J. Dairy Sci. 106:4121–4132
https://doi.org/10.3168/jds.2022-22735

Heritability and genetic correlations between enteric methane production and concentration recorded by GreenFeed and sniffers on dairy cows

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ABSTRACT

To reduce methane (CH_4) emissions of dairy cows by animal breeding, CH_4 measurements have to be recorded on thousands of individual cows. Currently, several techniques are used to phenotype cows for CH_4, differing in costs and applicability. However, there is uncertainty about the agreement between techniques. To judge the similarity and repeatability between measurements of different recording techniques, the repeatability, heritability, and genetic correlation are useful metrics. Therefore, our objective was to estimate (1) the repeatability and heritability for CH_4 and carbon dioxide production recorded by GreenFeed (GF) and for CH_4 and carbon dioxide concentration measured by cost-effective but less accurate sniffers, and (2) the genetic correlation between CH_4 recorded with these 2 different on farm and high throughput techniques. Data were available from repeated measurements of CH_4 production (grams/day) by GF units and of CH_4 concentration (ppm) by sniffers, recorded on commercial dairy farms in the Netherlands. The final data comprised 24,284 GF daily means from 822 cows, 170,826 sniffer daily means from 1,800 cows, and 1,786 daily means from 75 cows by both GF and sniffer (in the same period). Additionally, CH_4 records were averaged per week. For daily and weekly mean GF CH_4 the heritabilities were 0.19 ± 0.02 and 0.33 ± 0.04, and for daily and weekly mean sniffer CH_4 the heritabilities were similar and were 0.18 ± 0.01 and 0.32 ± 0.02, respectively. Phenotypic correlations between GF CH_4 production and sniffer CH_4 concentration were moderate (0.39 ± 0.03 for daily means and 0.37 ± 0.05 for weekly means). However, genetic correlations were high; 0.71 ± 0.13 for daily means and 0.76 ± 0.15 for weekly means. The high genetic correlation indicates that selection on low CH_4 concentrations (ppm) recorded by the cost-effective sniffer method, will result in reduced CH_4 production (grams/day) as recorded with GF.
Key words: methane emissions, genetics, dairy cows, GreenFeed, sniffer

INTRODUCTION

Cattle and other ruminants contribute to methane (CH_4) that is emitted into the atmosphere, which is a significant driver in global warming (Smith and Bustamante, 2014). Various strategies have been suggested to reduce emissions from cattle, such as through advances in gut microbiology, nutrition, improved animal health, and genetic improvement by animal breeding (Hill et al., 2016). To breed for cows that emit less CH_4, a large number of individual cows need to be phenotyped first. Several techniques exist to phenotype cows for enteric CH_4 emissions and each method has its advantages and disadvantages (Hammond et al., 2016).

Methods installed on farm, such as the GreenFeed (GF; C-lock Inc.; Zimmerman, 2011) and "sniffers" (Teye et al., 2009; Madsen et al., 2010), show promise to be used in large-scale recording of dairy cows. Both techniques repeatedly measure CH_4 and carbon dioxide (CO_2) concentrations from the breath of a cow during measurements that generally last a few minutes, and additionally GF units measure quantitative airflow, which is used to calculate CH_4 and CO_2 production (grams/day) based on mass flux calculations (Huhtanen et al., 2015). However, GF units are currently prohibitive for large-scale recording, due to purchase and running costs, and the limitation of the number of cows that can be recorded (15 to 25 cows per unit as recommended by C-lock). Sniffer systems, however, are cheaper with low running costs, are high throughput, and only limited to the number of cows that have access to the automatic milking station (AMS) where the sniffer is installed (generally 40 to 70 cows; Garnsworthy et al., 2019).

Estimates for the heritability of CH_4 production measured by GF units have been reported, and ranged

Received September 5, 2022.
Accepted January 5, 2023.
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from 0.12 ± 0.06 to 0.35 ± 0.19 for daily and 0.22 ± 0.11 to 0.43 ± 0.12 for weekly CH_4 production (Lopes et al., 2022; Manzanilla-Pech et al., 2021; Ryan et al., 2022; Tiezzi et al., 2022; Wethal et al., 2022). Estimates for the heritability of CH_4 concentration (ppm) measured by sniffers were similar, and ranged between 0.11 ± 0.02 and 0.32 ± 0.03 (van Engelen et al., 2018; Saborío-Montero et al., 2020; Difford et al., 2020; van Breukelen et al., 2022). Some studies estimated CH_4 production (grams/day or liters/day) from sniffer concentration measurements, based on CO_2 as a tracer gas in combination with the CH_4/CO_2 ratio (Madsen et al., 2010), or based on an average tidal respiratory volume (Chagunda et al., 2009). For CH_4 production estimated from sniffer measurements, the heritability estimates are again similar and range between 0.12 ± 0.04 and 0.45 ± 0.11 (Lassen and Løvendahl, 2016; Pszczola et al., 2017; Difford et al., 2018; Zetouni et al., 2018; Breider et al., 2019; López-Paredes et al., 2020).

Not only is the heritability of CH_4 sampling techniques important, but also how measurements of different techniques correlate. Both GF systems and sniffers are spot-sampling methods and do not measure the total "true" emissions per day. Nonetheless, both CH_4 recorded by GF and recorded by sniffers has been shown to be highly correlated with CH_4 measured in respiration chambers (RC; 0.75–0.96; Velazco et al., 2016; Hristov et al., 2018; Difford et al., 2019). The correlations indicate that measurements by either system are correlated with a cow's total emission as are measured in RCs. However, Huhtanen et al. (2015) investigated the phenotypic correlation between CH_4 recorded by GF and by sniffers, and reported a low correlation of 0.30 (transformed from r^2). Nonetheless, only phenotypic correlations between the CH_4 sampling techniques have been reported in the literature. To be able to judge the similarity between the sampling techniques, the genetic correlation is more useful and can be used as a measure of repeatability between sampling techniques (Veerkamp et al., 2002).

