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Longitudinal modeling of residual carbon dioxide and residual feed intake in the Nordic Red dairy cattle

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ABSTRACT

Feed utilization efficiency is an important trait in dairy production playing a significant role in reducing feed costs and lowering methane emission. One of the metrics used to measure feed efficiency in dairy cows is residual feed intake (**RFI**). This metric requires routine measurement of feed intake. Since there is a positive high correlation between heat production and carbon dioxide (**CO_2**) production on the one hand and heat production and efficiency on the other hand, residual carbon dioxide (**RCO_2**) might be a useful metric to improve feed efficiency. The objectives of this study were to model the trajectories of RCO_2 and RFI as well as to estimate their repeatabilities and correlations at different stages of lactation. Daily CO_2 output and feed intake were recorded from 46 primiparous Nordic Red dairy cows using two Greenfeed Emissions Monitoring™ systems from 2 to 305 days in milk (**DIM**). Edited data comprised 5 995 daily averages. To calculate predicted values of CO_2 and DM intake (**DMI**), prediction models were developed by fitting multiple regression models to observations. Subsequently, RCO_2 and RFI were calculated by subtracting predicted values of CO_2 and DMI from their corresponding actual observations. A random regression bivariate model was fitted to estimate repeatabilities and animal correlations within lactation at different DIMs between RCO_2 and RFI traits. The model fitted included fixed effects of year-month of recording, lactation month, fixed regressions as well as random regressions for the animal effect. The residual variance was considered to be heterogeneous. Repeatabilities and animal correlations of RCO_2 and RFI between selected DIM (for every 30 DIM i.e., 6, 36,. . ., 246 and 276) were calculated. Repeatability of RCO_2 was high at the beginning of lactation (0.72 at DIM 6) and decreased around the peak of milk production (0.27 at DIM 96) and again increased gradually toward the end of lactation. Similarly, RFI also had high repeatability at the beginning (0.86 at DIM 6); however, it decreased in mid-lactation (0.37 at DIM 156) and then increased toward the end of lactation. Animal correlations between RCO_2 and RFI were moderate to high on the same DIM and ranged from 0.37 to 0.88. Overall, we found that animals with higher CO_2 production than expected also consume more DMI than expected, but the moderate correlation between RCO_2 and RFI found in this study calls for more research to assess the potential of RCO_2 to become a new feed efficiency metric.

Implications

Evaluating feed efficiency requires recording DM intake of dairy cows which is expensive and difficult to implement routinely in commercial herds. Alternative approaches are therefore of interest. In this study, using daily carbon dioxide measurements to build a residual carbon dioxide metric, which recently has been proposed as a potential feed efficiency trait, was investigated. Results showed that residual carbon dioxide has medium to high repeatability and moderate correlations with residual feed intake.

Introduction

In the last decade, much attention was directed toward improving the efficiency of feed utilization in dairy cattle (Berry et al., 2014; Hurley et al., 2017; Connor et al., 2019), not only to respond to the growing demand for animal products but also to decrease the byproduct of ruminal digestion such as methane (Hegarty et al., 2007; Manafiazar et al., 2017) and mitigate nitrogen excretion. To improve feed efficiency, the most commonly adopted strategy has been the selection for residual feed intake (**RFI**). This metric requires measuring daily individual feed intake by scales, which has been done so far mainly in research farms, due to the high recording costs. Collecting feed intake data from genomic ref-

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erence populations or large number of animals is expensive. Therefore, there have been attempts (e.g., Lassen et al., 2018) to develop metrics that have a lower cost of recording and a high correlation with dairy cows' feed utilization efficiency.

Huhtanen et al. (2021) analyzing respiration chamber data showed that carbon dioxide (**CO_2**) production was closely related to heat production and predicted DM intake (**DMI**) better than models based on energy-corrected milk (**ECM**) yield and BW. Between-cow variation in heat production explains the largest part of the genetic variation in residual energy intake and Huhtanen et al. (2021) found a high correlation (r = 0.98) between CO_2 production and heat production. This provides a theoretical basis for using residual carbon dioxide (**RCO_2**) as a metric of feed efficiency in lactating dairy cows without a need for measurement of individual cow's DMI. Although this requires the measurement of metabolic gasses such as CO_2, recent advances in measurement techniques have made it possible that metabolic gasses from individual animals can be measured more accurately than before and at a relatively low cost compared to respiration chambers (Garnsworthy et al., 2019). Therefore, the differences between actual and predicted CO_2 production might be an alternative to RFI. If there is a between cow variability in terms of feed utilization efficiency, there should also be a between cow variability in terms of heat production and hence CO_2 production as well.

Conventionally, RFI is defined as the difference between actual and predicted DMI. Similarly, RCO_2 can be defined as the difference between actual and predicted CO_2 production. With this definition, it would be expected that individuals with lower RCO_2 would direct a larger proportion of consumed energy to production rather than wasting it by producing more CO_2. However, one of the shortcomings of the RCO_2 is that it cannot capture between cow variation in efficiency of feed digestion. This is because CO_2 production is a function of metabolizable energy intake and not gross energy intake. However, several studies have confirmed that actual between-cow variation in digestibility is rather small (Cabezas-Garcia et al., 2017; Huhtanen et al., 2016; Mehtiö et al., 2019).

Most studies on gaseous traits were focused on investigating methane production and the ways to mitigate it (Negussie et al., 2012; Manafiazar et al., 2017; Denninger et al., 2019; Aldridge et al., 2022), and up to now, only a few studies have been conducted on CO_2 exhalation (Arthur et al., 2018; Huhtanen et al., 2021; Fodor et al., 2022). Manafiazar et al. (2017) and Arthur et al. (2018) estimated correlations between CO_2 production and DMI in beef cattle ranging from 0.62 to 0.89. However, there are only two estimates so far on the correlation between RFI and RCO_2, 0.27 for beef cattle (Arthur et al., 2018) and 0.83 for dairy cows (Huhtanen et al., 2021). In general, there is a lack of information on the repeatabilities and animal correlations between RCO_2 and RFI at different stages of lactation, and particularly, there are no estimates for the Nordic Red cattle. The objectives of this study were (1) to model lactation trajectories of CO_2, DMI, RCO_2 and RFI, (2) to estimate repeatabilities of and correlations within and between CO_2 and DMI as well as those of RCO_2 and RFI at different stages of lactation and (3) to identify the most suitable stages of lactation to measure CO_2 output.

