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Comparison of different residual carbon dioxide formulations as a means to select feed–efficient dairy cows

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ABSTRACT

Improving feed utilisation efficiency and environmental sustainability by the selection of superior animals are amongst the widely studied topics during the last decade. For the evaluation of individual's feed utilisation efficiency, residual feed intake (**RFI**) has become the common metric and is defined as the difference between actual and expected feed intake. Lately, a new metric for carbon dioxide (**CO_2**) called residual CO_2 (**RCO_2**) is being developed and similarly defined as RFI. However, the partial regression coefficients for expected feed intake obtained by regressing DM intake (**DMI**) on energy sinks may not be biologically plausible and this could also be the case for CO_2. The objective of this study was to compare RCO_2 and RFI formulations calculated using different partial regression coefficients of energy sinks obtained either from regression on energy sinks or from different energy requirement formulations used nationally or internationally. The correlations between these different formulations as well as production, efficiency, and BW measurements were also calculated. Repeated daily measurements of CO_2 production (n = 51 977) using two GreenFeed Emissions Monitoring system and records of DMI from 83 primiparous Nordic Red dairy cows were used. Three types of RCO_2 and RFI formulations were calculated. The first was by fitting a multiple linear regression (RCO_{2MLR} and RFI_{MLR}) whereas the second and third were based on the Finnish energy requirement formulation (RCO_{2FIN} and RFI_{FIN}) and National Research Council 2021 (NRC, 2021; RCO_{2NRC} and RFI_{NRC}), respectively. Correlations between different RCO_2 and RFI formulations were lower (from 0.37 to 0.44) than the correlation between CO_2 production and DMI (0.58) implying that selection based on different RFI formulations may lead to selection of different sets of animals. Selection based on RCO_2 formulations would lead to improvement in energy conversion efficiency (**ECE**) albeit with a slightly lower rate compared to selection based on RFI formulations. However, the decline in the trend of CO_2 production would be enhanced when selection is based on RCO_2 rather than RFI. Of all the residual formulations studied in Finnish dairy cows, the use of RCO_{2FIN} is preferred because it had higher favourable correlations with ECE, CO_2 and methane emission per unit of energy-corrected milk. Due to its high correlation with DMI, the conventional RFI could favour cows with lower DMI, regardless of their milk production. More data are needed to further verify the correlation between CO_2 production and feed intake.

Implications

The carbon dioxide output of a dairy cow can be used to evaluate the cow's metabolic efficiency. The aim of this study was to investigate different residual carbon dioxide formulations for their suitability to select feed–efficient cows. Three different residual carbon dioxide and corresponding three residual feed intake formulations were developed, and their correlations with energy conversion efficiency, methane and carbon dioxide intensity were studied. Results showed that residual carbon dioxide formulations could improve energy conversion efficiency as well as environmental sustainability. Findings from this study also indicate that the rate of improvements depends on the targeted formulation.

Introduction

In recent years, environmental issues have attracted a lot of attention and it has been accentuated to decrease harmful greenhouse gases produced by ruminants. A number of studies on this issue (Huhtanen et al., 2016; Danielsson et al., 2017; Negussie et al., 2017; Løvendahl et al., 2018; Arndt et al., 2022) have under-

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scored the timing and importance of this topic. Due to advances in digital and sensor technologies, recently, it has become possible to measure a host of new phenotypes in ruminants such as exhaled metabolic gases from cows. Good examples of such phenotypes are methane (**CH_4**) and carbon dioxide (**CO_2**) production in dairy cows.

Although many studies have so far focused on the biology of CH_4 emission and options for its mitigation (Danielsson et al., 2017; Negussie et al., 2017; Arndt et al., 2022), currently, there is also an interest towards the biology and attributes of total CO_2 production and its relationship to feed utilisation efficiency as a means to reduce CH_4 emissions in dairy cows (Renand et al., 2019; Huhtanen et al., 2021). In dairy cows, CO_2 production has a very high correlation with cow's heat production which is one of the main determinants of feed utilisation efficiency (Huhtanen et al., 2021). Animals that turn higher proportions of their input energy to heat are less efficient as heat is not the final product and is not saleable. Huhtanen et al. (2021) have reported a high correlation of 0.98 between CO_2 and heat production. In the same study, they carried out mixed model regression analysis and found a lower RMSE for a model where DM intake (**DMI**) was regressed on CO_2 production compared to a model where DMI was regressed on the energy sinks energy correct milk and BW. This indicates that CO_2 production could be utilised in developing a similar criterion to residual feed intake (**RFI**) called residual CO_2 (**RCO_2**) which has the potential to be used as an indicator to improve feed utilisation efficiency. This criterion could be calculated in the same way as RFI. When it is calculated in this way, RCO_2 reflects the amount of actual relative to expected CO_2 production. Negative RCO_2 values are favourable in terms of less environmental impact, and more importantly, it is also indicative of better feed utilisation efficiency (Renand et al., 2019; Fodor et al., 2022), as CO_2 is the end product of feed oxidation in the body. So far, there are only a few studies on RCO_2. One of the studies reported a correlation of 0.83 between RCO_2 and RFI in dairy cows (Huhtanen et al., 2021) which indicates that it is possible to use RCO_2 as an alternative metric to improve feed efficiency. Fodor et al. (2022) reported that a group of cows with higher CO_2 production than expected (i.e., high RCO_2; 1.92 kg higher CO_2/d) had higher feed intake (1.31 kg/d higher) than what was expected in their study.

