO_2 cows. As a result, the high-RCO_2-cows produced 15% more CH_4 per kilogram ECM than the low-RCO_2 cows.

DISCUSSION

The main objectives of the current study were to evaluate the potential of the GF system (1) by comparing FE traits determined in RC or GF, and (2) comparing the FE traits based on measured feed intake or gas exchanges determined by the GF system. We estimated residuals as the difference between observed ME intake, O_2 consumption, and CO_2 or HP and corresponding expected parameters based on Luke (2024) ME requirements (RMEI and RHP), or from O_2 consumption and CO_2 production estimated from HP associated with maintenance and milk production. Due to the wide range in milk production (20–46 kg ECM/d), the proportion of concentrate varied between the cows but was constant for each cow during the whole study. Because of this, residual feed intake was expressed as RMEI to consider differences in dietary ME concentration. Heat production from maintenance and milk production is more constant per MJ MEI than per

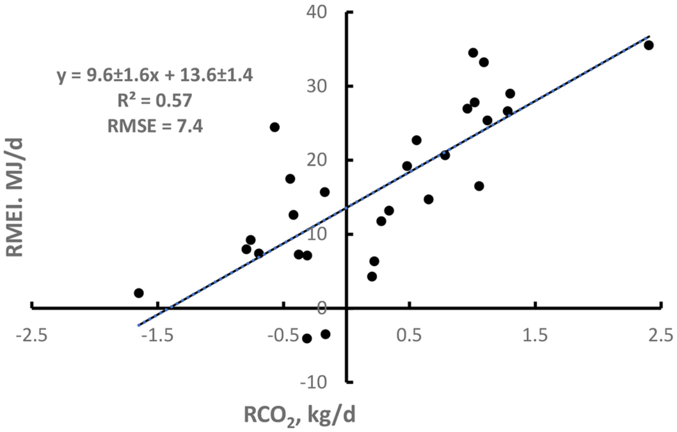

Figure 4. Relationship between RCO_2 determined by the GreenFeed system and RMEI in the barn conditions.

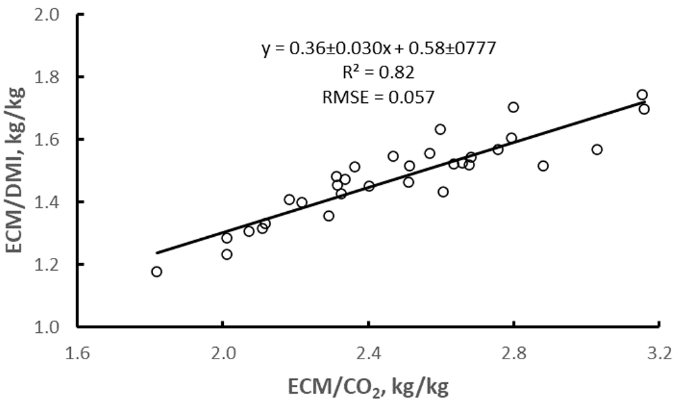

Figure 6. Relationship between gross feed efficiency of lactating dairy cows estimated as ECM /CO_2 and ECM/DMI.

Table 3. Mean of efficiency variables with SD and repeatability for dairy cows measured over 4 wk

Item[1]	Unit	Mean	SD	Repeatability
Intake based				
ECM/DMI	kg/kg	1.47	0.13	0.74
ECM/ME	g/MJ	129	11.1	0.74
$FCEI_{ME}$[1]	g/MJ	−9.1	5.6	0.73
RMEI[2]	MJ/d	16.3	11.0	0.93
GreenFeed based				
ECM/CO_2	kg/kg	2.48	0.354	0.92
ECM/O_2	kg/kg	3.60	0.495	0.94
$FCEI_{CO2}$	kg/kg	−0.01	0.180	0.84
RCO_2[2]	kg/d	0.13	0.707	0.87
RO_2[3]	kg/d	0.20	0.668	0.92
RHP[4]	MJ/d	3.0	9.79	0.91

[1] Feed conversion efficiency index (difference between observed and requirement-based ECM/MEI, g/MJ.