Material and methods

Data

Carbon dioxide measurement

Spot gas samples from cows' eructation and respiration were analyzed for daily CO_2 emissions from 46 primiparous Nordic Red dairy cows from October 2021 to May 2022 at the Natural Resources Institute (Luke) dairy cattle research herd in Jokioinen, Finland. The spot gas samples in combination with airflow were measured using two Greenfeed Emissions Monitoring™ (**GEM**) systems (C-Lock Inc., Rapid City, SD, USA) to calculate daily CO_2 production. A mass balance approach was used to calculate the CO_2 emission for the GEM systems. The records of concentrations were deducted from each peak concentration. The resulting differences were converted to concentrations, and then multiplied by the airflow values and conversion factors to obtain an emission rate in g/d. Details about the calculations of CO_2 production are given in McGinn et al. (2021). The GEM systems were installed about 15 m apart in the dairy barn and were connected to the concentrate feed dispenser unit which dispensed 320 g of pelleted concentrates per visit, in eight drops, as bait to attract cows to the measurement units. All cows had access to both units, and the baits had the same ingredients as the concentrate (explained below). The maximum number of times per day that cows could receive concentrate in GEM systems was five. The total number of individual visits to the GEM systems was 23 128. On average, each individual visited the GEM systems 3.43 ± 1.11 times per day and there were 6 735 daily averages of CO_2 production measurements. Observations after days in milk (**DIM**) 305 were sparse and therefore not included in the final analyses. The data editing also involved the identification and removal of outliers from the final data. For this, mean ± 2.5 × SD of daily CO_2 production within each month of lactation was used as a criterion and all observations outside this range were excluded from the final dataset. After editing, the final data included 20 753 individual visits that resulted in 5 995 daily averages from 2 to 305 DIM, i.e., on average 130 daily averages per cow during the considered 304−day lactation period. Then, weekly averages of CO_2, DMI, RCO_2 and RFI were calculated to assess the effect of the period of averaging records on the repeatability of the studied traits.

Feed intake, milk yield and BW

The individual cow's DMI was recorded using automated bins (44 RCI feed weigh troughs, Hokofarm Group, The Netherlands). Cows were kept in a freestall barn and were fed separate grass silage (timothy-meadow fescue sward) and concentrate (a mixture of barley, wheat, molassed sugar beet pulp, rapeseed meal and mineral and vitamin premix) *ad libitum*. The silage was delivered four times a day and the amount of concentrate was adjusted for each cow to keep the ratio of concentrate to silage constant at 48%. Cows were milked twice daily, at 0645 and 1600 h, in a milking parlour and received 0.3 kg of concentrate during each milking. All cows were under continuous feed intake recording for the entire lactation period. The concentrate intake in the milking parlour and GEM systems were considered in the DMI calculations. Feed refusals were weighted, and samples for DM analysis were collected daily. The data recording included daily measurements of individual feed intake, BW (two records per day), and milk yield. Daily milk production was calculated as the sum of milk yield from the morning and evening milking. The milk composition (fat, protein, lactose, somatic cell count, and mid-infrared spectroscopy (**MIR**)) was analyzed on lactation weeks 2 and 3, and thereafter, once a month and also BWs of cows were taken after each milking. Milk compositions were used to calculate ECM using the formula by Sjaunja et al. (1990). A random regression model was fitted to the BW observations (Mäntysaari and Mäntysaari, 2015) to smoothen for each cow the cow-specific daily weights and thereby minimize fluctuations and errors. These estimated daily weights were used to calculate BW gain (**BWG**) and BW loss (**BWL**), as a difference in BW between subsequent days. Finally, the edited CO_2 production data were merged with the production and feed intake data. These data included variables such as recording date, calving date, DIM, milk yield, ECM, DMI, BW, BWG and BWL. A summary and descriptive statistics of the final data are presented in Table 1.

Analysis

Residual carbon dioxide and residual feed intake

In analogy to RFI, four traits, namely ECM, metabolic BW (**MBW**), BWL and BWG that predict the energy use of the cow and are often called energy sinks, were used to predict CO_2 production. A multiple linear regression analysis was performed to regress CO_2 on ECM, MBW, BWL and BWG. The same traits were also used for the prediction of DMI. Subsequently, RCO_2 was defined as a difference between actual and predicted CO_2 production and it was calculated as follows:

$$\mathrm{RCO}_{2\mathrm{i}} = \mathrm{CO}_{2\mathrm{i}} - \widehat{\mathrm{CO}}_{2\mathrm{i}} \tag{1}$$

Likewise, RFI was calculated as:

$$\mathrm{RFI}_{\mathrm{i}} = \mathrm{DMI}_{\mathrm{i}} - \widehat{\mathrm{DMI}}_{\mathrm{i}} \tag{2}$$

The MIXED procedure of SAS software (version 9.4., SAS Institute Inc., Cary, NC) was used to fit the models.

Estimation of repeatabilities and correlations

To calculate animal (genetic plus permanent environmental) and phenotypic correlations of CO_2, DMI, RCO_2 and RFI between selected DIM (6, 36, …, 276; every 30 DIM), the following bivariate random regression model was fitted to the data:

$$\mathrm{Y}_{\mathrm{t:dijk}} = \mathrm{YM}_{\mathrm{t:i}} + \mathrm{LM}_{\mathrm{t:j}} + \sum_{\mathrm{l=0}}^{5} \beta_{\mathrm{t:l}} \varnothing_{d1l} + \sum_{\mathrm{n=0}}^{2} \alpha_{\mathrm{t:kdn}} \varnothing_{d2n} + \varepsilon_{\mathrm{t:dijk}} \tag{3}$$

where $\mathrm{Y}_{\mathrm{t:dijk}}$ is the daily observations for trait t (CO_2, DMI, RCO_2, RFI) of cow k made on DIM d within year-month (YM) i and lactation month (LM) j; $\sum_{\mathrm{l=0}}^{5}\beta_{\mathrm{t:l}}\varnothing_{d1l}$ is the fixed regression function on DIM d, where $\varnothing_{d1}$ is a vector containing the covariates of a fourth-order Legendre polynomial plus exponential term (Wilmink, 1987) for DIM d (i.e., $e^{-0.05d}$); $\sum_{\mathrm{n=0}}^{2}\alpha_{\mathrm{t:kdn}}\varnothing_{d2n}$ is the random regression function for animal effects, where $\varnothing_{d2}$ is a vector containing the covariates of a first-order Legendre polynomial plus exponential term; var ($\boldsymbol{\alpha}$) = MVN ($\mathbf{0}$, $\mathbf{I} \otimes \mathbf{K}_a$) where $\mathbf{K}_a$ is a 6 × 6 covariance matrix for the animal effect regression coefficients; and $\varepsilon_{\mathrm{t:dijk}}$ is the random residual where var ($\boldsymbol{\varepsilon}$) = MVN ($\mathbf{0}$, $\mathbf{I} \otimes \mathbf{R}$), where $\mathbf{R}$ is a 2 × 2 covariance matrix for the residual effect. Residual variance was considered to be heterogeneous between different lactation months. The model selection was based on the Akaike information criterion, Bayesian information criterion and predictive ability (correlation between actual observations and expected values). Comparing different orders of Legendre Polynomials and homogenous versus heterogeneous residual variances, Li et al. (2020) observed small differences in the Akaike information criterion and Bayesian information criterion between models with second and higher orders of Legendre polynomials, especially when heterogeneous residual variance was applied. The MiX99 program suite (Strandén and Lidauer, 1999) was used to fit the above-mentioned model to the data.