RFI has been the most commonly used trait to improve feed utilisation efficiency in dairy cows (Li et al., 2017; Løvendahl et al., 2018; Fodor et al., 2022). It indicates that an individual with lower feed consumption than expected (i.e., low RFI) will have better feed utilisation efficiency than its contemporaries with higher RFI. The classical approach to calculate RFI is by subtracting expected feed intake from actual feed intake. Expected feed intake is obtained by regressing DMI on energy sinks, namely energy-corrected milk (**ECM**), metabolic BW (**MBW**), and BW gain (**BWG**) and loss (**BWL**). In animal breeding, it is common to regress DMI on the same data that are used for breeding value estimation, which allows a one-step approach (Tempelman et al., 2015). Alternatively, expectations can be obtained from energy requirement formulations built from nutritional studies nationally or internationally. Regressing DMI on energy sinks has some advantages and disadvantageous. The advantage is that it is easy to implement and generates partial regression coefficients specific to the data available. However, the partial regression coefficients calculated in this way are often too small (Mehtiö et al., 2018; Lidauer et al., 2023) and therefore resulting metrics based on required energy may be even lower than the energy content of one unit of energy sink trait, which is in conflict with the first law of thermodynamics that energy cannot be created. It can be expected that this shortcoming would also hold true for predicting RCO_2 by partial regression coefficients using the same procedure. However, there are different energy requirement formulations that are developed over several years of large nutritional studies with biologically reasonable partial regression coefficients for each energy sink (e.g., NRC, 2021; Luke, 2022). We hypothesised that the use of such regression coefficients from energy requirement formulations may avoid the problem associated with implausible partial regression coefficients resulting from the classical calculation of RFI and RCO_2 using multiple linear regression. So far, however, not much has been reported on the use of these partial regression coefficients from different energy requirement formulations and their comparisons to the direct regression method particularly information from the Finnish feeding norms is lacking.

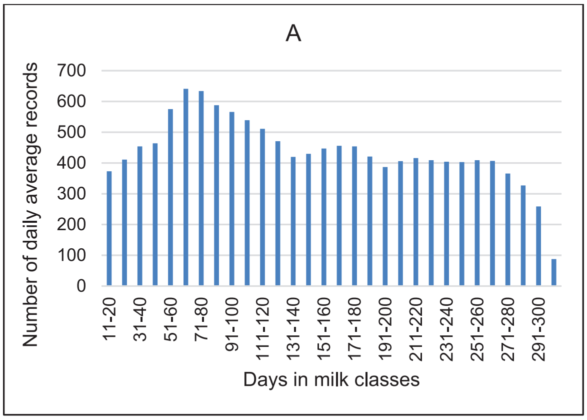
The objectives of this study were 1) to develop different RCO_2 formulations by calculating the expectations either based on regressing CO_2 production on energy sinks or by obtaining corresponding coefficients from National Research Council (NRC, 2021) or from Finnish energy requirement formulation tables (Luke, 2022), 2) to assess the correlations between RCO_2 and RFI formulations and efficiency traits, and, 3) to compare the performances of different residual formulations in two divergent groups of superior and inferior animals in terms of feed efficiency.

Material and methods

Data

The data used in this study were collected from 83 primiparous Nordic Red dairy cows from October 2021 to May 2023 at the Natural Resources Institute Finland (Luke) dairy research farm. Spot air samples from cows' respiration collected using two GreenFeed emissions monitoring systems (C-Lock Inc., Rapid City, SD, USA), which were installed in a corral with 15 m distance, were used to determine their daily CO_2 and CH_4 production. These units were connected to a concentrate feed dispenser that dispensed some pelleted feed as a bait to attract cows to the measurement units. During the visit to the GreenFeed emissions monitoring units, cows received 320 g of concentrate pellet supplements per visit for up to five visits per day. In total, there were 51 977 repeated individual visits to the GreenFeed emissions monitoring units. All visits of a cow that lasted less than 2 min were discarded by the GreenFeed emissions monitoring system as invalid measurements. Diurnal distribution of visits had four peaks at 0100, 0700, 1400 and 2000 h, however, it was uniform with 53 and 47% of visits occurred between 1200–2400 h and 2400–1200 h, respectively. Only records between days in milk 11–305 were included. On average, each cow visited the GreenFeed emissions monitoring units 3.41 ± 1.12 times per day and daily averages were computed as the mean of measurements from all visits. Less than 5 percent of the daily averages were based on one single visit. The raw data were edited, and outliers were identified and removed. All observations outside the range of mean $\pm 2.5 \times$ SD for daily CO_2 production within each month of lactation were identified as an outlier and removed. After editing, the final dataset included 49 155 repeated individual visits, resulting in 13 136 daily averages of CO_2 and CH_4 production measurements. This corresponds to on average 592.2 visits and 158.3 daily average records per cow. Distribution of observations throughout lactation is shown in Fig. 1.

The experimental cows were under daily feed intake (44 RCI feed weigh troughs, Hokofarm Group, The Netherlands) and production performance recording and their BW were measured twice a day right after milking using an automatic scale (Pellon Group Oy, Ylihärmä, Finland). The cows were housed in a freestall barn and provided with unlimited access to grass silage (timothy-meadow fescue sward). The grass silage was delivered to the cows four times daily at 0630, 1300, 1530 and 1800 h, and the quantity



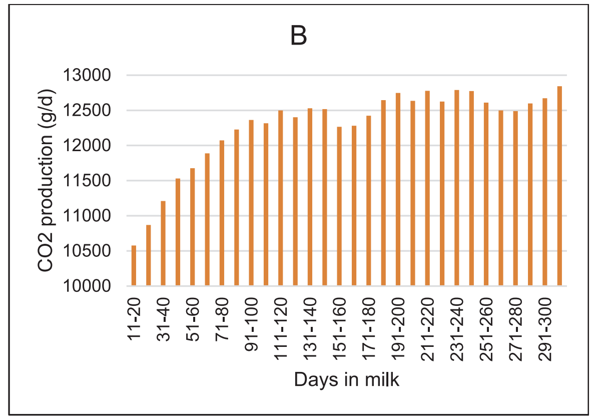


Fig. 1. Distribution of records of carbon dioxide (CO_2; A) and mean of daily averages of CO_2 production (B) throughout lactation in primiparous Nordic Red dairy cows.

of concentrate given to each cow was adjusted accordingly to maintain a consistent forage–to–concentrate ratio of 52:48 on a DM basis. The concentrate was a mixture of barley, wheat, oat, molassed sugar beet pulp, rapeseed meal, and a premix of minerals and vitamins (Table 1). Feed refusals were weighted and samples for DM analysis were collected daily. To minimise fluctuations and errors in BW measurements, a method described in Mäntysaari and Mäntysaari (2015) was used to calculate smoothed daily BW and subsequently daily BW gains and losses.