[2] RCO_2 = Residual CO_2 production.

[3] RO_2 = Residual O_2 production.

[4] RHP = Residual heat production.

kilogram DMI making comparisons of FE traits based on measured intake and gas data more comparable.

The RQ value of 1.0 was assumed for maintenance (Yan et al., 1997), and a value of 1.18 for ECM production was estimated from the current RC data. Jentsch et al. (2009) assumed RQ values of 0.85 and 1.20 for maintenance and milk production. However, it is unlikely that lactating cows derive a large proportion of their maintenance requirement from lipid oxidation (RQ <1.0). In growing pigs, RQ was 1.26 when most of the retained energy was fat synthetized from carbohydrates (Jakobsen and Thorbekt, 1993).

Recently, Lidauer et al. (2023) concluded that the FE metric based on expected ME intake resulted in a different ranking of cows compared with those based on RFI estimated from partial regression coefficient, and it was superior in selecting the most efficient cows. Partial regression coefficients of RFI models have varied between studies (e.g., Tempelman et al., 2015) or even between different stages of lactation (Li et al., 2017; Løvendahl et al., 2018; Mehtiö et al., 2018). Partial regression coefficient of ECM (Li et al., 2017; Mehtiö et al., 2018) varied more than 2-fold at different stages of lactation, and sometimes it was less on gross energy basis than ECM (i.e., feed gross energy was converted with >100% efficiency to milk energy). Partial regression coefficients of MBW have consistently been higher than maintenance requirements in different feed evaluation systems. Even when based on whole lactation data, the partial regression coefficients were not biologically meaningful compared with the NRC (2001) energy requirements (Connor et al., 2019). Energy requirements based on large datasets from respiration chamber studies vary only marginally between feed evaluation systems. Therefore, there is no biological basis for large variation in partial regression coefficients of RFI models between studies, and especially between different stages of lactation. Most likely, the variation in partial regression coefficients is related to random errors in estimating BWC, and especially variation in energy content of BWC at different stages of lactation. When analyzed from respiration chamber studies (Guinguina et al., 2020), partial regression coefficients of DMI on energy sinks were more consistent with energy requirements in different systems (e.g., NRC, 2001) but still higher for MBW and lower for ECM than in feed energy systems.

We made the method comparison ignoring the effects of BW change. The effects of BW change on FE traits would be similar for the MEI-based estimates and for those estimated from gas exchanges when the traits are estimated as the difference between observed and expected values. Unrealistically low and variable partial regression coefficients of DMI on BWC at different stages of lactation can be related to collinearity of variables (Lidauer et al., 2023). With short measurement periods, random errors in estimating BWC relative to between-cow variation in FE traits are large, and cause biologically biased coefficients of energy sinks. In our study, mean ± SE of BWC was 0.30 ± 0.42 kg/d when estimated by regression of day on BW from 5-wk BW. On ME basis the SE is about 12

Table 4. Production characteristics of low (n = 10), medium (n = 12) and high RCO_2 cows (n = 10) measured by the GreenFeed system

	LSM				Contrast	
Item	Low	Medium	High	SEM	Linear	Quadratic
RCO_2,[1] kg/d	−0.78	0.16	0.99	0.22	<0.001	0.80
DMI, kg/d	21.4	21.2	22.3	1.00	0.45	0.49
Milk, kg/d	28.7	27.0	27.7	2.31	0.65	0.49
ECM, kg/d	33.0	31.2	32.1	2.13	0.68	0.44
Milk fat, g/kg	49.2	51.0	50.6	1.73	0.54	0.55
Milk protein, g/kg	39.3	40.6	41.7	1.39	0.10	0.94
BW, kg	621	633	652	20.0	0.25	0.88
BW change, g/kg	−0.05	0.21	0.13	0.132	0.17	0.11
DIM	163	182	174	22.8	0.35	0.20

[1] RCO_2 = residual CO_2 production.