For calculating correlations, the (co)variance matrix for the selected days in milk was calculated by pre- and postmultiplying $\mathbf{K}_a$ by the matrix of Legendre polynomials plus exponential term constructed for the days in milk (i.e., $\varnothing \times \mathbf{K}_a \times \varnothing'$). Animal and phenotypic correlations were calculated as follows:

$$\mathrm{r}_{anim.(t1i,t2j)} = \frac{\varnothing_{(t1i)}\mathbf{K}_a\varnothing_{(t2j)}}{\sqrt{\varnothing_{(t1i)}\mathbf{K}_a\varnothing_{(t1i)} + \varnothing_{(t2j)}\mathbf{K}_a\varnothing_{(t2j)}}}, \text{ and}$$

$$\mathrm{r}_{pheno.(t1i,t2j)} = \frac{\varnothing_{(t1i)}\mathbf{K}_a\varnothing_{(t2j)} + \sigma_{e(t1i)}\sigma_{e(t2j)}}{\sqrt{\left(\varnothing_{(t1i)}\mathbf{K}_a\varnothing_{(t1i)} + \sigma^2_{e(t1i)}\right)\cdot\left(\varnothing_{(t2j)}\mathbf{K}_a\varnothing_{(t2j)} + \sigma^2_{e(t2j)}\right)}},$$

where *i* and *j* correspond to the selected DIM and *t1* and *t2* correspond to the traits. $\text{É¸}_{(it1)}\mathbf{K}_a\text{É¸}_{(jt2)}$ is the covariance between trait *t1* in DIM *i* and trait *t2* in DIM *j* and $\text{É¸}_{(it1)}\mathbf{K}_a\text{É¸}_{(it1)}$ is the variance of trait *t1* in DIM *i*. To calculate phenotypic variances, the residual variance was added to the diagonals of the (co)variance matrix into the corresponding DIM. Repeatabilities for each of the traits were calculated as follows:

$$\mathrm{Repeatability}_{ti} = \frac{\varnothing_{(ti)}\mathbf{K}_a\varnothing_{(ti)}}{\varnothing_{(ti)}\mathbf{K}_a\varnothing_{(ti)} + \sigma^2_{e(ti)}}$$

where *i* corresponds to the DIM. As residual variance was heterogeneous between months of lactation, for each selected DIM corresponding residual variance was allocated according to the lactation month in which the DIM was located. To assess whether using weekly averages leads to higher correlations and repeatabilities, the analyses were carried out using also weekly averages of the daily CO_2, DMI, RCO_2 and RFI observations. From these analyses, only repeatability estimates are estimated and reported.

Results and discussion

Descriptive statistics

The average daily CO_2 production, DMI, ECM and MBW throughout lactation were 12.01 kg/day, 19.6 kg/d, 29.9 kg/d and 123.2 kg, respectively (Table 1). Previous studies reported 11.38–

Table 1
Average and SD (in parentheses) of daily carbon dioxide production, DM intake, and energy sinks in different months of lactation for Nordic Red dairy cattle.

Lactmonth	N	CO_2 (kg/d)	DMI (kg/d)	ECM (kg/d)	MBW (kg)	BWG[1] (kg/d)	BWL[1] (kg/d)
1	567	10.7 (1.20)	15.9 (2.48)	29.4 (5.96)	122.9 (8.13)	0.028 (0.102)	1.289 (1.262)
2	683	11.4 (1.23)	18.7 (2.18)	31.9 (5.05)	119.8 (7.85)	0.141 (0.226)	0.191 (0.287)
3	939	12.0 (1.26)	19.9 (2.26)	30.7 (4.14)	119.9 (7.59)	0.228 (0.228)	0.070 (0.160)
4	791	12.3 (1.27)	20.8 (2.15)	31.1 (3.77)	121.0 (7.92)	0.262 (0.204)	0.020 (0.070)
5	655	12.4 (1.31)	20.9 (1.91)	30.9 (4.19)	122.9 (8.18)	0.301 (0.178)	0.006 (0.032)
6	602	12.2 (1.56)	20.8 (2.37)	29.6 (3.54)	124.2 (8.43)	0.322 (0.156)	0.001 (0.005)
7	477	12.6 (1.61)	21.0 (2.30)	30.2 (3.20)	125.4 (8.89)	0.321 (0.182)	0.004 (0.015)
8	452	12.6 (1.20)	20.1 (1.96)	29.3 (2.91)	127.6 (7.54)	0.356 (0.179)	0.001 (0.011)
9	462	12.2 (1.29)	19.2 (2.17)	26.8 (3.16)	127.2 (8.44)	0.476 (0.292)	0.003 (0.013)
10	345	11.9 (1.11)	18.3 (2.09)	24.9 (2.80)	128.2 (8.22)	0.652 (0.373)	0.045 (0.388)
11	22	12.2 (0.86)	18.2 (1.46)	27.3 (5.56)	124.4 (8.23)	0.591 (0.473)	0.469 (0.987)
Total	5 995	12.0 (1.41)	19.6 (2.65)	29.9 (4.45)	123.2 (8.57)	0.282 (0.259)	0.163 (0.560)

Abbreviations: Lactmonth = Lactation months; n = Number of daily observations; CO_2 = carbon dioxide production; DMI = DM intake; ECM = energy-corrected milk; MBW = metabolic body weight = (BW)^0.75; BWG = BW gain; BWL = BW loss, DIM = days in milk.

[1] In a certain DIM, when the BWG was positive, the BWL was zero and vice versa.

13.7 kg CO_2/d in dairy cows with similar production levels and measurement methods (Huhtanen et al., 2013; Huhtanen et al., 2020; Fodor et al., 2022) which is close to the results of the present study.