The genetic relationship between CH_4 production recorded by GF and CH_4 concentration recorded by sniffers is important to investigate if selection on low CH_4 concentrations (ppm) recorded by the sniffer method, will result in reduced CH_4 production (grams/day). Therefore, the objective of this study was to estimate (1) the repeatability and heritability for CH_4 and CO_2 production recorded by GreenFeed (GF) units and for CH_4 and CO_2 concentration measured by sniffers, and (2) the genetic correlation between CH_4 recorded by these 2 different techniques.

MATERIALS AND METHODS

Methane Recording

GreenFeed units and sniffers were used to noninvasively record enteric CH_4 and CO_2 emissions from lactating dairy cows on commercial farms in the Netherlands. Ethical approval was not needed for this study because no animal procedures were performed, as only existing data were used. Emissions were recorded with GF units on 16 farms (with 19 to 293 recorded cows per farm) and with sniffers on 15 farms (with 14 to 96 recorded cows per farm). On 6 of the farms, measurements were taken with both GF units and sniffers. The GF units were used to estimate CH_4 and CO_2 production (CH_4p and CO_2p, respectively) as grams per day in the barn or on pasture, for either 2 wk or 3 mo, between September 2018 and February 2020. In total 161,825 visits from 1,184 cows were recorded by GF units. The technical specifications of the GF units had a measurement range for CH_4 concentrations in between 0 and 4,000 ppm, and for CO_2 concentrations between 0 and 20,000 ppm. Full details on the data collection with GF were reported by Koning et al. (2020). Sniffers (WD-WUR v1.0, manufactured by Carltech BV) were installed in the feed bin of AMS and measured CH_4 and CO_2 concentrations (CH_4c and CO_2c, respectively) in ppm, with recording periods from 64 up to 436 d, between March 2019 and January 2021. The concentration measurements were not used to estimate production, because of problems in sensor drift which occurred for CH_4 and CO_2 independently (van Breukelen et al., 2022). In total 461,223 AMS visits from 2,271 cows were recorded by sniffers. The technical specifications of the sniffers had a measurement range forCH_4 concentrations between 0 and 2,000 ppm, and for CO_2 concentrations between of 0 and 10,000 ppm. A detailed description of the data recording by sniffers is given in van Breukelen et al. (2022).

Data Editing

Sniffers do not record cow ID, therefore, the sniffer records were first aligned with ID recorded by the AMS [for more details see van Breukelen et al. (2022)]. Thereafter, the GF data set and sniffer data set were filtered to only include cows for which pedigree data were available, provided by the cooperative cattle improvement organization CRV (Arnhem, the Netherlands). Furthermore, the data sets were filtered to only include cows that were 75% Holstein or more. Records for cows up to 305 d in milk (DIM) were retained to cor-

Table 1. The number of farms, cows, and daily or weekly methane and carbon dioxide records, recorded by GreenFeed (GF), sniffers, or by both methods (in total or with overlapping recording)

	Daily				Weekly			
Number	GF	Sniffer	GF and sniffer	GF and sniffer overlap[1]	GF	Sniffer	GF and sniffer	GF and sniffer overlap[1]
Farms	16	15	6	4	16	15	6	4
Cows	822	1,800	184	75	822	1,800	176	73
Records	24,284	170,826		1,786	4,358	30,982		334

[1]The number of farms, cows, and daily or weekly records for which GF units and sniffers recorded emissions within the same day, note these are a subset of GF and sniffer records.

rectly match the recorded AMS visits to calving dates and the corresponding parity. The data were not log-transformed, as this did not result in normality of the data. Nonetheless, previous analysis on the same data showed that the residuals were normally distributed. A linear model was used to correct both the data recorded by GF units and by sniffers for diurnal variation with a Fourier series approach (Løvendahl and Bjerring, 2006; Lassen and Løvendahl, 2016) using the following model:

$$\mathbf{y}_{ik} = \boldsymbol{\mu} + \mathbf{Farm}_i \cdot \sum_{j=1}^{1} (\mathbf{sinj\theta 2\pi} + \mathbf{cosj\theta 2\pi}) + \mathbf{e}_{ik},$$

where $\boldsymbol{y}_i$ is GF or sniffer recorded CH_4 or CO_2 per visit; **Farm** is the fixed effect for the ith farm and is fitted as an interaction with the 24-h diurnal cycle, where $\boldsymbol{\theta}$ is the time at recording as a decimal fraction (i.e., $\boldsymbol{\theta}$ = hour at recording/24), and j is the order of regression; and $\mathbf{e}$ is the residual error, $e_i \sim N\left(0, \mathbf{I}\sigma_e^2\right)$, where σ_e^2 is the error variance. The estimated fixed effects were subtracted from the corresponding records to derive the corrected estimates from each visit.

After correction for diurnal variation, the recorded GF and sniffer visits were combined in one data set with daily means and one data set with weekly means. In the data set with weekly means, records with less than 3 records per cow per week were discarded. The number of remaining daily and weekly records and cows used for the analyses are summarized in Table 1. Recording by GF and sniffers was mostly carried out on different farms, because the GF data were collected for different research objectives in other studies.

Pedigree and Genomic Data

Pedigree and genotype data were made provided by CRV. In total 1,817 animals were genotyped with the Eurogenomics 10k chip and imputed to 76,439 SNPs by CRV as part of a routine process. The pedigree was pruned to include all phenotyped animals and their ancestors, using the R-packages "optisel" in R v3.6.1 (Wellmann, 2020). In total, the pruned pedigree included 41,290 animals from 29 generations.

Parameter Estimation

Pearson correlation coefficients were estimated to visually inspect the relationship between CH_4 emissions of 75 cows measured by GF units and by sniffers, without a correction for environmental influences. Fisher's transformation was used to derive the Confidence Intervals (CI) for the transformed Pearson correlation estimates (Fisher, 1921).