Calculation of phenotypes and analysis

Residual feed intake formulations

Prior to introducing RCO_2 formulations, we present the applied RFI reference formulations, as these serve as a basis for the studied and later introduced RCO_2 formulations. The RFI formulations were calculated by subtracting expected DMI from actual DMI as follows:

$$RFI_{ij} = DMI_{ij} - \text{expected}\,DMI_{ij}$$

where RFI_{ij} is the i^{th} RFI observation of individual j and expected DMI_{ij} was calculated either by regressing DMI_{ij} on energy sinks or by using regression coefficients from other sources such as NRC 2021 and Finnish energy requirement formulations (Luke, 2022). It should be noted that the data of this study were not considered for the derivation of the Finnish energy requirement formulation. In the first RFI formulation (RFI_{MLR}), a multiple linear regression model that included four energy sinks (ECM, MBW, BWG and BWL) was fitted on DMI to obtain a data-based formulation for expected DMI. The RFI_{MLR} was calculated as follows:

$$RFI_{MLR_i} = DMI_i - [\hat{\mu} + \hat{\gamma}_1 \times ECM_i + \hat{\gamma}_2 \times MBW_i - \hat{\gamma}_3 \times BWL_i + \hat{\gamma}_4 \times BWG_i]$$

RFI_{MLR_i} is the repeated observations for each individual and is similar to conventional RFI in the literature; $\hat{\mu}$ is the estimated intercept and $\hat{\gamma}_1$ to $\hat{\gamma}_4$ are the estimated partial regression coefficients from the multiple linear regression analysis. The second formulation was RFI_{FIN} which was based on Finnish energy requirement formulations and was calculated as follows:

$$RFI_{FIN} = DMI - [0.477 \times ECM + 0.0477 \times MBW - 2.588 \times BWL + 3.142 \times BWG]$$

where 0.477 kg was calculated by dividing the energy content of 1 kg of ECM (3.145 MJ; Sjaunja et al., 1990) by the conversion efficiency of metabolisable energy (**ME**) of feed to net energy lactation based on Finnish energy requirement formulation (i.e., 0.61) and dividing the outcome by energy density of diet (10.82 MJ ME/kg DM). The coefficients for the remaining sinks were calculated by dividing the energy requirements for MBW = 0.515, BWL = –28.0, and BWG = 34.0 (Luke, 2022; which are energy requirement for 1 kg MBW, the energy released from 1 kg BWL and energy required for 1 kg BWG, respectively) by the energy density. The third RFI formulation, RFI_{NRC}, was based on the latest National Research Council (NRC, 2021) energy requirements and was calculated as follows:

$$RFI_{NRC} = DMI - [0.440 \times ECM + 0.0586 \times MBW - 3.292 \times BWL + 3.292 \times BWG]$$

where 0.440 kg was calculated as the energy content of 1 kg milk (3.145 MJ) which is equivalent to 4.765 MJ ME (considering energy conversion efficiency of 0.66 for ME of feed to net energy lactation based on NRC). Dividing this number by energy density yields 0.440 kg as the partial coefficient for ECM. Also, the energy requirement for maintenance of 1 kg of MBW is 0.418 MJ net energy lactation per day which is equal to 0.634 MJ ME/d and the energy content of 1 kg body reserve is 26.36 MJ retained energy (NRC, 2021). Knowing that the conversion efficiency of ME to retained energy is 0.74, the ME requirement for 1 kg gain (or released in case of 1 kg loss) is 35.62 MJ. Dividing the above-mentioned values by energy density gave the following partial regression coefficients for MBW, BWL and BWG 0.0586 kg, 3.292 kg and 3.292 kg, respectively.

Residual carbon dioxide formulations

We developed RCO_2 formulations that are corresponding to the presented RFI formulations. The first one (RCO_{2MLR}) was based on regression of total CO_2 on energy sinks, and the second formulation was based on partial regression coefficients from Finnish energy requirement formulations. The third one was based on the latest National Research Council (NRC, 2021) energy requirements. Similar to RFI, the general equation used to calculate the RCO_2 formulations was:

Table 1
Ingredients and their composition in the concentrate of primiparous Nordic Red dairy cows in the present study.

Ingredient[1]	Content (% of concentrate, as fed)
Barley	16
Wheat	14
Oat	22
Molassed sugar beet pulp	10
Rapeseed meal	35
Mineral and vitamin premix	3

[1] DM content of the diet was 55.36%.

$$RCO_2 = CO_2 - \text{expected}\,CO_2$$

where expected CO_2 production was calculated either by regressing CO_2 on energy sinks or regression coefficients taken from other sources (i.e., NRC, 2021; Luke, 2022). The first formulation which is the multiple linear regression resulted in the following RCO_2 formulation (RCO_{2MLR}):

$$RCO_{2MLR_i} = CO_{2i} - [\hat{\mu} + \hat{\alpha}_1 \times ECM_i + \hat{\alpha}_2 \times MBW_i - \hat{\alpha}_3 \times BWL_i + \hat{\alpha}_4 \times BWG_i]$$