The partial regression coefficients of the model which was employed to predict CO_2 was as follows:

$$\widehat{CO_2} = -1.065 + 0.110 \times ECM + 0.077 \times MBW - 0.471 \times BWL + 1.287 \times BWG$$

where CO_2 and ECM are in kg/d and MBW, BWL and BWG are in kg. The coefficient of determination for the above-mentioned model was 0.482. All partial regression coefficients for energy sinks were highly significant at $P < 0.0001$. Also, the corresponding model for the prediction of DMI was as follows:

$$\widehat{DMI} = 0.621 + 0.276 \times ECM + 0.087 \times MBW - 1.849 \times BWL + 1.130 \times BWG$$

where DMI was in kg/d. The R^2 for the above-mentioned model was 0.474. Similarly, all partial regression coefficients for energy sinks to predict DMI were highly significant at $P < 0.0001$. The partial regression coefficient for ECM to predict DMI was very low which from a biological point of view is not rational, i.e., the metabolizable energy content of 0.276 kg DMI is less than the energy requirement for the production of 1 kg ECM. Similar findings have been reported in previous studies (Tempelman et al., 2015; Lidauer et al., 2023).

Lactation trajectories

Trajectories of DM intake and carbon dioxide production

Fig. 1 shows the trajectories of DMI and CO_2 production. As shown, DMI and CO_2 have a similar curve. However, the DMI trajectory is slightly higher than the trajectory of CO_2 production in the first half of lactation and afterward, CO_2 production is slightly higher than DMI. The reason for this may be the negative energy balance of the cows in the first part of lactation, i.e., using their body reserves to produce milk which has higher efficiency compared to converting feed energy to milk and as a consequence lower amount of CO_2 would be produced.

Trajectories of residual feed intake and residual carbon dioxide

The trajectories of RCO_2 and RFI as weekly averages are similar (Fig. 2). Cows consume more feed and produce more CO_2 than predicted for the 1st week of lactation. However, this changed when cows experienced negative energy balance in weeks 2–10, because the increase in DMI is not as fast as the increase in milk production and cows begin to mobilize body reserves. Residual measurements become on average positive in the middle of lactation (weeks 11–31) when cows have regained rumen volume, after parturition, to consume more feed not only to meet requirements of current production but also to compensate for the lost reserves at earlier stages. The trajectory of RFI from our study is similar to the trajectory of genetic SD of residual energy intake reported by Hurley et al. (2017). The reason for the average negative RCO_2 and RFI at the beginning of lactation may indicate that including only a partial regression coefficient for BWL in the prediction models was not sufficient to properly predict CO_2 production and DMI when a cow is in negative energy status. Also including a partial regression coefficient on body condition score, in case this information is available, might improve the fit of the model. The reason for average negative RCO_2 and RFI in late lactation is not clearly known. It might be due to an increase in digestibility in the later part of lactation (Mehtiö et al., 2016) along with an increase in the efficiency of using metabolizable energy for lactation or growth.

Correlations and repeatabilities

Carbon dioxide

Animal and phenotypic correlations between CO_2 production in selected DIM as well as animal and phenotypic SDs and repeatabilities of CO_2 production in selected days of lactation are shown in Table 2. As expected, phenotypic correlations were lower than their corresponding animal correlations. Animal correlations ranged from 0.18 to 0.99 during lactation. Phenotypic correlations ranged from 0.12 to 0.73 during lactation. The closer the selected DIM, the higher their correlations. In general, CO_2 production in DIM 6 was less correlated with CO_2 production in other DIMs and correlations in mid-lactation were high, ranging from 0.89 to 0.99. Differences could be due to a rapid increase in milk production and higher BW changes in the 1st month of lactation. Repeatability and animal SD were high at the beginning of lactation (0.61 and 0.94, respectively) and decreased at peak yield (DIM 36; 0.50 and 0.83, respectively) and again increased constantly toward the end of lactation. This means that the ratio of variance among records of individuals to total variance is higher in late lactation. In other words, there is a higher similarity between records of an individual in late lactation. To our knowledge, there is no study about the repeatability of CO_2 at different stages of lactation, therefore, direct comparisons with the results of this study are not possible. However, the repeatability of CO_2 production measured with GEM systems was reported as 0.83 for dairy cows (Huhtanen et al., 2013). Using a Photoacoustic IR Spectroscopy gas analyzer (F10 multigas analyzer), Negussie et al. (2012) found a repeatability of 0.54 for CO_2 production. In the present study, the average of repeatability of CO_2 over lactation using daily and weekly average records were 0.61 and 0.80, respectively.

The repeatability of CO_2 production in beef cattle was higher for 7-day averaging period than the daily average (0.82 vs 0.58; Manafiazar et al., 2017). The same trend has been reported in methane studies. For instance, higher repeatability was estimated for weekly methane production (0.68) compared to per visit measurement (0.3) by Aldridge et al. (2022). Similarly, Denninger et al. (2019) found higher repeatability for the average of 14-day methane production measured by GEM systems compared to 7-day and 28-day averages (0.68 vs 0.64 and 0.59). The findings of the present study show that the repeatability of CO_2 production varied over the stages of lactation with the highest estimates in mid to late lactation.

DM intake

Table 3 shows the animal and phenotypic correlations between DMI in selected DIM as well as its SDs and repeatability. Similar to CO_2, animal correlations were higher than phenotypic correlations (ranging from 0.16 between DIM 6 and 96–0.85 between DIM 246 and 276) and followed a similar pattern. Animal correlations between DMI in selected DIM were slightly lower than the corresponding animal correlations between CO_2 production in selected DIM, whereas the opposite was true for phenotypic correlations, with relatively higher correlations for DMI. DMI in DIM 6 had lower correlations with other selected DIMs. Similar findings were reported in previous studies (Liinamo et al., 2012; Manzanilla Pech et al., 2014; Li et al., 2016). DMI had higher repeatability throughout lactation than CO_2, with 0.70 at the beginning of lactation followed by a drop at DIM 66–0.61 and a gradual increase toward the end of lactation. This indicates that the ratio of temporary environmental variance to animal variance for DMI decreases toward the end of lactation. A similar trend for repeatability of DMI, but with a lower mean, was reported for German Holstein cows (Tetens et al., 2014). Working on data from the first 24 weeks of lactation (4-week periods) from Nordic Red cows, Li et al. (2016) reported a repeatability of DMI ranging from 0.68 for the first period to 0.85