Variance components were estimated with pairwise bivariate repeatability animal models, using a restricted maximum likelihood procedure in ASReml 4.2 (Gilmour et al., 2015). The variance components were used to estimate the heritability, repeatability, and phenotypic, genetic, permanent environmental, and residual correlations. As input, a genetic relationship matrix was used which combines the pedigree and genotype data ($\mathbf{H}^{-1}$). The $\mathbf{H}^{-1}$ matrix was constructed following the method of Aguilar et al. (2010) and Christensen and Lund (2010) using calc_grm version r1.143 (Calus and Vandenplas, 2016). The $\mathbf{H}^{-1}$ matrix comprised all 41,290 animals that were in the pedigree.

The statistical significance of fixed effects was tested in ASReml before including the fixed effects in the final model. The random effects included were the additive genetic, permanent environmental, and residual effect. In the bivariate models between a GF and a sniffer trait the permanent environmental covariance was fixed to zero. This was done because the permanent environmental covariances in the analyses between a GF and sniffer trait were not statistically significant and resulted in spurious estimates, most likely due to the low number of cows that had both records by GF units and by sniffers (Table 1). For the bivariate models with 2 GF or 2 sniffer traits, the permanent environmental covariances were significantly different from zero and therefore the permanent environmental covariance was

not fixed to zero. The bivariate model used in the final analysis was defined as:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & 0\\ 0 & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Za}_1 & 0\\ 0 & \mathbf{Za}_2\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Zp}_1 & 0\\ 0 & \mathbf{Zp}_2\end{bmatrix}\begin{bmatrix}\mathbf{pe}_1\\ \mathbf{pe}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Ze}_1 & 0\\ 0 & \mathbf{Ze}_2\end{bmatrix}\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix},$$

where $\mathbf{y}_i$ is a vector with records on trait i (GF CH_4p or CO_2p and sniffer CH_4c or CO_2c, as daily or weekly mean); $\mathbf{b}_i$ is a vector containing fixed effects for trait i, which were farm × unit × year × week of the measurement, second breed fraction × second breed, DIM which was modeled using third-order Legendre polynomials, and parity (from parity 1 to 4, where 4 is parity 4 or higher); $\mathbf{a}_i$ is a vector containing additive genetic effects for trait i; $\mathbf{pe}_i$ is a vector containing permanent environmental effects within parity (from parity 1 to 11) for trait i; $\mathbf{e}_i$ is a vector with the residuals for trait i; and $\mathbf{X}_i$, $\mathbf{Za}_i$, $\mathbf{Zp}_i$, and $\mathbf{Ze}_i$ are identity matrices linking the records in $\mathbf{y}_i$ to the fixed effects, the additive genetic effects, and the permanent environmental effects, respectively. The additive genetic, permanent environmental and residual effects for all traits were assumed normally distributed with a mean of zero, a variance of σ^2_{ji} for random effect j and trait i, and a covariance between 2 traits of $\sigma_{j_1j_2}$:

$$\begin{bmatrix}j_1\\ j_2\end{bmatrix}\sim N\left[\begin{pmatrix}0\\ 0\end{pmatrix},\mathbf{I}\otimes\begin{pmatrix}\sigma^2_{j_1} & \sigma_{j_1j_2}\\ \sigma_{j_1j_2} & \sigma^2_{j_2}\end{pmatrix}\right].$$

From the variance estimates, heritabilities and repeatabilities were estimated and reported as means of all bivariate runs. The heritability was defined as:

$$h^2=\frac{\sigma^2_a}{\sigma^2_a+\sigma^2_{pe}+\sigma^2_e},$$

where σ^2_a is the additive genetic variance, σ^2_{pe} is the permanent environmental variance, and σ^2_e is the residual variance.

The repeatability was defined as:

$$t=\frac{\sigma^2_a+\sigma^2_{pe}}{\sigma^2_a+\sigma^2_{pe}+\sigma^2_e}.$$

RESULTS

The daily mean CH_4p measured by GF units was 436 g/d (Table 2) with a coefficient of variation (CV) of 28%. The weekly mean CH_4p was 435 g/d and had a lower CV of 23%. The daily mean CH_4c measured by sniffers was 325 ppm with a high CV of 77%. The weekly mean CH_4c was 331 ppm with a CV of 66%. The repeatability of CH_4 and CO_2 was higher in the scenarios with weekly means than with daily means, both when measured as production by GF units or as concentrations by sniffers. The repeatability of CH_4p measured by GF units compared with CH_4c measured by sniffers was equal for daily means (0.34), but higher for weekly mean CH_4p than weekly mean CH_4c (0.77 and 0.66, respectively).

Both CH_4p measured by GF units and CH_4c measured by sniffers decreased during the night and were lowest around 06.00h, whereafter the measured CH_4p and CH_4c increased (Figure 1). Additionally, both showed a dip around 16.00h. This dip was larger for CH_4c measured by sniffers. Both CH_4p and CH_4c increased rapidly during the first DIM (Figure 2). However, after 100 DIM average CH_4c measured by sniffers started to decrease, whereas the average CH_4p measured by GF units was relatively consistent after 100 d.

In total 75 dairy cows were measured with both GF units and sniffers within the same days (Table 1), with on average 24 d with measurements by both techniques. Of these cows, 73 dairy cows had weekly mean measurements, with at least 3 visits recorded per week, by both techniques within the same week. These 73 cows had on average 5 wk of measurements by both GF units and sniffers. The Pearson correlations between GF CH_4p and sniffer CH_4c for these cows were low (0.20 (95% CI [0.15, 0.24]) and 0.19 (95% CI [0.08, 0.29])), for daily and weekly means respectively) (Figure 3A). Similarly, the Pearson correlations between GF CO_2p and sniffer

Table 2. The mean ± SD, minimum (Min), maximum (Max), and repeatability (t) of daily or weekly methane (CH_4) and carbon dioxide (CO_2) emissions, recorded by GreenFeed (GF, grams/day) or sniffer (ppm)

		CH_4				CO_2			
Item		Mean ± SD	Min	Max	t[1]	Mean ± SD	Min	Max	t[1]
GF (g/d)	Daily	436 ± 120	38	1,929	0.34	13,159 ± 2,041	2,590	22,399	0.45
	Weekly	435 ± 98	148	834	0.77	13,169 ± 1,760	7,931	19,971	0.81
Sniffer (ppm)	Daily	325 ± 251	0.3	1,964	0.34	3,725 ± 1,865	3	9,683	0.39
	Weekly	331 ± 218	0.5	1,566	0.66	3,684 ± 1,586	65	9,257	0.69

[1]All repeatabilities had a SE of 0.01 and were reported as means of all bivariate analyses.