RCO_{2MLR_i} is the repeated observations for each individual; $\hat{\mu}$ is the estimated intercept and $\hat{\alpha}_1$ to $\hat{\alpha}_4$ are the estimated partial regression coefficients from the multiple linear regression analysis. The second RCO_2 formulation that uses the Finnish energy requirement formulation (RCO_{2FIN}) was calculated as follows:

$$RCO_{2FIN} = CO_2 - [201.3 \times ECM + 51.6 \times MBW - 1287.7 \times BWL + 601.2 \times BWG]$$

where 201.3 g was calculated as: $\varphi = \gamma.(1 - k_l).\tau$ where φ is partial regression coefficients for ECM; γ is MJ ME consumed for production of 1 kg ECM (5.15 according to Luke, 2022); k_l is conversion efficiency of ME to net energy lactation in Finnish energy requirement formulation (0.61); and τ is 100.2 g CO_2/MJ heat production according to Bayat A.R. (unpublished data, personal communication). The "$1 - k_l$" stands for the portion of consumed energy that will be excreted as heat and is highly correlated with CO_2 production. The coefficients for MBW, BWL and BWG were calculated using their corresponding conversion efficiencies and energy requirements (or release in the case of BWL). For instance, 0.515 MJ ME is required for maintenance of 1 kg of MBW and as all of it is turned into heat, the partial regression coefficient for MBW becomes 51.6 g. For BWG, regarding the difference between 34 MJ ME which is needed for 1 kg body reserve and 28 MJ which will be reserved in tissues (Luke, 2022), the coefficient would be 601.2 g. As there are no k_l values estimated for BWL (i.e., conversion efficiency of retained energy to net energy lactation) from Finnish energy requirement formulation, corresponding values from NRC (2021) were used. Transferring retained energy to net energy lactation results in 11% loss (i.e., 28 × (1 – 0.89) × 100.2 = 308.6 g). However, as one unit of BWL provides energy for production of 7.93 kg ECM, the coefficient would be: 308.6 – 7.93 × 201.3 = –1287.7. Finally, the third RCO_2 formulation (RCO_{2NRC}) was based on the latest NRC (2021) energy requirements and resulted in the following RCO_{2NRC} formulation:

$$RCO_{2NRC} = CO_2 - [162.3 \times ECM + 63.5 \times MBW - 920.2 \times BWL + 927.9 \times BWG]$$

The coefficients for this formulation were calculated in the same way as for RCO_{2FIN}. The only difference is that in this case, conversion efficiencies were extracted from NRC (2021) which were 0.66, 0.66, 0.89 (conversion efficiency of retained energy to net energy lactation) and 0.74 (conversion efficiency of ME to retained energy), respectively. Additionally, the amount of energy needed to produce 1 kg of ECM, maintain 1 kg of MBW and 1 kg gain of BW as well as the amount of energy released for catabolism of 1 kg of body tissue were according to NRC (2021), 4.765 MJ ME, 0.634 MJ ME/d, 35.62 MJ ME and 26.36 MJ retained energy, respectively. For instance, the partial regression coefficient for BWG was calculated as: 35.62 × (1 – 0.74) × 100.2 = 927.9 g. One unit of BWL provides energy for production of 7.46 kg ECM, according to NRC (2021). Therefore, the partial regression coefficient for BWL became: 26.36 × (1 – 0.89) × 100.2 – (7.46 × 162.3) = –920.2.

In addition to the above-mentioned formulations, different efficiency traits were also calculated. These included energy conversion efficiency, CO_2 intensity and CH_4 intensity. Energy conversion efficiency was defined as ECM divided by metabolisable energy intake. Also, CO_2 intensity and CH_4 intensity were calculated by dividing CO_2 and CH_4 production by energy-corrected milk, respectively. SAS software version 9.4 (SAS Institute, 2016) was used to fit multiple linear regressions to calculate the partial regression coefficients to predict DMI and CO_2 production using energy sinks. Also, it was used to calculate the correlations between different formulations of RCO_2, RFI and efficiency traits. As a validation tool to test the possible outcomes of selection based on each of the different residual formulations, the best half (low) and worst half (high) of the animals in terms of RFI and RCO_2 were compared. Some of the experimental animals had less than 100 daily averages. In order to have an unbiased comparison, an individual should have had at least 100 daily averages for CO_2 production to be included in one of the above-mentioned groups.

Results

Summary statistics of the traits considered in this study are in Table 2. Means (SD) of CO_2 production, DMI, ECM and MBW were 12 240.5 (1 466.6) g/d, 19.7 (2.52) kg/d, 30.7 (4.31) kg/d and 120.4 (9.33) kg, respectively. Cows produced on average 0.145 kg ECM for each MJ ME in their diet. The analyses of raw data show that the average of CO_2 and CH_4 production for each kg ECM was about 406 g and 14.3 g, respectively, and cows produced about 620 g CO_2 for each kg DMI. Animals showed higher variability in terms of CO_2 production per unit of ECM produced than that of per unit of DM consumed. Averages of expected DMI and expected CO_2 production using multiple linear regressions (19.7 and 12 240.5) were exactly similar to their corresponding actual values.

Partial regression coefficients of different RFI formulations were relatively different from each other. For instance, ECM had lower and MBW had higher relative weights in RFI_{MLR} (Table 3) compared to RFI_{FIN} and RFI_{NRC} (0.309 vs 0.477 and 0.440 for ECM; 0.067 vs 0.0477 and 0.0586 for MBW). A similar trend was also observed for RCO_2 formulations (106.1 vs 201.3 and 162.3 for ECM; 47.6 vs 51.6 and 63.5 for MBW). In addition, the ratio of partial regression coefficient of ECM to that of MBW was lowest for RFI_{MLR} and RCO_{2MLR} among all formulations.

The Pearson correlations between energy sinks, efficiency measures and different residual formulations are presented in Table 4. There was a moderate correlation between CO_2 production and DMI (0.58). There were moderate to highly significant correlations (0.74–0.80) between CO_2 production and RCO_2 formulations. Although low, correlations between CO_2 production and RFI formulations were positive and significant (0.15–0.28).