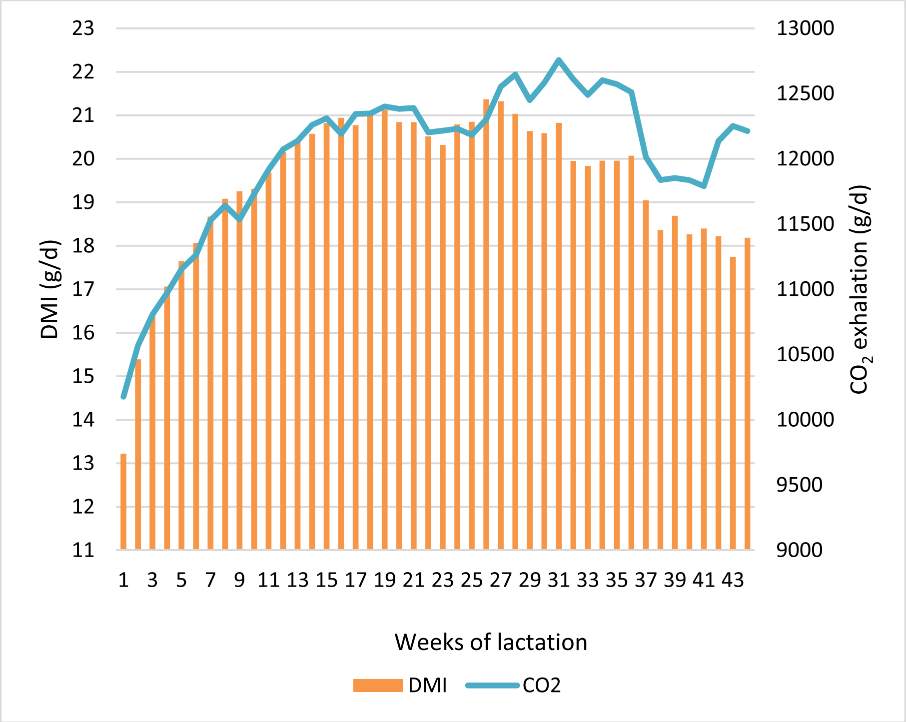

Fig. 1. Trajectories of carbon dioxide (CO_2; g/d; blue solid line) and DM intake (DMI; kg/d; orange bars) throughout lactation for Nordic Red dairy cattle using the whole dataset (number of daily records = 5 995).

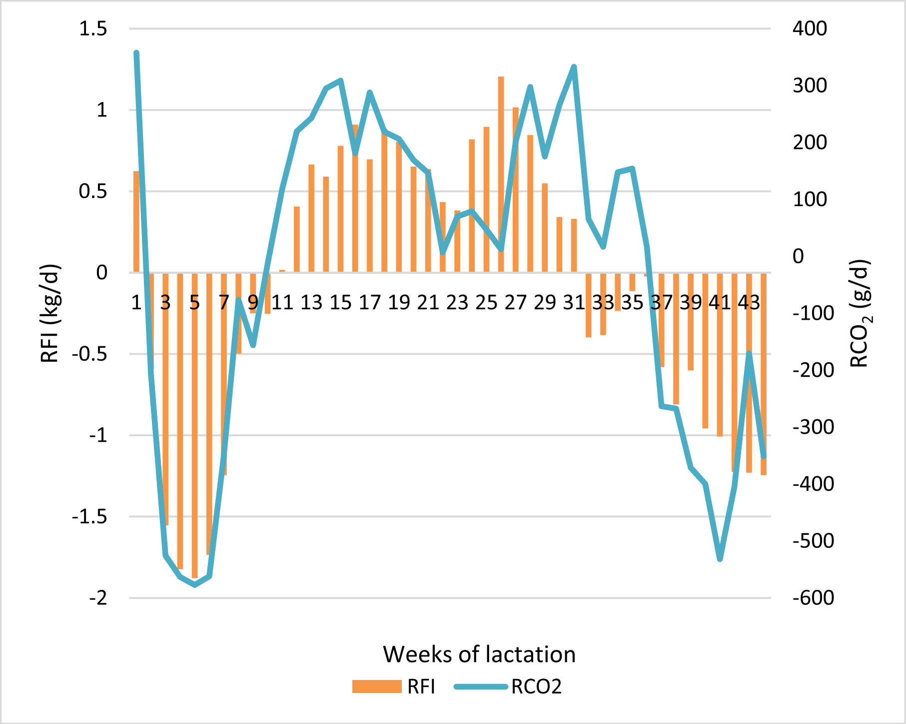

Fig. 2. Trajectories of residual carbon dioxide (RCO_2; g/d; blue solid line) and residual feed intake (RFI; kg/d; orange bars) throughout lactation for Nordic Red dairy cattle using the whole dataset (number of daily records = 5 995).

Table 2

Animal correlations (± SE) (above diagonal) and phenotypic correlations (below diagonal) between CO_2 in selected DIM (daily observations were used) for Nordic Red dairy cattle.

DIM	6	36	66	96	126	156	186	216	246	276
6		0.66^{b}	0.49^{b}	0.43^{b}	0.38^{c}	0.33^{c}	0.29^{c}	0.25^{c}	0.21^{c}	0.18^{c}
36	0.36^{c}		0.97^{a}	0.93^{a}	0.88^{a}	0.82^{a}	0.76^{b}	0.70^{b}	0.64^{b}	0.59^{c}
66	0.28^{c}	0.50^{b}		0.99^{a}	0.96^{a}	0.92^{a}	0.87^{a}	0.82^{b}	0.77^{b}	0.72^{b}
96	0.24^{c}	0.48^{b}	0.53^{b}		0.99^{a}	0.97^{a}	0.93^{a}	0.89^{a}	0.85^{a}	0.81^{b}
126	0.23^{c}	0.48^{b}	0.54^{b}	0.56^{b}		0.99^{a}	0.97^{a}	0.95^{a}	0.92^{a}	0.89^{a}
156	0.20^{c}	0.44^{b}	0.51^{b}	0.54^{b}	0.59^{b}		0.99^{a}	0.98^{a}	0.96^{a}	0.94^{a}
186	0.18^{c}	0.42^{c}	0.50^{b}	0.54^{b}	0.59^{b}	0.60^{b}		0.99^{a}	0.98^{a}	0.97^{a}
216	0.16^{c}	0.40^{c}	0.49^{c}	0.54^{b}	0.60^{b}	0.61^{b}	0.64^{b}		0.99^{a}	0.99^{a}
246	0.14^{c}	0.38^{c}	0.47^{c}	0.52^{b}	0.59^{b}	0.61^{b}	0.65^{b}	0.68^{b}		0.99^{a}
276	0.12^{c}	0.36^{c}	0.46^{c}	0.52^{c}	0.60^{b}	0.63^{b}	0.67^{b}	0.71^{b}	0.73^{b}	
σ_U	0.935	0.825	0.890	0.930	0.977	1.038	1.113	1.199	1.295	1.399
σ_P	1.200	1.172	1.219	1.269	1.268	1.356	1.411	1.464	1.547	1.599
r	0.61	0.50	0.53	0.54	0.59	0.59	0.62	0.67	0.70	0.77
r*	0.77	0.73	0.79	0.76	0.78	0.79	0.83	0.87	0.82	0.89

Abbreviations: DIM = days in milk; σ_U = animal SD (sqrt [diag ($\varnothing_{(i)} \times K_a \times \varnothing_{(i)}$)]); σ_P= phenotypic SD (sqrt [diag ($\varnothing_{(i)} \times K_a \times \varnothing_{(i)} + \sigma^2_{e(i)}$)]); r = repeatabilities; r* = repeatabilities using weekly averages of records for lactation months 1–10.