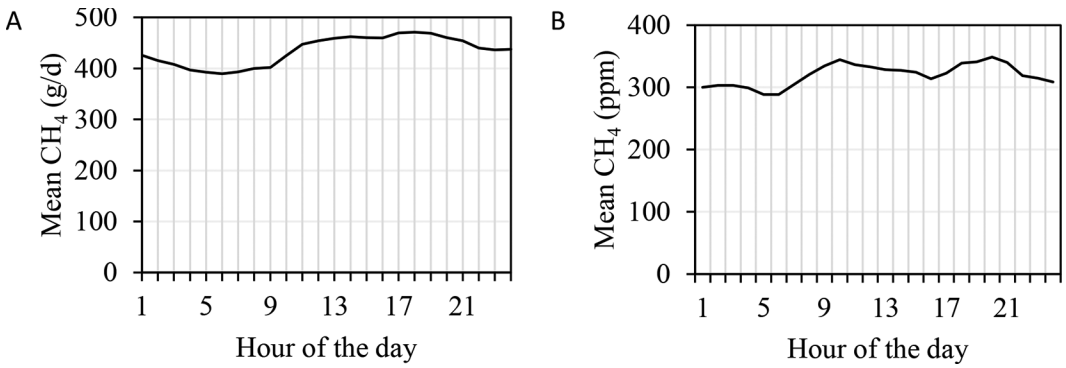

Figure 1. The mean CH_4 emissions measured as (A) production (grams/day) on 16 farms by GreenFeed units and (B) concentration (ppm) on 15 farms by sniffers per hour of the day.

CO_2c were low for daily (0.08 (95% CI [0.03, 0.12])), and for weekly means (−0.01 (95% CI [-0.12, 0.0.10])) (Figure 3B).

Variance components were estimated with bivariate repeatability animal models and were used to estimate the repeatability, heritability, and phenotypic and genetic correlations. The heritability of CH_4p measured by GF units was 0.20 for daily means and 0.33 for weekly means (Table 3). The heritability of CH_4c measured by sniffers was similar; and was 0.18 for daily means and 0.32 for weekly means, albeit the repeatability was slightly lower for the weekly sniffer measures compared with the GF. The phenotypic correlation between daily mean CH_4 measured by GF or sniffer was 0.39 ± 0.03, and 0.37 ± 0.05 between weekly mean CH_4 measured by GF or sniffer. The genetic correlation between daily mean CH_4 measured by GF or sniffer was high (0.71 ± 0.13), and was similar for weekly mean CH_4 measured by GF or sniffer (0.76 ± 0.15). Residual correlations were moderate and ranged from 0.06 ± 0.03 to 0.77 ± < 0.01 (Appendix Table A1).

The heritability of CO_2p measured by GF units was 0.24 for daily means and 0.34 for weekly means and the heritability of CO_2c measured by sniffers was 0.20 for daily means and 0.32 for weekly means (Table 3). The genetic correlations between CO_2p and CH_4p measured by GF were moderate (0.64 and 0.65, for daily and weekly means, respectively), and were higher between CO_2c and CH_4c recorded by sniffers (0.93 for daily and weekly means). Furthermore, the genetic correlations between CO_2p and CO_2c (0.52 and 0.60, for daily and weekly means, respectively) were lower than the genetic correlations between CH_4p and CH_4c (0.71 and 0.76, for daily and weekly means, respectively).

DISCUSSION

The aim of this study was to estimate (1) the repeatability and heritability for CH_4 and CO_2 production recorded by GreenFeed (GF) units and for CH_4 and CO_2 concentration measured by sniffers, and (2) the genetic correlation between CH_4 recorded by these 2 different techniques. In the results we showed that CH_4 and CO_2 emissions recorded by either GF units or sniffers had a moderate heritability and that the genetic correlation between CH_4p measured by GF units and CH_4c measured by sniffers was high.

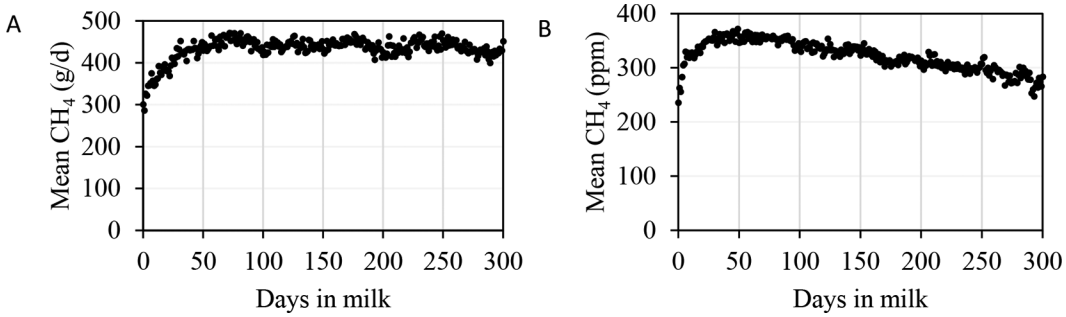

Figure 2. The mean CH_4 emissions measured as (A) production (grams/day) on 16 farms by GreenFeed units and (B) concentration (ppm) on 15 farms by sniffers per DIM.