Table 5. Energy metabolism and methane emissions of low (n = 10), medium (n = 12) and high (n = 10) RCO_2 cows measured by the GreenFeed system

	LSM				Contrast	
Item[1]	Low	Medium	High	SEM	Linear	Quadratic
RCO_2,[1] kg/d	0.78	0.16	0.99	0.22	<0.001	0.80
RO_2,[2] kg/d	0.76	−0.29	0.23	0.18	<0.001	0.87
RHP,[3] MJ/d	−6.4	1.7	9.9	2.45	<0.001	0.97
OM digestibility, g/kg	697	689	680	5.3	0.03	0.97
Heat production, MJ/d	123	126	137	4.0	0.01	0.33
RMEI,[4] MJ/d	10.9	18.0	25.2	3.32	0.004	0.98
ECM/ME, g/MJ	134	127	125	3.3	0.01	0.50
ECM/CO_2, kg/kg	2.71	2.44	2.31	0.097	<0.001	0.37
$FCEI_{ME}$,[5] g ECM/MJ ME	−6	−10	−14	1.8	0.004	0.97
$FCEI_{CO2}$,[6] kg ECM /kg CO_2	0.16	−0.03	−0.17	0.041	<0.001	0.62
CH_4, g/d	444	455	487	20.4	0.03	0.46
Residual CH_4, g/d	−16	1	16	9.2	0.02	0.93
CH_4, g/kg ECM	13.6	15.0	15.6	0.55	0.01	0.45

[1] RCO_2 = residual CO_2 production.

[2] RO_2 = residual O_2 consumption.

[3] RHP = residual heat production.

[4] RMEI = residual ME intake.

[5] $FCEI_{ME}$ = feed conversion efficiency index based on ME intake.

[6] $FCEI_{CO2}$ = feed conversion efficiency index based on CO_2 production.

MJ/d, equal to the requirement of 2.3 kg ECM. Even if BWC could be estimated without random errors, variable energy content of BWC at different stages of lactation (Gibb et al., 1992), and at different BCS (NRC, 2001) make estimating of body energy change difficult, even impossible, especially when the cows are at different stages of lactation as in our study.

Accurate and precise prediction of FE of individual cows on-farm conditions requires that DMI or HP production can be accurately estimated. Although coefficient of O_2 is about 3-fold compared with CO_2 in Brouwer (1965) equation, high correlation between the 2 gasses (0.96–0.97 in the present study), HP in lactating dairy cows can be estimated accurately from CO_2 production. In the current study, RMSE of HP was 1.8 MJ/d with both systems when calculated from CO_2 production compared with the complete Brouwer (1965) model.

Intake Predictions

Better predictions of DMI from ECM + O_2 or ECM + CO_2 compared with DMI = ECM + BW model can be attributed to variation in FE; efficient cows consume less O_2 and produce less CO_2 per kg DMI. In the present study, RMSE values of DMI prediction from ECM + CO_2 or O_2 with RC were similar to those estimated from a larger RC dataset (Huhtanen et al., 2021). Similar RMSE values of the DMI predictions with the bivariate gas models in the RC and GF data suggest that O_2 consumption and CO_2 production measured by the GF system has a biological meaningful relationship to DMI and ECM production. Observed regression coefficient of DMI on ECM in DMI = ECM + CO_2 model (0.30) was close to that calculated according to Luke (2024) requirements assuming 11 MJ ME/kg DM.

Comparison Between RC and GF

Good agreement between GF and RC in estimating CO_2 (R^2 = 0.84), O_2 (R^2 = 0.89), and HP (R^2 = 0.88) was observed (Bayat et al., 2025). The effects of environmental factors comparing the systems was minimized as the chambers and GF systems were located in the same barn. The effects of diet composition were also minimized by conducting chamber measurements between the 2-wk GF periods. It was observed that there were significant differences between the chambers in the difference of GF and RC in the gas data. Because there were no differences between the 2 GF units, it was more likely the differences were between the chamber units, most likely in gas flow measurements. in estimating the relationships between RC and GF measurements.