Range of SEs are shown with different superscripts (^{a}: 0–0.01, ^{b}: 0.02–0.03 and ^{c}: 0.04–0.05).

Table 3

Animal correlations (± SE) (above diagonal) and phenotypic correlations (below diagonal) between DM intake in selected DIM (daily observations were used) for Nordic Red dairy cattle.

DIM	6	36	66	96	126	156	186	216	246	276
6		0.42^{b}	0.25^{c}	0.23^{c}	0.23^{c}	0.23^{c}	0.23^{c}	0.23^{c}	0.22^{c}	0.21^{c}
36	0.29^{c}		0.98^{a}	0.94^{a}	0.89^{a}	0.81^{a}	0.73^{b}	0.65^{b}	0.58^{b}	0.51^{c}
66	0.16^{c}	0.62^{b}		0.99^{a}	0.95^{a}	0.89^{a}	0.82^{b}	0.75^{b}	0.68^{b}	0.61^{b}
96	0.16^{c}	0.62^{b}	0.63^{b}		0.99^{a}	0.95^{a}	0.90^{a}	0.84^{a}	0.78^{b}	0.73^{b}
126	0.17^{c}	0.62^{b}	0.65^{b}	0.69^{b}		0.99^{a}	0.96^{a}	0.92^{a}	0.87^{a}	0.83^{b}
156	0.16^{c}	0.55^{b}	0.58^{b}	0.64^{b}	0.72^{b}		0.99^{a}	0.97^{a}	0.94^{a}	0.90^{a}
186	0.17^{c}	0.53^{b}	0.57^{b}	0.65^{b}	0.74^{b}	0.74^{b}		0.99^{a}	0.98^{a}	0.95^{a}
216	0.17^{c}	0.47^{c}	0.52^{b}	0.61^{b}	0.71^{b}	0.72^{b}	0.79^{b}		0.99^{a}	0.98^{a}
246	0.17^{c}	0.43^{c}	0.48^{c}	0.58^{b}	0.69^{b}	0.71^{b}	0.79^{b}	0.81^{b}		0.99^{a}
276	0.16^{c}	0.37^{c}	0.43^{c}	0.52^{c}	0.64^{b}	0.67^{b}	0.76^{b}	0.78^{b}	0.81^{b}	
σ_U	1.944	1.744	1.949	2.007	2.069	2.175	2.326	2.516	2.735	2.978
σ_P	2.317	2.154	2.494	2.478	2.381	2.598	2.613	2.812	3.002	3.339
r	0.70	0.66	0.61	0.66	0.76	0.70	0.79	0.80	0.83	0.80
r*	0.70	0.81	0.76	0.76	0.89	0.83	0.90	0.88	0.83	0.85

Abbreviations: DIM = days in milk; σ_U = animal SD (sqrt [diag ($\varnothing_{(i)} \times K_a \times \varnothing_{(i)}$)]); σ_P= phenotypic SD (sqrt [diag ($\varnothing_{(i)} \times K_a \times \varnothing_{(i)} + \sigma^2_{e(i)}$)]); r = repeatabilities; r* = repeatabilities using weekly averages of records for lactation months 1–10.

Range of SEs are shown with different superscripts (^{a}: 0–0.01, ^{b}: 0.02–0.03 and ^{c}: 0.04–0.05).

for the fifth period. Phenotypic variance also had an increasing trend toward the end of lactation and phenotypic correlations between consecutive periods were higher in late lactation, which is in agreement with the results of the present study. In general, repeatability of DMI ranging between 0.46 and 0.84 for data from different countries has been reported (Søndergaard et al., 2002; Berry et al., 2014).

DM intake and carbon dioxide

Animal correlations between CO_2 production and DMI in selected DIM are shown in Table 4. The average of modeled animal correlations (0.77) was higher than the raw correlation between daily records of CO_2 production and DMI (0.60). Phenotypic correlations followed the same pattern; however, they were slightly lower than the animal correlations (not shown). Averages of the correlations for each row or column are shown in the margins of Table 4. Generally, CO_2 production and DMI had a higher correlation in the second half compared to the first half of lactation. A correlation of 0.85 between DMI and CO_2 production has been reported by a study on beef cows (Arthur et al., 2018). On the other hand, Huhtanen et al. (2021) reported a very high correlation of 0.93 between CO_2 production and DMI in dairy cows using respiration chamber data. The discrepancy between correlations estimated in different studies could be due to the differences in breed, measurement techniques and duration of recording.

Residual carbon dioxide

Animal correlations within RCO_2 and RFI in selected DIM as well as their corresponding repeatabilities are shown in Table 5. Correlations between selected DIM were higher toward the end of lactation compared to those in early lactation stages. Moreover, correlations between DIMs close to each other were higher. Generally, correlations between RCO_2 in selected DIM were lower than those of CO_2 in corresponding DIM. Accumulation of errors when modeling CO_2 by four energy sinks would result in lower correlations between RCO_2 in selected DIMs. This implies that RCO_2 in different lactation stages should be considered as different traits; therefore, specific weights should be allocated to each stage for selection. As expected, animal variances were lower for RCO_2 than CO_2 in different DIMs, except for DIM 6. The RCO_2 had lower repeatability (ranging from 0.27 to 0.72) than CO_2, and the lowest repeatability was observed at DIM 96. As the R^2 for the regression of CO_2 on energy sinks was below unity, it is expected that also some of the animal variance would have been lost. Up to now, we have not been able to find any repeatability estimates for RCO_2 in scientific literature and comparative assessments of the results were not possible.

Table 4
Animal correlations (±SE) between daily DMI and CO_2 in selected DIM for Nordic Red dairy cattle.