Correlations between DMI and different residual formulations ranged from 0.17 to 0.75. Correlations between energy conversion efficiency with different RFI formulations (ranging from –0.59 to –0.76) were stronger than those with RCO_2 formulations (ranging from –0.23 to –0.47). Using Finnish energy requirement formulations to calculate RFI and RCO_2, higher correlations were obtained between RFI and RCO_2 (i.e., 0.41 between RFI_{FIN} and RCO_{2FIN}; Table 4) compared to using partial regression coefficients from the data (i.e., 0.37 between RFI_{MLR} and RCO_{2MLR}). High and favourable correlations between energy conversion efficiency with CO_2 intensity and CH_4 intensity were observed (–0.71 and –0.65, respectively). Also, there was a high correlation of 0.88 between CO_2 intensity and CH_4 intensity. Surprisingly, RFI_{MLR} and RCO_{2MLR} had higher correlations with CH_4 intensity (0.22 and 0.55) than with CO_2 intensity (0.20 and 0.51). Comparison between groups of best and worst individuals based on different residual formulations showed that selection based on RFI_{MLR} and RCO_{2MLR} would result in a set of animals with lower DMI (Table 5). In general, RFI formulations were slightly better able to find animals with

Table 2
Summary of descriptive statistics of the traits in primiparous Nordic Red dairy cows under study.

Trait	Unit	N	Mean	SD	Min	Max	CV
CO_2	g/d	13 136	12240.5	1466.63	7422.6	16677.1	11.98
CH_4	g/d	13 136	431.6	75.12	156.1	753.2	17.41
DMI	kg/d	16 060	19.7	2.52	8.9	28.2	12.81
ECM	kg/d	16 517	30.7	4.31	8.3	54.7	14.07
MBW	$kg^{0.75}$	16 517	120.4	9.33	95.9	147.6	7.75
BWL	kg/d	16 517	0.11	0.325	0	3.8	284.88
BWG	kg/d	16 517	0.27	0.254	0	1.3	93.28
ECE	kg/MJ ME[1]	16 060	0.145	0.023	0.044	0.298	15.74
CO_2I	g/kg	13 136	405.5	77.18	192.9	1456.8	19.03
CH_4I	g/kg	13 136	14.3	3.11	4.18	45.89	21.80
eCO_{2MLR}	g	13 136	12240.5	874.00	7958.9	15170.9	7.14
eCO_{2FIN}	g	13 136	12470.8	1011.35	7269.2	17581.5	8.11
eCO_{2NRC}	g	13 136	12840.3	974.84	8817.3	17046.0	7.59
$eDMI_{MLR}$	kg	16 060	19.7	1.67	7.8	25.4	8.44
$eDMI_{FIN}$	kg	16 060	20.9	2.11	9.1	28.6	10.11
$eDMI_{NRC}$	kg	16 060	21.1	2.14	7.1	28.6	10.14
RCO_{2MLR}	g	13 136	0.0	1178.98	−4181.3	4849.0	NA[2]
RCO_{2FIN}	g	13 136	−231.0	1292.80	−5481.8	5484.4	−559.54
RCO_{2NRC}	g	13 136	600.6	1233.08	−5255.1	4899.0	−205.32
RFI_{MLR}	kg	16 060	0.0	1.89	−11.6	7.85	NA[2]
RFI_{FIN}	kg	16 060	−1.2	2.02	−13.6	9.5	−169.25
RFI_{NRC}	kg	16 060	−1.4	1.97	−13.8	8.8	−143.49

Abbreviations: CO_2 = carbon dioxide production; CH_4 = methane production; DMI = DM intake; ECM = energy-corrected milk; MBW = metabolic BW ($BW^{0.75}$); BWL = BW loss; BWG = BW gain; ECE = ECM / metabolisable energy intake (energy conversion efficiency); CO_2I = CO_2 / ECM (carbon dioxide intensity); CH_4I = methane production / ECM (methane intensity); eCO_{2MLR} = expected CO_2 calculated by fitting a multiple linear regression (MLR); eCO_{2FIN} = expected CO_2 calculated using Finnish energy requirement formulation (FIN); eCO_{2NRC} = expected CO_2 calculated using NRC (2021); $eDMI_{MLR}$ = expected DMI calculated by MLR; $eDMI_{FIN}$ = expected DMI calculated using FIN; $eDMI_{NRC}$ = expected DMI calculated using NRC (2021); RCO_{2MLR} = residual CO_2 calculated by MLR; RCO_{2FIN} = residual carbon dioxide calculated using FIN; RCO_{2NRC} = residual carbon dioxide calculated using NRC (2021); RFI_{MLR} = residual feed intake calculated by MLR; RFI_{FIN} = residual feed intake calculated using FIN; RFI_{NRC} = residual feed intake calculated using NRC 2021.

[1] Metabolisable energy.

[2] Not applicable.

Table 3
Estimated partial regression coefficients predicting DM intake and CO_2 production in primiparous Nordic Red dairy cows by fitting a multiple linear regression or using inputs from Finnish energy requirement formulation and National Research Council for four energy sinks.

Formulation	Unit	μ	ECM (kg)	MBW (kg $^{0.75}$)	BWL (kg)	BWG (kg)	Corr
RFI_{MLR}	(kg)	2.014	0.309	0.0670	−3.004	1.900	0.66
RFI_{FIN}	(kg)	–	0.477	0.0477	−2.588	3.142	0.63
RFI_{NRC}	(kg)	–	0.440	0.0586	−3.292	3.292	0.65
RCO_{2MLR}	(g)	2825.0	106.1	47.6	−970.6	1769.1	0.60
RCO_{2FIN}	(g)	–	201.3	51.6	−1287.7	601.2	0.51
RCO_{2NRC}	(g)	–	162.3	63.5	−920.2	927.9	0.55

Abbreviations: μ = intercept; ECM = energy-corrected milk; MBW = metabolic BW ($BW^{0.75}$); BWL = BW loss; BWG = BW gain; Corr = correlation between actual and estimated value using each method; RFI_{MLR} = residual feed intake calculated by fitting a multiple linear regression (MLR); RFI_{FIN} = residual feed intake calculated using Finnish energy requirement formulation (FIN); RFI_{NRC} = residual feed intake calculated using NRC (2021); RCO_{2MLR} = residual CO_2 calculated by MLR; RCO_{2FIN} = residual carbon dioxide calculated using FIN; RCO_{2NRC} = residual carbon dioxide calculated using NRC (2021).

higher energy conversion efficiency than RCO_2 formulations. However, selection based on RCO_2 formulations would result in higher selection differentials for CO_2 intensity and CH_4 intensity compared to selection based on RFI formulations. The difference between the best and worst groups for energy conversion efficiency, CO_2 intensity and CH_4 intensity was higher for residual formulations calculated using Finnish energy requirements and NRC (2021) than residuals calculated using multiple linear regressions.