Feeding pattern was slightly different between the GF and RC systems (for more details, see Bayat et al., 2025) but this is unlikely to affect differences in gas exchanges. On average, calculated ME requirements were equal, but SD of the difference (8 MJ/d) and the range (from −19 to 15 MJ/d) can increase random variation between the systems. Physical activity of the cows differs between the 2 systems. Fischer et al. (2018) estimated that physical activity contributed 26.5% to variation in residual NE intake. However, some activities such as eating and rumination behavior may not be different in respiration chambers and barn conditions. 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. The contribution of physical activity to RFI is likely to be small 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 requirements of walking relative to the total energy requirements. According to the NRC (2001), ME requirement for 1 km of walking for a 600-kg cow is about 1.2 MJ of ME. In pasture, energy expenditure was 1.7 MJ ME/km (Martin et al., 2015). Repeatability of daily measurements of CO_2 production (0.98) and O_2 consumption (0.96) in RC were high suggesting that the contribution of random errors in chambers measurements to the differences between the methods was insignificant. Most likely, random errors in GF measurements were the main factor causing the differences between the methods in gas measurements, probably with some contributions of physical activity related to different environment and differences in ME requirements between the measurements. However, the GF system ranked the cows according to FE well compared with the RC measurements with 75% of the top 50% in GF ranking were ranked as the top 50% according to the RC ranking with none of the top 50% cows ranked among the lowest 30%.

The relationship between RC and GF was better for RO_2 than RCO_2. This can partly reflect higher repeatability of O_2 compared with CO_2 measurements by the GF system. Eructation peaks increase variability in CO_2 concentration compared with the more stable O_2 concentration. Oxygen-based system can also be recommended because the coefficient of O_2 in HP equation is greater (i.e., it could be expected to be more closely related to HP [and efficiency] than CO_2). Oxygen can also be expected to be influenced by diet composition less than CO_2. Using preformed fatty acids to milk fat synthesis produce less CO_2 than de novo synthesis from acetate. Increased lipid synthesis is associated with RQ greater than 1.0 (Blaxter, 1989). Morris et al. (2020) reported a higher RQ (1.09 vs. 1.05) for cows fed high-starch diet compared with high-fat diet. Previously, abomasal infusion of glucose increased RQ, whereas an isoenergetic abomasal infusion of fat decreased RQ in Holstein cows (Nichols et al., 2019). Even relatively small increase in dietary fat concentration by replacement of barley with oats decreased RQ significantly when measured by the GF system (Ramin et al., 2021).

One possible source of error in GF gas measurements is improper muzzle position during the visits. Muzzle position was a highly repeatable trait and strongly related to CH_4 flux when unacceptable head position data were not filtered (Huhtanen et al., 2015). However, the system is equipped with head position sensors to exclude the unacceptable data. When tested with a model cow, the distance from sampling point (0–30 cm) had no effect on the relative response of CV of CH_4 concentrations (Huhtanen et al., 2015). Similar between-cow SD values of the gas data during RC and GF measurements also suggest that random variability was not markedly different between the systems. The random variation in gas exchange data were smaller than that for DMI (3% vs. 5%) indicating that the suitability of using gas data instead of on-farm DMI measurements should be evaluated further.

Comparison of RMEI and Gas Production–Based Efficiency Traits

The relationship between RCO_2 and RMEI was reasonably good, especially during period 2. Both intake and gas data are likely to have some measurement errors. Lower repeatability of DMI compared with CO_2 production and O_2 consumption do not suggest greater errors in gas compared with DMI data. In the mixed-model regression analysis predicting period 2 values from period 1 data, the block variance of DMI was 1.9-fold compared with random variance and ranged from 0.6 to 1.3 for the gas data and ECM yield. Also, the SD of block variance of observed mean was greater for DMI (4.4%) than for O_2, CO_2, HP, and ECM yield (2.9%–3.2%). This may indicate greater random errors in DMI determination compared with production and gas data. Silage sampling is probably the most critical point affecting the accuracy of DMI determination, especially when silage DM concentration is low as in our study. The intake of ME was calculated using feeding values based on maintenance intake. This explains the positive intercept of regression of RCO_2 on RME as ME concentration at production intake is lower due to reduced digestibility and its negative associative effects with increased DMI (Huhtanen et al., 2009)