		DMI										
	DIM	6	36	66	96	126	156	186	216	246	276	Avg.[1]
CO_2	6	0.85^{a}	0.40^{b}	0.22^{c}	0.18^{c}	0.16^{c}	0.14^{c}	0.12^{c}	0.10^{c}	0.08^{c}	0.07^{c}	0.23^{c}
	36	0.36^{c}	0.68^{b}	0.65^{b}	0.63^{b}	0.59^{b}	0.55^{b}	0.50^{b}	0.44^{c}	0.40^{c}	0.35^{c}	0.53^{b}
	66	0.18^{c}	0.68^{b}	0.70^{b}	0.70^{b}	0.68^{b}	0.65^{b}	0.60^{b}	0.56^{b}	0.51^{b}	0.47^{c}	0.57^{b}
	96	0.14^{c}	0.66^{b}	0.71^{b}	0.73^{b}	0.73^{b}	0.71^{b}	0.68^{b}	0.64^{b}	0.61^{b}	0.57^{c}	0.62^{b}
	126	0.12^{c}	0.64^{b}	0.71^{b}	0.74^{b}	0.76^{b}	0.76^{b}	0.74^{b}	0.71^{b}	0.68^{b}	0.65^{b}	0.65^{b}
	156	0.10^{c}	0.61^{b}	0.69^{b}	0.74^{b}	0.77^{b}	0.78^{b}	0.78^{b}	0.76^{b}	0.73^{b}	0.71^{b}	0.67^{b}
	186	0.09^{c}	0.58^{b}	0.67^{b}	0.73^{b}	0.78^{b}	0.80^{b}	0.80^{b}	0.79^{b}	0.77^{b}	0.75^{b}	0.68^{b}
	216	0.08^{c}	0.55^{b}	0.64^{b}	0.72^{b}	0.77^{b}	0.80^{b}	0.81^{b}	0.81^{b}	0.80^{b}	0.78^{b}	0.68^{b}
	246	0.07^{c}	0.51^{b}	0.62^{b}	0.70^{b}	0.76^{b}	0.80^{b}	0.82^{b}	0.82^{b}	0.81^{b}	0.80^{b}	0.67^{b}
	276	0.06^{c}	0.48^{c}	0.59^{b}	0.68^{b}	0.75^{b}	0.79^{b}	0.82^{b}	0.83^{b}	0.82^{b}	0.82^{b}	0.66^{b}
	Avg.[1]	0.21^{c}	0.58^{b}	0.62^{b}	0.66^{b}	0.68^{b}	0.68^{b}	0.67^{b}	0.65^{b}	0.65^{b}	0.60^{b}	

Abbreviations: DMI = DM intake; DIM = days in milk; CO_2 = carbon dioxide production (kg/d).
Range of SEs are shown with different superscripts (^{a}: 0–0.01, ^{b}: 0.02–0.03 and ^{c}: 0.04–0.05).

[1] Averages of rows and columns are shown in margins.

Table 5
Animal correlations (± SE) between RCO_2 in selected DIM (above diagonal) and between RFI in selected DIM (below diagonal) for Nordic Red dairy cattle (daily observations were used).

DIM	6	36	66	96	126	156	186	216	246	276
6		0.59^{b}	0.22^{c}	0.15^{c}	0.15^{c}	0.16^{c}	0.17^{c}	0.17^{c}	0.18^{c}	0.18^{c}
36	0.44^{b}		0.91^{a}	0.84^{a}	0.78^{a}	0.70^{b}	0.62^{b}	0.53^{b}	0.45^{c}	0.38^{c}
66	-0.02^{c}	0.88^{a}		0.98^{a}	0.93^{a}	0.86^{a}	0.76^{b}	0.67^{b}	0.58^{b}	0.50^{c}
96	-0.07^{c}	0.81^{a}	0.98^{a}		0.98^{a}	0.93^{a}	0.86^{a}	0.78^{b}	0.71^{b}	0.64^{b}
126	-0.02^{c}	0.74^{b}	0.91^{a}	0.97^{a}		0.98^{a}	0.94^{a}	0.89^{a}	0.83^{a}	0.77^{b}
156	0.06^{c}	0.63^{b}	0.77^{b}	0.87^{a}	0.96^{a}		0.99^{a}	0.96^{a}	0.91^{a}	0.87^{a}
186	0.14^{c}	0.48^{b}	0.59^{b}	0.72^{b}	0.87^{a}	0.97^{a}		0.99^{a}	0.97^{a}	0.94^{a}
216	0.19^{c}	0.34^{c}	0.41^{c}	0.57^{b}	0.75^{b}	0.90^{a}	0.98^{a}		0.99^{a}	0.98^{a}
246	0.23^{c}	0.22^{c}	0.27^{c}	0.43^{c}	0.64^{b}	0.82^{b}	0.94^{a}	0.99^{a}		0.99^{a}
276	0.25^{c}	0.13^{c}	0.15^{c}	0.32^{c}	0.54^{c}	0.75^{b}	0.89^{a}	0.96^{a}	0.99^{a}	
r_{RCO2}	0.72	0.29	0.28	0.27	0.30	0.30	0.32	0.39	0.44	0.48
r_{RFI}	0.86	0.46	0.38	0.40	0.48	0.37	0.51	0.58	0.63	0.63
r^{*}_{RCO2}	0.67	0.53	0.54	0.51	0.51	0.52	0.47	0.62	0.51	0.62
r^{*}_{RFI}	0.72	0.64	0.60	0.60	0.76	0.52	0.75	0.75	0.66	0.67

Abbreviations: RCO_2: residual carbon dioxide; DIM = days in milk; RFI: residual feed intake; r = repeatabilities; r* = repeatabilities using weekly averages of records for lactation months 1–10.
Range of SEs are shown with different superscripts (^{a}: 0–0.01, ^{b}: 0.02–0.03 and ^{c}: 0.04–0.05).

Residual feed intake

The size and trend of our repeatability estimates throughout lactation were in good agreement with the report for Holstein dairy cows in the Netherlands (Tempelman et al., 2015). Animal correlations between RFI in selected DIM were lower than their corresponding values for RCO_2. However, phenotypic correlations were higher for RFI than RCO_2. This implies that the correlation between records of an individual (within-animal correlation) is higher for RCO_2 than for RFI. This might be due to a higher number of records for CO_2 compared to DMI. Several repeated measures per day might cancel out the effect of error in recording to some extent compared to a situation in which there is only one record per day (i.e., DMI). Also, correlations of RFI between different DIMs and its repeatability were lower than those of DMI. Nehme Marinho et al. (2021) studied the relationship between RFI in early and mid-lactation with performance and health. They estimated a correlation of 0.43 between RFI in two stages and reported that selection based on RFI phenotype improves efficiency without impairing health. Correlations of residual energy intake ranged from 0.21 (between weeks 2–10 and 21–30) to 0.58 (between weeks 2–10 and 11–20) have been reported for Nordic Red dairy cows by Mäntysaari et al. (2012). Repeatability of residual energy intake ranging between 0.30 and 0.35 was found using different feeding standards in the same study. Investigating the effect of the quantity of starch in the diet on the repeatability of RFI, Potts et al. (2015) obtained a high (0.73) across-diet repeatability for RFI in primiparous and multiparous Holstein cows. Furthermore, Olijhoek et al. (2020) estimated average repeatability of 0.63 and 0.65 for Holstein cows over the first and second lactation, respectively. Similar to the results of our study, they found a lower correlation between RFI in the first 3 weeks and other weeks across the lactation. Working to identify the best period for recording DMI, Connor et al. (2019) found that DIM between 150 and 214 to be the best period, which has a correlation of 0.9 between RFI calculated within this period and RFI for the entire lactation. It seems that similar to RCO_2, RFI in different lactation stages have different attributes and should be considered as separate traits. In general, the discrepancies observed between results from various studies could be due to differences in methods of RFI calculation, accuracy of recording as well as differences in diet, breeds and population.