Discussion

Summary statistics and partial regression coefficients

In this study, we investigated different RCO_2 formulations based on data collected from 83 cows. Cows under this study had production level and BW that is within the range of previous reports on Nordic Red dairy cows (Huhtanen et al., 2021; Lidauer et al., 2023), and Dutch and Scottish Holstein cows (Tempelman et al., 2015) and consumed a similar amount of DMI (Table 2). Also, CO_2 production level and energy conversion efficiency were consistent with Huhtanen et al. (2021) and Fodor et al. (2022).

So far there are very few studies on CO_2 production in dairy cows and comparison to the results from other studies in scientific literature will be limited. Our expected CO_2 production partial regression coefficients of 106.1 for ECM and 47.6 for MBW (Table 3) were lower than the corresponding values of 135 g/kg ECM and 78 g/kg MBW reported by Huhtanen et al. (2021). The variation could be attributed primarily to variances in the types of measurement equipment used (GreenFeed emissions monitoring versus respiration chamber). Additionally, disparities in the breed and parity of the animals being studied may also contribute to the differences.

There is a wide range for partial regression coefficients of energy sinks predicting DMI in the literature. In our study, partial regression coefficients estimated by fitting multiple linear regression were 0.309 for ECM, 0.067 for MBW, −3.004 for BWL and 1.900 for BWG. In a comprehensive study using pooled data from different countries, Tempelman et al. (2015) showed that partial

Table 4
Pearson correlations between energy sinks, performance efficiency measures and different residual formulations using data from primiparous Nordic Red dairy cows.

Trait	DMI	ECM	MBW	BWL	BWG	ECE	CO_2I	CH_4I	RCO_{2MLR}	RCO_{2FIN}	RCO_{2NRC}	RFI_{MLR}	RFI_{FIN}	RFI_{NRC}
CO_2	0.58	0.17	0.43	−0.25	0.40	−0.31	0.50	0.55	0.80	0.74	0.75	0.28	0.19	0.15
DMI		0.36	0.31	−0.32	0.25	−0.47	−0.06	0.13	0.29	0.17	0.21	0.75	0.59	0.57
ECM			−0.02[b]	0.27	−0.33	0.63	−0.72	−0.59	0.00[ns]	−0.36	−0.25	0.00[ns]	−0.32	−0.21
MBW				0.00[ns]	0.37	−0.21	0.30	0.27	0.00[ns]	0.06	−0.06	0.00[ns]	0.04	−0.02
BWL					−0.38	0.55	−0.29	−0.32	0.00[ns]	−0.07	−0.11	0.00[ns]	−0.11	0.04
BWG						−0.51	0.51	0.46	0.00[ns]	0.28	0.19	0.00[ns]	0.02	−0.09
ECE							−0.71	−0.65	−0.23	−0.47	−0.41	−0.59	−0.76	−0.64
CO_2I								0.88	0.51	0.77	0.68	0.20	0.40	0.30
CH_4I									0.55	0.76	0.69	0.22	0.39	0.29
RCO_{2MLR}										0.91	0.96	0.37	0.35	0.36
RCO_{2FIN}											0.98	0.35	0.41	0.38
RCO_{2NRC}												0.36	0.40	0.37
RFI_{MLR}													0.94	0.96
RFI_{FIN}														0.98

Abbreviations: CO_2 = carbon dioxide production (g/d); DMI = DM intake (kg/d); ECM = energy-corrected milk (kg/d); MBW = metabolic BW ($BW^{0.75}$); BWL = BW loss (kg/d); BWG = BW gain (kg/d); ECE = ECM / metabolisable energy intake (energy conversion efficiency; kg/MJ metabolisable energy); CO_2I = CO_2 / ECM (carbon dioxide intensity; g/kg); CH_4I = methane production / ECM (methane intensity; g/kg); RCO_{2MLR} = residual CO_2 calculated by fitting a multiple linear regression (MLR) (g); RCO_{2FIN} = residual carbon dioxide calculated using Finnish energy requirement formulation (FIN) (g); RCO_{2NRC} = residual carbon dioxide calculated using NRC (2021) (g); RFI_{MLR} = residual feed intake calculated by MLR (g); RFI_{FIN} = residual feed intake calculated using FIN (g); RFI_{NRC} = residual feed intake calculated using NRC (2021) (g).
Correlations without superscript were significantly different from zero at $P < 0.01$, superscript b was significant at $P < 0.05$, and [ns] stood for nonsignificant.

Table 5
Differences in production, CO_2 exhalation, BW measurements and different residual formulations between low and high groups of primiparous Nordic Red dairy cows based on studied formulations.