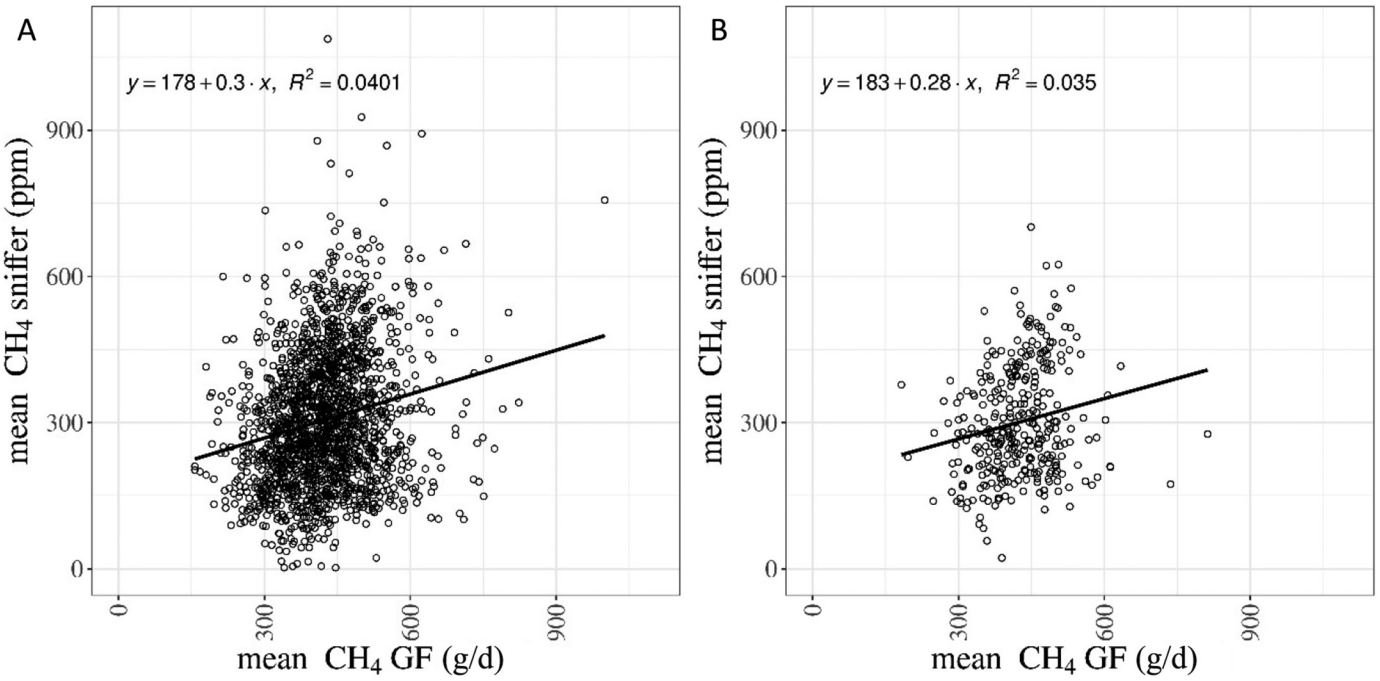

Figure 3. The relationship between methane (CH_4) production measured by GreenFeed (GF, grams/day) units and CH_4 concentrations measured by sniffers (ppm) from repeated measurements on (A) 75 dairy cows as means per day and (B) 73 dairy cows as means per week.

Heritability and Repeatability

The heritability that we estimated for CH_4p recorded by GF units was moderate, and was 0.19 ± 0.02 for daily means and 0.33 ± 0.04 for weekly means (Table 3). The first published estimates of the heritability for CH_4 production measured by GF units ranged from 0.12 ± 0.06 to 0.35 ± 0.19 for daily and 0.22 ± 0.11 to 0.43 ± 0.12 for weekly CH_4 production (Lopes et al., 2022; Manzanilla-Pech et al., 2021; Ryan et al., 2022; Tiezzi et al., 2022; Wethal et al., 2022). In addition, many studies have reported heritability estimates for various traits for CH_4 recorded by sniffers (Lassen and Difford, 2020). Some studies using sniffers attempted to estimate CH_4p from sniffer CH_4c measurements by using mass flux calculations (Madsen et al., 2010) or based on tidal volume (Chagunda et al., 2009). The estimated heritability for GF CH_4p reported in this study, is within the range of the in the literature reported heritabilities for estimated sniffer CH_4p, which ranged between 0.12 ± 0.04 and 0.45 ± 0.11 (Lassen and Løvendahl, 2016; Difford et al., 2018; Zetouni et al., 2018; Breider et al., 2019; López-Paredes et al., 2020).

The repeatability of similar trait definitions for CH_4p measured by GF units and CH_4c measured by sniffers was comparable (0.34 for daily mean CH_4p and CH_4c, Table 2). For both sampling techniques, the repeatability was higher when using multiple measurements of weekly mean CH_4, and was 0.77 for CH_4p measured by GF units and 0.66 for CH_4c measured by sniffers. The higher repeatability for weekly means is a result of averaging a larger number of records, which reduces the temporary environmental variance (Falconer and Mackay, 1996). In the literature, many repeatability estimates for CH_4 emissions measured on dairy cows are reported. The literature estimates reported depend largely on trait definition, which is confirmed by the results in this study, where the repeatability estimates are higher for the traits based on weekly mean CH_4 emissions than for daily mean CH_4 emissions. This highlights the importance of carefully defining the trait when reporting parameter estimates.