Correlations between residual feed intake and residual carbon dioxide

Correlations between RCO_2 and RFI are presented in Table 6. These correlations followed the same pattern as the correlations between CO_2 and DMI, although the size of the correlation estimates is smaller. The combined lactation average correlation

Table 6
Animal correlations (± SE) between daily RFI and RCO_2 in selected DIM for Nordic Red dairy cattle.

		RFI										
	DIM	6	36	66	96	126	156	186	216	246	276	Avg.[1]
RCO_2	6	0.88^{a}	0.57^{b}	0.14^{c}	0.05^{c}	0.02^{c}	0.02^{c}	0.01^{c}	0.01^{c}	0.00^{c}	0.00^{c}	0.17^{c}
	36	0.45^{b}	0.61^{b}	0.40^{b}	0.31^{b}	0.24^{c}	0.15^{c}	0.06^{c}	-0.01^{c}	-0.07^{c}	-0.11^{c}	0.22^{c}
	66	0.13^{c}	0.44^{b}	0.41^{b}	0.37^{b}	0.31^{c}	0.23^{c}	0.15^{c}	0.07^{c}	0.01^{c}	-0.04^{c}	0.21^{c}
	96	0.09^{c}	0.38^{b}	0.39^{b}	0.37^{b}	0.35^{b}	0.30^{c}	0.24^{c}	0.17^{c}	0.12^{c}	0.08^{c}	0.25^{c}
	126	0.11^{c}	0.35^{b}	0.35^{b}	0.37^{b}	0.37^{b}	0.36^{c}	0.33^{c}	0.28^{c}	0.24^{c}	0.20^{c}	0.30^{c}
	156	0.15^{c}	0.32^{c}	0.31^{c}	0.35^{c}	0.39^{b}	0.41^{b}	0.40^{c}	0.37^{c}	0.35^{c}	0.32^{c}	0.34^{c}
	186	0.18^{c}	0.28^{c}	0.27^{c}	0.32^{c}	0.39^{c}	0.43^{c}	0.45^{c}	0.45^{c}	0.43^{c}	0.41^{c}	0.36^{c}
	216	0.20^{c}	0.24^{c}	0.22^{c}	0.29^{c}	0.38^{c}	0.45^{c}	0.49^{c}	0.50^{c}	0.49^{c}	0.48^{c}	0.37^{c}
	246	0.22^{c}	0.20^{c}	0.18^{c}	0.26^{c}	0.36^{c}	0.46^{c}	0.51^{b}	0.54^{b}	0.54^{b}	0.53^{c}	0.38^{c}
	276	0.23^{c}	0.17^{c}	0.15^{c}	0.23^{c}	0.35^{c}	0.46^{c}	0.53^{c}	0.56^{c}	0.57^{c}	0.57^{c}	0.38^{c}
	Avg.[1]	0.26^{c}	0.36^{c}	0.28^{c}	0.29^{c}	0.32^{c}	0.33^{c}	0.35^{c}	0.29^{c}	0.27^{c}	0.27^{c}	

Abbreviations: RFI = residual feed intake; DIM = days in milk; RCO_2 = residual carbon dioxide.
Range of SEs are shown with different superscripts (^{a}: 0–0.01, ^{b}: 0.02–0.03 and ^{c}: 0.04–0.05).

[1] Averages of rows and columns are shown in margins.

between RCO_2 and RFI was 0.50. Garnsworthy et al. (2019) reported a correlation of 0.81 between records measured by GEM system and respiration chamber, which gives an indication that the correlations between RCO_2 and RFI found in our study were also affected by the accuracy of the GEM system. Huhtanen et al. (2021) reported a high partial correlation coefficient of 0.83 between RCO_2 and RFI in dairy cows.

Animal correlations between RCO_2 and RFI were generally higher in the second half of lactation. When the weekly averages of CO_2, DMI and energy sinks were used to calculate the modeled correlation between RCO_2 and RFI, the average of animal correlations was lower (result not shown). However, the average of animal correlations between RCO_2 in different months was slightly higher using weekly averages (0.75 vs 0.70) and similarly, a slightly higher average of animal correlations between RFI in different months was observed (0.62 vs 0.58).

Although correlations did not increase substantially, the repeatabilities of studied traits were significantly higher when data on weekly averages was used. The increase in repeatabilities was higher for residual traits than CO_2 and DMI. Also, the amount of increase was higher for CO_2 and RCO_2 (31.3 and 45.0%, respectively) compared to DMI and RFI (12.4 and 26.1%, respectively).

Conclusions

In this pilot study, we estimated the repeatabilities and correlations between RCO_2 and RFI at different stages of lactation for the Nordic Red dairy cattle. Within trait correlations for CO_2 at different stages of lactation ranged from 0.18 to 0.99 depending on the distance between DIM. Similar patterns were also observed for the within RCO_2 and RFI correlations at different stages of lactation. A moderate animal correlation was estimated between RCO_2 and RFI. Excluding early lactation, the average of animal correlations between RCO_2 and RFI was significantly higher in the second half of lactation. This might be due to the less confounding effect of BW change on DMI and CO_2 production in this part of lactation. The repeatabilities of RCO_2 and RFI were high at the beginning of lactation and then decreased until peak lactation and increased again toward the end of lactation. This variability indicates that temporary environmental effects on RCO_2 and RFI decrease as the end of lactation approaches. In general, the results of this study show that animals with higher CO_2 production than expected also consumed more DMI than expected. Nevertheless, considering that in this study, we found only a moderate correlation between RCO_2 and RFI, more research is needed to assess whether an RCO_2 formulation that is based on daily CO_2 measurements from individual cows can be used as a feed efficiency metric.

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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