	RCO_{2MLR}		RCO_{2FIN}		RCO_{2NRC}		RFI_{MLR}		RFI_{FIN}		RFI_{NRC}	
Trait	Low	high	low	high	low	high	low	high	low	high	low	high
CO_2	11731.5[a]	12868.6	11728.3[a]	12871.8	11768.0[a]	12832.1	12037.7[b]	12562.4	12042.4[b]	12557.7	12187.1[ns]	12413.0
DMI	19.55[b]	20.34	19.61[c]	20.28	19.62[c]	20.27	19.32[a]	20.57	19.55[b]	20.33	19.73[ns]	20.16
ECM	31.17[ns]	30.33	31.45[ns]	30.05	31.36[ns]	30.14	30.53[ns]	30.96	31.65[b]	29.84	31.56[c]	29.94
MBW	121.1[ns]	121.1	120.6[ns]	121.6	121.4[ns]	120.7	121.2[ns]	121.0	119.5[ns]	122.7	121.2[ns]	121.0
BWL	0.099[ns]	0.069	0.097[ns]	0.070	0.094[ns]	0.073	0.062[ns]	0.105	0.072[ns]	0.096	0.062[ns]	0.105
BWG	0.206[a]	0.326	0.186[a]	0.346	0.193[a]	0.339	0.262[ns]	0.269	0.245[ns]	0.287	0.278[ns]	0.254
ECE	0.149[a]	0.139	0.150[a]	0.138	0.150[a]	0.138	0.147[c]	0.141	0.150[a]	0.138	0.149[a]	0.139
CO_2I	380.7[a]	433.4	376.8[a]	437.3	379.4[a]	434.7	398.0[ns]	416.1	383.9[a]	430.2	389.7[b]	424.5
CH_4I	13.35[a]	15.30	13.23[a]	15.42	13.35[a]	15.31	13.98[ns]	14.67	13.41[a]	15.24	13.75[b]	14.91
RCO_{2MLR}	−456.8[a]	534.4	−428.8[a]	506.4	−440.7[a]	518.3	−239.1[a]	316.7	−222.5[a]	300.1	−222.8[a]	300.4
RCO_{2FIN}	−818.7[a]	374.2	−842.5[a]	398.0	−837.8[a]	393.2	−489.1[ns]	44.6	−582.2[a]	137.7	−545.4[a]	100.9
RCO_{2NRC}	1155.4[a]	−18.7	−1154.3[a]	−19.8	−1165.4[a]	−8.7	−857.3[b]	−316.8	−884.3[a]	−289.9	−879.6[a]	−294.5
RFI_{MLR}	−0.307[a]	0.431	−0.268[a]	0.393	−0.313[a]	0.437	−0.564[a]	0.688	−0.496[a]	0.620	−0.492[a]	0.616
RFI_{FIN}	−1.446[a]	−0.708	−1.438[a]	−0.716	−1.461[a]	−0.693	−1.651[a]	−0.503	−1.784[a]	−0.370	−1.767[a]	−0.387
RFI_{NRC}	−1.617[a]	−0.946	−1.591[a]	−0.972	−1.629[a]	−0.934	−1.880[a]	−0.683	−1.945[a]	−0.618	−1.963[a]	−0.600

Abbreviations: CO_2 = carbon dioxide production (g/d); DMI = DM intake (kg/d); ECM = energy-corrected milk (kg/d); MBW = metabolic BW ($BW^{0.75}$); BWL = BW loss (kg/d); BWG = BW gain (kg/d); ECE = ECM / metabolisable energy intake (energy conversion efficiency; kg/MJ metabolisable energy); CO_2I = CO_2 / ECM (carbon dioxide intensity; g/kg); CH_4I = methane production / ECM (methane intensity; g/kg); RCO_{2MLR} = residual CO_2 calculated by fitting a multiple linear regression (MLR) (g); RCO_{2FIN} = residual carbon dioxide calculated using Finnish energy requirement formulation (FIN) (g); RCO_{2NRC} = residual carbon dioxide calculated using NRC (2021) (g); RFI_{MLR} = residual feed intake calculated by MLR (g); RFI_{FIN} = residual feed intake calculated using FIN (g); RFI_{NRC} = residual feed intake calculated using NRC (2021) (g).
Comparison of means between low and high groups for each formulation was tested, and significant difference levels are shown in superscripts ([a] = $P < 0.01$; [b] = $P < 0.05$; [c] = $P < 0.1$; [ns] = non-significant).

regression coefficients of energy sinks ranged from 0.29 to 0.47 for ECM and from 0.06 to 0.16 for MBW. In a recent study, Lidauer et al. (2023) reported a low regression coefficient of 0.249 for ECM and Li et al. (2017) revealed that there are fluctuations in the partial regression coefficient of DMI on ECM at different lactation stages ranging from around 0.03–0.18.

Correlations between residual formulations, energy sinks and efficiency traits

Residual formulations calculated using Finnish energy requirements and NRC 2021 had higher correlations with efficiency traits (i.e., energy conversion efficiency, CO_2 intensity and CH_4 intensity) than residual formulations calculated using multiple linear regressions. The reason is differences in the partial regression coefficients that create different correlations. For instance, the summation of correlations between ECM and CO_2 with RCO_{2FIN} was higher than with RCO_{2MLR}. Therefore, improving RCO_{2FIN} would increase the denominator (i.e., ECM) and decrease the nominator (i.e., CO_2 and CH_4) in CO_2 intensity and CH_4 intensity and subsequently leads to higher correlations with these traits. Also, CH_4 intensity and CO_2 intensity had higher correlations with RCO_2 formulations than RFI formulations. However, energy conversion efficiency had higher correlations with RFI formulations compared to RCO_2 formulations. This is due to the discrepancies in components of these ratio traits. In addition, it might be that CH_4 intensity, CO_2 intensity and RCO_2 are more closely related to ME content rather than DMI. In other words, RFI can better account for the efficiency of feed digestion (Potts et al., 2017). Correlations between RCO_2 and RFI were higher when formulations were based on Finnish energy requirements. Cows with lower RFI_{MLR} have higher digestibility; therefore, they produce and exhale higher amounts of gases (CO_2 and CH_4) per kg of DMI than expected. This could weaken the correlation between RFI_{MLR} and RCO_{2MLR} to some extent. Unexpectedly, residual correlations calculated by fitting multiple linear regressions had a higher correlation with CH_4 intensity than with CO_2 intensity. Due to the complexity of these composite traits, it is hard to explain the exact reason behind these higher correlations. However, most probably, the residuals obtained by multiple linear regressions select animals with higher digestibility and digestibility has a higher correlation with CH_4 than with CO_2. It has been stated that the majority of CH_4 produced by cows is because of enteric fermentation (~ 85%; Hindrichsen et al., 2005), while most of the produced CO_2 is due to the metabolism of nutrients and only a small fraction (~ 20%) comes from digestive fermentation (Hoernicke et al., 1965).