The literature also reports several repeatability estimates for CH_4p measurements by GF units. The estimates from this study, fall within the range of estimates reported in the literature. For example, Manafiazar et al. (2016) averaged CH_4p measurements in 1 to 14 d means, and estimated repeatabilities ranging from 0.33 to 0.79. Also Coppa et al. (2021) reported that the repeatability of CH_4p increased when averaging records over longer periods of time (0.60 to 0.78, for one to 8-wk means). On the contrary, a study by Denninger et al. (2019) analyzed 7, 14, and 28 d means (0.64, 0.68, and 0.59, respectively) and showed that the repeatability for CH_4p was highest for 14 d means . Thus, it is uncertain which length of recording period for averag-

Table 3. Phenotypic (above the diagonal) and genetic correlations (below the diagonal) between methane (CH_4) and carbon dioxide (CO_2) recorded by GreenFeed (GF, production: CH_4p in grams/day) units or sniffers (concentration: CH_4c in ppm) and averaged per day or per week (±SE)[1]

Item	GF CH_4p day	GF CO_2p day	GF CH_4p week	GF CO_2p week	Sniffer CH_4c day	Sniffer CO_2c day	Sniffer CH_4c week	Sniffer CO_2c week
GF CH_4p day	*0.19 ± 0.02	0.72 ± 0.01	0.70 ± 0.01[2]	0.53 ± 0.01	0.39 ± 0.03	0.20 ± 0.04	0.37 ± 0.04	0.18 ± 0.04
GF CO_2p day	0.68 ± 0.04	*0.24 ± 0.03	0.58 ± 0.01	0.77 ± 0.01[2]	0.32 ± 0.04	0.25 ± 0.04	0.35 ± 0.04	0.27 ± 0.04
GF CH_4p week	0.99 ± 0.01[2]	0.66 ± 0.05	*0.33 ± 0.04	0.75 ± 0.01	0.27 ± 0.04	0.15 ± 0.05	0.37 ± 0.05	0.19 ± 0.06
GF CO_2p week	0.64 ± 0.05	1.00 ± 0.01[2]	0.65 ± 0.05	*0.34 ± 0.05	0.22 ± 0.04	0.18 ± 0.04	0.31 ± 0.05	0.24 ± 0.06
Sniffer CH_4c day	0.71 ± 0.13	0.54 ± 0.15	0.74 ± 0.15	0.69 ± 0.16	*0.18 ± 0.01	0.78 ± >0.01	0.73 ± <0.01[2]	0.62 ± 0.01
Sniffer CO_2c day	0.39 ± 0.16	0.51 ± 0.15	0.47 ± 0.17	0.63 ± 0.16	0.93 ± 0.01	*0.20 ± 0.01	0.65 ± 0.01	0.76 ± <0.01[2]
Sniffer CH_4c week	0.71 ± 0.14	0.60 ± 0.15	0.76 ± 0.15	0.72 ± 0.16	1.00 ± <0.01[2]	0.92 ± 0.01	*0.32 ± 0.02	0.84 ± <0.01
Sniffer CO_2c week	0.35 ± 0.17	0.51 ± 0.15	0.41 ± 0.18	0.60 ± 0.17	0.91 ± 0.01	1.00 ± <0.01[2]	0.93 ± 0.01	*0.32 ± 0.02

[1]The heritabilities are reported on the diagonal and marked with an asterisk. The heritabilities were reported as the mean of all runs.
[2]Estimate with the highest likelihood but with convergence problems due to closeness to unity of the correlation.

ing records yields the highest repeatability. Nonetheless, when measurements are used to estimate breeding values from repeated measurements in a repeatability model averaging visits over longer periods of time, by using weekly means, may increase the heritability and repeatability but will not result in higher reliabilities (van Breukelen et al., 2022).

Genetic and Phenotypic Correlations

For the second objective, we successfully estimated a genetic correlation between CH_4c measurements by sniffers and CH_4p measurements by GF units. This is the first study to estimate a genetic correlation between CH_4 recorded by sniffers and any other CH_4 recording technique in dairy cows. Our results showed that the genetic correlation between CH_4p measured by GF units and CH_4c measured by sniffers was high, and was 0.71 ± 0.13 for daily means and 0.76 ± 0.15 for weekly means (Table 3). The genetic correlations between weekly means of CH_4p or CH_4c and daily means of the other trait were similar to the estimates within daily or weekly means (0.71 ± 0.14 and 0.74 ± 0.15).

These high genetic correlations indicate that when cows are selected based on low breeding values for CH_4c measured by sniffers, this would result in reducing the average CH_4p in grams per day as measured by GF units. However, regardless of the large data set and that the phenotypes are genetically linked, the results of this study were based on a relatively small data set, with 184 cows recorded by both GF units and sniffers and only 75 cows with records overlapping in time. The permanent environmental covariance was fixed to zero in the bivariate models between a GF and a sniffer trait, because the permanent environmental covariances in these analyses were not significantly different from zero, most likely due to the low number of cows (n = 184) that had both records by GF units and by sniffers (Table 1). Furthermore, the low number of records did not allow to fit an across lactation permanent environmental effect, next to the within lactation permanent environmental effect. Therefore, the results should be interpreted with caution and further analyses will be required to gain confidence in these estimates. Nonetheless, the correlation estimates remained similar when the permanent environmental covariance was not fixed to zero, although these analyses did not converge. This does suggest that the reported results are likely to provide a good indication of the expected direction of the correlations, and this study sets the basis of future research on the genetic correlations between different techniques to measure enteric methane emissions.

The phenotypic correlations were moderate between CH_4p measured by GF units and CH_4c measured by sniffers, and were 0.39 ± 0.03 for daily means and 0.37 ± 0.05 for weekly means. The moderate phenotypic correlations suggest that environmental effects segregate the measurements by the 2 systems. For example, measurements could be affected by differences in the biology and behavior of the cow (Wu et al., 2018), or are a result of the different samplings techniques used. Nonetheless, the high genetic correlations show that pedigree and genomic information help to link measurements between related individuals, making it possible to disentangle the genetic background of CH_4 emissions from environmental factors. Whereas genetic correlations are missing in the literature, previous studies have investigated phenotypic relationships between CH_4 measurements from different CH_4 recording techniques. As was mentioned in the introduction, it has been shown that both CH_4p measured by GF units and CH_4c measured by sniffers are phenotypically correlated with CH_4p measured in RCs. Studies using GF reported high correlations of 0.85 and 0.96 (0.96 is transformed from r^2; Velazco et al., 2016; Hristov et al., 2018). A study using sniffers reported a moderate phenotypic correlation of 0.34 ± 0.22 and a high individual level correlation 0.75 ± 0.20 between CH_4c and CH_4p measured in RCs (Difford et al., 2019). The initial study that investigated the phenotypic relationship between GF and sniffer measurements reported a moderate phenotypic correlation of 0.30 (transformed from r^2) on a limited number of cows (n = 20; Huhtanen et al., 2015). The phenotypic correlation estimated by Huhtanen et al. (2015), is similar to the phenotypic correlation reported in this study and the Pearson correlation estimates from the same data (Pearson's r = 0.20 (95% CI [0.15, 0.24])and 0.19 ± 0.05 (95% CI [0.08, 0.29]) for daily and weekly means, respectively). The phenotypic correlations estimated from REML, were higher compared with the estimated Pearson correlations, which suggests the measurements are influenced by environmental factors. Environmental factors that play a role may be amplified by the fact that cows were measured at different times of day with GF and sniffers, and were not measured simultaneously. Some environmental factors can be successfully corrected for by using fixed effects in mixed models as was done in this study, where fixed effects for hour of measurement and week of measurement were included, which resulted in higher phenotypic correlations. Other techniques to improve the accuracy of sniffer systems should be further investigated, for example, by using video to record cows' head position.