The relationship between RMEI and GF based measurements was not better for RO_2 and RHP compared with RCO_2, in contrast to comparison of FE traits determined in RC or by GF, despite higher repeatability of O_2 and HP than CO_2. It is possible that block differences in DMI have masked this. Although CO_2 predicted HP accurately in RC data reflecting rather small variability in RQ of lactating dairy cows, RO_2 and RHP could be more reliable proxies of FE because of higher repeatability of O_2 and its greater coefficient in Brouwer (1965) HP equation. Using RO_2 or RHP as proxies of FE makes the comparison data from different diets more uniform as de novo milk fat synthesis produces more CO_2 than incorporation of dietary fatty acids directly to milk fat as discussed before. In line with this, retained fat synthetized from dietary carbohydrates increased RQ in pigs much more than retained fat from a high-oil diet (Jakobsen and Thorbekt, 1993).

Gross FE Traits

Provided that gas measurements by the GF system are accurate enough, FE traits based on gas exchanges should have some advantages compared with measured DMI in genetic evaluation of the cows in on-farm conditions, even when DMI could be measured without difficulty. Calibration of the GF system is uniform between the farms as they are made centrally by the company (C-Lock Ltd.). The FE traits are based on energy losses, which are less sensitive to ME concentration of the diet, as energetic efficiency in ad libitum fed ruminants is rather constant (Tolkamp, 2010). This means that metabolizability of diet affects less HP or gas-based traits than RFI based on measured DMI. Therefore, FE traits based on the gas data are likely to be more uniform between the farms than those based on RFI. In addition, in contrast to FE traits based on measured DMI, feed sampling and analysis are not required. Representative silage sampling is essential for accurate estimation of DMI that can be a challenge in the farm conditions. Lassen et al. (2023) introduced 3D camera measuring feed intake for FE purposes. Repeatability values between 0.62 and 0.65 were lower than those observed for CO_2 (Huhtanen et al., 2015; Manafiazar et al., 2017; Ryan et al., 2022) and O_2 in the current study. The system measures feed intake on volume basis that is then converted to weight. However, for the genetic evaluation of cows for FE traits based on fresh weight of feed is not accurate as DM concentration of feed can be highly variable within short period of time.

Differences Between RFI Groups

The low-RCO_2 cows had numerically lower DMI and higher ECM yield than the high-RCO_2 cows, but the differences were not significant. In the study of Lidauer et al. (2023) with a large number of cows, 10% superior cows had significantly lower DMI and higher ECM when RMEI was estimated as the difference between observed and predicted MEI. In the current study, the Low-RCO_2 cows had a higher gross FE both in terms of ECM per MJ ME and kg CO_2 production, in agreement with Lidauer at al. (2023). The effects were similar when FCE were expressed as indexes between observed and expected FCE. The differences between low- and high-RCO_2 groups in RCO_2 (1.77 vs. 2.33 kg/d) and RFI (1.24 kg/d = 14.3 MJ/11.5 MJ/kg DM vs. 1.87) were smaller than in the analysis of RC data (Huhtanen et al., 2021), probably reflecting more uniform diets and cows. Reduced HP was the main contributor to the differences in FE between the low- and high-RCO_2 groups. Reduced HP accounted for approximately two-thirds of the differences between the low- and high-RFI groups and metabolizability (ME/GE) about one-third with digestibility accounting for about 80% of the ME/GE effect (Guinguina et al., 2020). Reduced HP in efficient cows can be related to lower maintenance requirement, improved ME utilization for lactation or both. Linear regressions of milk energy corrected for zero energy balance (MJ/d) on ME intake (MJ/d), both scaled to MBW, suggested that the difference between the high- and medium-RFI cows was the higher maintenance requirement of the high-RFI cows, and the better utilization of ME above maintenance for lactation of the low-RFI cows compared with the medium-RFI-cow (Guinguina et al., 2020).