The correlation of CO_2 production with residual formulations was the highest with RCO_{2MLR} (0.80), and the correlation of DMI was the highest with RFI_{MLR} (0.75). This was expected as the multiple linear regression results in partial regression coefficient estimates which are specific to the data. The high correlation between RFI_{MLR} and DMI shows that this formulation favours animals with low feed intake even if they are low producers. In first parity Jersey cows Løvendahl et al. (2018) reported a correlation of 0.80 between RFI and DMI. This implies in a selection index with high economic weight for RFI_{MLR}, there will be a risk that animals undergo a higher negative energy balance by lowering their DMI. The correlation between DMI and energy conversion efficiency (−0.47) indicates that cows with higher feed consumption generally are less energy efficient, however, there might be cows with higher DMI that are more efficient than their counterparts as the correlation between them is far from unity. Liinamo et al. (2015) reported a high negative correlation between DMI and energy conversion efficiency. Also, in a study conducted by Coleman et al. (2010) on Holstein-Friesian cows in pasture-based systems, they found that the group of cows with higher feed conversion efficiency had on average lower DMI. However, it is important to carefully consider which target trait(s) to focus on in order to enhance feed efficiency. Since RCO_{2MLR} and RFI_{MLR} have the highest correlations with DMI among the different residual formulations, it could also be expected that selection based on these traits could result in animals with more negative energy balance compared to the other formulations studied here.

In an earlier study, Huhtanen et al. (2021) reported no association between negative energy balance and CO_2 production. In the present study, cows with higher BWL produced significantly lower amount of CO_2. This might be due to the higher conversion efficiency of energy stored in body tissues than the feed energy to net energy of lactation. This is probably because an animal that uses body reserves to produce a part of its ECM would exhalate less CO_2 relative to its counterparts, with similar BW and ECM, that receive all its energy requirements from feed sources. The negative correlation between CO_2 production and BWL should be taken into consideration when selecting for CO_2 production. However, RCO_2 formulations had lower correlations with energy balance, which is favourable, than their corresponding RFI formulations (results not shown). Correlations between the different RCO_2 formulations were high (0.91–0.99). Correlations between different RFI formulations were also high (0.94–0.98). However, it can be expected that selection based on each of the residual formulations leads to the selection of different sets of animals with different characteristics. For instance, the difference in ECM between low and high groups was lower for RCO_{2MLR} than RCO_{2FIN} and RCO_{2NRC}. Also, Spearman correlations between different RFI formulations, calculated for animals with at least 100 daily averages, were 0.83–0.98 and those between RCO_2 formulations were 0.88–0.97.

Animals with higher DMI produced lower CO_2 per kg of feed consumed (results not shown). This might be due to that higher DMI reduces ruminal retention time and subsequently reduces feed digestion (Huhtanen et al., 2016; Løvendahl et al., 2018). The high correlation between CO_2 intensity and CH_4 intensity agrees with the reported correlation of 0.87 between CO_2 and CH_4 production by Huhtanen et al. (2021). The high correlations between RCO_2 formulations and CH_4 intensity found here give some indication that there might be great potential for lowering CH_4 production by selecting based on RCO_2 formulations.

Comparison of residual formulations

Animals with lower RCO_2 and RFI had a better feed utilisation efficiency. When the cows were ranked based on ECM production, the highest ECM producers had unfavourable RFI_{MLR} (0.127) compared to the group with the lowest ECM (−0.001). This implies that selection based on partial regression coefficients of RFI_{MLR}, which was calculated by regressing DMI on energy sinks, may not be an optimal formulation to select for more feed–efficient animals. However, selection based on RFI formulations generally would result in lower CO_2 exhalation. On the other hand, selection based on RCO_2 formulations would improve energy conversion efficiency. Our results in general agree with the previous study by Huhtanen et al. (2021) who reported that cows with lower RCO_2 produced more ECM per unit of DMI.

The low group based on RFI_{MLR} produced a lower amount of ECM compared to their counterparts, whereas the low groups based on RFI_{FIN} and RFI_{NRC} produced a higher amount of ECM compared to their corresponding high groups. This can be attributed to the low partial regression coefficient for ECM. In general, since the correlations between the different RCO_2 and RFI formulations are far from unity, such differences in their performance in relation to different efficiency measures are to be expected.

Cows with lower RFI had higher CO_2 production per unit of DMI (results not shown) and most probably also higher digestion ability. It can be speculated that cows in a herd with fewer feeding frequency generally would have better scores for RFI. Also, evaluating feeding behaviour and its associations with feed efficiency traits, Cavani et al. (2022) concluded that it is likely that cows with a slower rate of intake would be more feed efficient. This is in line with the report of Løvendahl et al. (2018) who stated that the rate of digesta passage affects digestibility and CH_4 yield and therefore, it might be difficult to improve digestibility and CH_4 emission by selection simultaneously. However, our results indicate that cows with lower RCO_2 value produce a lower amount of CO_2 per unit of DMI or ECM and have also a lower total CO_2 emission. Also, the CH_4 intensity would be improved by selecting based on the studied residual formulations, especially when applying RCO_2 formulations.

Conclusion

In this study, we investigated different RCO_2 formulations and compared their effectiveness in identifying and selecting of cows with improved feed utilisation efficiency and reduced emissions. Residual formulations calculated based on energy requirement formulations had clearly higher correlations with energy conversion efficiency compared to residual formulation calculated using multiple linear regressions. Also, among the formulations in the studied, RCO_2 calculated based on energy requirement formulations had the highest correlation with CH_4 intensity. The results of this study give some indications that RCO_2 might be an alternative trait that has the potential not only to improve feed efficiency but also to lower CH_4 emission per unit of product. Nevertheless, more data are needed to conduct genetic analyses for evaluating the actual superiority of RCO_2 over RFI as a metric in selection for feed efficiency.

Ethics approval

Collecting the carbon dioxide and feed intake data complied with the ethical standards and did not require approval by the National Ethics Committee.

Data and model availability statement

The data and developed models were not deposited in an official repository. They are available upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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