Parameters for CO_2

The genetic correlation between CH_4p and CO_2p was 0.68 ± 0.04 for daily means and 0.65 ± 0.05 for weekly means, and the phenotypic correlations were higher and were 0.72 ± 0.01 for daily means and 0.75 ± 0.01 for weekly means (Table 3). The genetic correlations between CH_4c and CO_2c were high (0.93 ± 0.01, for both daily and weekly means), and so were the phenotypic correlations (0.78 ± < 0.01 and 0.84 ± < 0.01, for daily and weekly means respectively). High phenotypic and genetic correlations between CH_4 and CO_2 emissions of dairy cows have been reported in the literature previously. A study by Difford et al. (2020) reported correlations between log-transformed CH_4c and CO_2c, and reported phenotypic correlations of 0.87 ± < 0.01 and 0.96 ± < 0.01, and genetic correlations of 0.96 ± 0.03 and 0.97 ± 0.03. Additionally, a study using RC measurements also reported high phenotypic correlations between CH_4p and CO_2p (0.93 (Aubry and Yan, 2015). This indicates that there is a strong relationship between CH_4 and CO_2 emissions from dairy cows.

Genetic and phenotypic correlations between CH_4p measured by GF units and CO_2c measured by sniffers were moderate to low. The genetic correlations were 0.39 ± 0.16 for daily means and 0.41 ± 0.18 for weekly means, and were thus associated with large SE. The phenotypic correlations were 0.20 ± 0.04 for daily means and 0.19 ± 0.06 for weekly means. Therefore, although the genetic correlations between CH_4p and CH_4c, and between CH_4c and CO_2c were high, the genetic correlations between CH_4p and CO_2c were relatively low. This indicates that CH_4c measurements from sniffers would be a more suitable indicator for GF CH_4p, than using CO_2c measurements as a predictor. Regardless of the larger stability and less drift that we observed for measurements from the sniffer CO_2 sensor.

The Relationship Between CH_4 and DIM

Both the mean CH_4p measured by GF units and the CH_4c measured by sniffers increased steeply in the first weeks of lactation (Figure 2). Most likely this effect is caused by a low and increasing DMI that occurs in the first days of lactation (Krattenmacher et al., 2019). After the initial increase, the CH_4p measured by GF units remained stable over the further lactation, whereas the CH_4c measured by sniffers started to decrease after approximately 100 DIM. In the parameter estimations a fixed effect for DIM was fitted to correct for differences between DIM, similar to what has been used in and was recommended by previous studies (van Engelen et al., 2018). Phenotypic lactation patterns of CH_4 emissions

that have been reported in the literature are inconsistent in the later weeks of lactation (Garnsworthy et al., 2012; Bell et al., 2014; Lassen and Løvendahl, 2016; Pszczola et al., 2017). The study by Bell et al. (2014), showed that CH_4 emissions remained stable in the later weeks of lactation whereas other studies reported a decrease of CH_4 emissions in later weeks of lactation (Garnsworthy et al., 2012; Lassen and Løvendahl, 2016). The study by Pszczola et al. (2017) split the data between first and later parity cows. The data in the study by Pszczola et al. (2017) suggested that the pattern may differ per parity, and that the decrease is only observed for first parity cows, however, this could not be confirmed by the data recorded by GF units or sniffers from this study (results not shown). The deviation in lactation patterns could have resulted from other undefined differences between the for this study recorded farms, as the majority of measurements were taken on different farms for GF units and sniffers.

Implications for Implementing CH_4 Emissions in Breeding Goals

Both GF units and sniffers can be used to record multiple short-term CH_4 and CO_2 measurements from the breath of dairy cows. The main difference in functionality is the ability of GF units to record airflow, which is used in mass flux calculations to estimate CH_4p from concentration measurements (Madsen et al., 2010). Additionally, GF units record head position to ensure that the cow's muzzle is in close proximity to the air inlet. For measurements taken by sniffers, the position of the head of the cow in relation to the air inlet is unknown. A study by Huhtanen et al. (2015) showed that head movements have a high repeatability (0.74 for daily observations), indicating that there is systematic muzzle movement behavior of cows. This systematic head movement could in theory lead to lower average concentrations that are measured for cows that frequently move their muzzle away from the air inlet. Nonetheless, the study by Huhtanen et al. (2015) found a weak correlation between muzzle position and CH_4c measured by a sniffer method including 95 cows ($r = 0.26$) and no significant relationship including only the 59 cows which had acceptable muzzle data. However, as muzzle movements have shown to be highly repeatable, the relationship between muzzle movement and CH_4c measured by sniffers should be investigated further to prevent that breeding for reduced CH_4c will result in changes in cow behavior.