The difference (15%) in CH_4 intensity (g CH_4 / kg ECM) between the high- and low-RCO_2 cows was similar to that reported from respiration chamber studies when RCO_2 was estimated from partial regression coefficients (Huhtanen et al., 2021). When the cows were ranked according to RFI based on partial regression analysis, the high-RFI cows produced 13% more CH_4 per kg ECM than the low-RFI cows (Guinguina et al., 2020). When the cows were grouped in 2 equal groups of 16 cows according to RCO_2 and RCH_4, the difference between the high- and low-RCO_2 groups in CH_4 intensity was greater than between high- and low-RCH_4 cows (11% vs. 9%). Our results suggest that improving efficiency will improve CH_4 intensity but decreasing CH_4 does not improve efficiency.

Future Perspectives

Breeding cows for improved FE has been hampered by difficulties of measuring feed intake of individual cows in on-farm conditions. Accurate estimation of body energy balance is another challenge, especially when measurement periods are short. Even if the estimate of BW change is accurate, variable energy content of BW change at different stages of lactation (Gibb et al., 1992) and at different BCS (NRC, 2001) make estimation of body energy balance challenging. One option to minimize this problem is to determine FE at established stages of lactation when the energy balance is likely to be close to zero. Hooven et al. (1972) reported high (0.85–0.87) correlations of monthly gross FE measured at 60 to 180 DIM with the whole lactation FE.

It is important to identify the cows that are mobilizing body energy that influences apparent FE. Milk fatty acid composition analyzed routinely by mid-infrared spectroscopy can be used as an estimation of energy status of the cows (Mäntysaari et al., 2022). Milk fatty acid composition was more strongly related to energy balance in early lactation when the cows were in negative energy balance (Guinguina et al., 2021). One option is to install acetone sensors to the GF system. Neither milk MIR analysis nor acetone sensors cannot estimate the extent of positive energy balance. Identifying the cows in negative energy balance can help to avoid selecting them as efficient cows. However, from practical point of view the cow is not economical if she partitions a large proportion of ME to body fat or is metabolically inefficient.

One month measurement period in mid-lactation can give a reliable estimate of whole lactation FE. Studies in respiration chambers do not indicate differences in ME utilization for milk production at different stages of lactation, even more unlikely that there is cow × DIM interactions. Ellis et al. (2006) reported that maintenance requirement was dependent of the stage of lactation increasing from 0.335 MJ NE/kg MBW at onset of lactation to 0.40 MJ NE at wk 15 of lactation, but in mid-lactation maintenance requirement was constant. Also, maintenance requirement is variable between the cows, but it is also unlikely that there is cow × DIM interactions as the increase is related to replacement of metabolically inactive fat tissues with high active visceral tissues.

CONCLUSIONS

A good relationship between the GF system and RC in FE traits based on gas exchanges was observed with the relationships being slightly better for RO_2 and RHP compared with RCO_2. Ranking of the cows according to efficiency traits was consistent between the systems. Repeatability of different efficiency traits on GF measurements were similar or greater than corresponding values based on measured DMI. The FE values determined by the GF system were highly correlated to those based on measured DMI. Our results suggest that the cows can be ranked according to FE reliably based on gas exchanges determined by the GF system. Compared with intake-based FE traits, the values based on gas exchanges can have some benefits in on-farm conditions as the method is automated and does not require feed sampling and analysis. The values are less related to energy concentration of the diet making between-farm comparison less biased. Additionally, diet selection would be a smaller problem when the efficiency traits are based on gas data rather than measured intake.

NOTES

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Nonstandard abbreviations used: BWC = body weight change; FCE = feed conversion efficiency; FCEI = FCE indexes; FE = feed efficiency; GF = GreenFeed; HP = heat production; MBW = metabolic BW; MEI = ME intake; P1 = period 1; P2 = period 2; RC = respiration chamber; RCH_4 = residual CH_4; RCO_2 = residual CO_2; Rep = repeatability values; RFI = residual feed intake; RHP = residual heat production; RMEI = residual ME intake; RMSE = root means squared error; RO_2 = residual O_2, RQ = respiratory quotient; 3D = 3-dimensional.

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