Additionally, GF units and sniffers are spot-sample techniques, and are unable to measure the total emissions of cows. At this moment, there is no technique that can measure the "true" CH_4 emissions of dairy cows. Often RCs are considered to be the gold standard for recording CH_4 emissions of individual cows, as they are able to accurately record total emissions (Hammond et al., 2016). However, RC measurements may not reflect true CH_4 emissions (Hill et al., 2016). Cow behavior, such as feed intake, can change when cows are isolated from the herd to be measured in a RC. Therefore, RC measurements may deviate from a cows' emissions in the herd on a commercial dairy farm. Furthermore, cows in RCs are usually recorded for a short period of time, lasting a few hours and up to 3 d, whereas CH_4 emissions do change over time. For example, by diurnal variation in CH_4 emissions (Figure 1), which can be a result of changes in feed intake during the day (Crompton et al., 2011). Additionally, studies by Pszczola et al. (2017), Breider et al. (2019), and Sypniewski et al. (2021) have shown that the heritability of CH_4 emission changes over a lactation. A technique that measures the true total amount of CH_4, can provide longitudinal data, and is cost-effective does not exist. The limitations in the different techniques that measure CH_4 have important implications for the application of a metric for CH_4 emissions in breeding goals that aim to reduce a cows' total emissions.

Instead of having available measurements of cows' true total CH_4 emissions, multiple measurements by different, genetically correlated, techniques and other predictors can be combined in genetic evaluations to realize the highest genetic gain and thus the highest reduction in CH_4 emissions (de Haas et al., 2017). Possible predictors can be for example rumination time (López-Paredes et al., 2020), composition of the rumen microbiome (Difford et al., 2018), feed intake, and digestibility (de Haas et al., 2017). In this study we focused on using sniffer CH_4c measurements as a predictor for CH_4p as recorded by GF units. The results from this study suggest that CH_4 measurements on CH_4p by GF and on CH_4c sniffers are highly genetically correlated, and indicate that selection on low CH_4c will reduce CH_4p. Because of the high genetic correlation, measurements from the 2 techniques could therefore be used to strengthen each other in genetic evaluations. In practice, sniffers are able to record CH_4c cost-effectively on thousands of dairy cows, which could complement the more expensive recording by GF units that measure CH_4p in grams per day. Furthermore, the high genetic correlation indicates that data could be shared between countries which have measurements available from either only GF units or sniffers. Sharing CH_4 data across countries is of interest to build a large genomic reference population. A large reference population across countries can increase the power of QTL detection and increase the accuracy of genomic prediction, as was shown in a previous project for scarcely

recorded feed intake data (global Dry Matter Initiative; Banos et al., 2012; de Haas et al., 2012). An initial study by Manzanilla-Pech et al. (2021) has successfully explored combining CH_4 measurements across countries and from different methods of measuring CH_4 (i.e., GF, sniffer, and SF_6), although more data are needed to better disentangle the use of different methods in different countries which was in some cases confounded.

CONCLUSIONS

To phenotype cows for CH_4 emissions, many different methods have been developed and are currently used in research practices. To be able to judge the similarity and repeatability between CH_4 measurements of different recording techniques, the genetic correlation can be a useful metric. Combining measurements by highly genetically correlated CH_4 recording techniques can help to enlarge existing data sets, for example by sharing data across countries, which is needed for accurate genetic evaluations. In this study, we have shown that the genetic correlation between CH_4p measured by GF units and CH_4c measured by sniffers was high (0.71 ± 0.13 for daily means and 0.76 ± 0.15 for weekly means). In addition, the heritability for CH_4p recorded by GF units was moderate and was similar to the heritability estimated for CH_4c measured by sniffers, 0.19 ± 0.02 and 0.33 ± 0.04 for daily and weekly means for GF, and 0.18 ± 0.01 and 0.32 ± 0.02 for daily and weekly means for sniffers, respectively. These results indicate that genetic selection on low CH_4c (ppm) recorded by the cheaper sniffer method, will result in reduced CH_4p (grams/day).

ACKNOWLEDGMENTS

This study was financially supported by the Climate Approach project funded by the Dutch ministry for agriculture, nature and food quality (LNV; project number BO-53-003) and was supported by the TKI Agri & Food project LWV19155 and the partners CRV and FrieslandCampina. The authors gratefully acknowledge the farmers for participating in this research, Johan Ploegaert, Theo van Hattum, and Henk Gunnink (Wageningen Livestock Research, Wageningen, the Netherlands) for installing and maintaining the sniffers and GreenFeed units, Hendrik Jan van Dooren (Wageningen Livestock Research, Wageningen, the Netherlands) for setting up data collection for sniffers, and CRV (Arnhem, the Netherlands) for providing the pedigree and genotype data. The authors have not stated any conflicts of interest.

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APPENDIX

Table A1. Residual correlations between methane (CH_4) and carbon dioxide (CO_2) recorded by GreenFeed (GF, production: CH_4p in grams/day) units or sniffers (concentration: CH_4c in ppm) and averaged per day or per week (± SE)

Item	GF CH_4p day	GF CO_2p day	GF CH_4p week	GF CO_2p week	Sniffer CH_4c day	Sniffer CO_2c day	Sniffer CH_4c week	Sniffer CO_2c week
GF CH_4p day		0.70 ± <0.01	0.43 ± 0.01[1]	0.29 ± 0.01	0.39 ± 0.02	0.19 ± 0.03	0.40 ± 0.02	0.21 ± 0.03
GF CO_2p day			0.33 ± 0.01	0.47 ± <0.01[1]	0.35 ± 0.03	0.24 ± 0.03	0.42 ± 0.02	0.31 ± 0.03
GF CH_4p week				0.70 ± <0.01	0.23 ± 0.03	0.07 ± 0.03	0.42 ± 0.02	0.21 ± 0.03
GF CO_2p week					0.14 ± 0.03	0.06 ± 0.03	0.29 ± 0.03	0.18 ± 0.03
Sniffer CH_4c day						0.72 ± <0.01	0.52 ± <0.01[1]	0.39 ± <0.01
Sniffer CO_2c day							0.42 ± <0.01	0.54 ± <0.01[1]
Sniffer CH_4c week								0.77 ± <0.01
Sniffer CO_2c week								

[1]Estimate with the highest likelihood but with convergence problems due to closeness to unity of the correlation.