



Genetic (co-)variation of methane emissions, efficiency, and production traits in Danish Holstein cattle along and across lactations

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ABSTRACT

Methane emissions in ruminant livestock has become a hot topic, given the pressure to reduce greenhouse gas emissions drastically in the European Union over the next 10 to 30 yr. During the 2021 United Nations Climate Change conference, countries also made collective commitments to curb methane emissions by 2050. Genetic selection for low-methane-emitting animals, particularly dairy cows, is one possible strategy for mitigation. However, it is essential to understand how methane emissions in lactating animals vary along lactation and across lactations. This understanding is useful when making decisions for future phenotyping strategies, such as the frequency and duration of phenotyping within and across lactations. Therefore, the objectives of this study were to estimate (1) genetic parameters for 2 methane traits: methane concentration (MeC) and methane production (MeP) at 2 parity levels in Danish Holstein cows across the entire lactation using random regression models; (2) genetic correlations within and between methane traits across the entire lactation; and (3) genetic correlations between the methane traits and economically important traits throughout first lactation. Methane concentration ($n = 19,639$) records of 575 Danish Holstein cows from a research farm measured between 2013 and 2020 were available. Subsequently, CH_4 production in grams/day (MeP; $n = 13,866$) was calculated; MeP and MeC for first and second lactation (L1 and L2) were analyzed as separate traits: MeC_L1, MeP_L1, MeC_L2, and MeP_L2. Heritabilities, variance components, and genetic correlations within and between the 4 CH_4 traits were estimated using random regression models with Legendre polynomials. The additive genetic and permanent environmental effects were modeled using second-order Legendre polynomial for lactation weeks.

Estimated heritabilities for MeP_L1 ranged between 0.11 and 0.49, for MeC_L1 between 0.10 and 0.28, for MeP_L2 between 0.14 and 0.36, and for MeC_L2 between 0.13 and 0.29. In general, heritability estimates of MeC traits were lower and more stable throughout lactation and were similar between lactations compared with MeP. Genetic correlations (within trait) at different lactation weeks were generally highly positive (0.7) for most of the first lactation, except for the correlation of early lactation (<10 wk) with late lactation (>40 wk) where the correlation was the lowest (<0.5). Genetic correlations between methane traits were moderate to highly correlated during early and mid lactation. Finally, MeP_L1 has stronger genetic correlations with energy-corrected milk and dry matter intake compared with MeC_L1. In conclusion, both traits are different along (and across) lactation(s) and they correlated differently with production, maintenance, and intake traits, which is important to consider when including one of them in a future breeding objective.

Key words: methane production, methane concentration, efficiency, genetic correlation, random regression

INTRODUCTION

Enteric fermentation by ruminants contributes to 44.3% of global livestock emissions (FAO, 2018). Methane gas has been classified as a short-lived air pollutant (Tong et al., 2015), making its reduction a possible solution for global warming in the short term. Reducing enteric methane (CH_4) emissions in ruminants is imperative, given the commitment by the European Commission (2019) to reduce greenhouse gas emissions by 55% in 2030 and become neutral by 2050. During the last decade, several approaches have been proposed to reduce methane in livestock (Knapp et al., 2014), including nutritional approaches such as feed additives (Roque et al., 2019), manure management (Hristov et al., 2013), genetic selection (Hegarty et al., 2007; González-Recio et al., 2020), reductions in the num-

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ber of animals, and reductions in meat consumption (Stoll-Kleemann and Schmidt, 2017). Genetic selection for low-CH₄-emitting cows can be an effective and sustainable approach to reduce greenhouse gas production from dairy cattle (Lassen and Difford, 2020), given that genetic progress is cumulative over generations. Thus, selecting low-CH₄-emitting animals could yield significant reductions in emissions within a few generations. However, this methane reduction should be achieved without affecting the health status of the cow or its production. For that reason, it is important to understand the genetic architecture behind methane traits and their relationship with other traits (i.e., health and production traits).

Despite the above-mentioned extensive research over the last decade, little is known about the variation of CH₄ emissions during lactation and across lactations. This can be partly attributed to the difficulty in recording CH₄ emissions and to the fact that considerable time and resources are needed to longitudinally record CH₄ emission over the typical 305-d lactation and over multiple lactations in cohorts of animals large enough to estimate genetic parameters. Thus, given the scarcity of longitudinal CH₄ data in adequately large populations, studies that have explored genetic variation along lactation and across lactations are limited to predicted CH₄ emissions from milk infrared spectra (Kandel et al., 2017) or short spot measurements of CH₄ emissions in a few herds (Pszczola et al., 2017; Sypniewski et al., 2021). From these studies (Breider et al., 2019; Sypniewski et al., 2021), it is clear that additive genetic variation changes within and across lactations for CH₄ production and CH₄ breath concentration in dairy cows.

The use of sniffers, which only measure the methane concentration in cow's breath (Garnsworthy et al., 2019), require more validation as a methane emission trait. This is a simpler alternative to calculation of production of CH₄ in grams per day, using the ratio CH₄:CO₂ of gas concentrations and ECM together with BW (Madsen et al., 2010). Evidence suggests that estimation of CH₄ production leads to an artificially induced covariance structure between CH₄ with ECM and BW, with high genetic correlations (Manzanilla-Pech et al., 2020, 2021). Previous studies have presented methane concentration as a trait that could be of use as proxy for methane emissions (Difford et al., 2020; González-Recio et al., 2020; Manzanilla-Pech et al., 2021).

Knowledge about the genetic variation in measured CH₄ emission traits during and across lactations from long-term experiments would be useful to better elucidate temporal genetic variation in CH₄ emission and its possible interaction with other traits. Additionally, this knowledge would help to form the basis for design-

ing efficient testing and selection schemes. Currently, in this study, we have gathered the largest amount of longitudinal data for CH₄ emission in Holstein cows, based on continuously recording over a period of 7 yr in a research farm with around 600 cows over first and second lactations.

Therefore, the objectives of this study were to estimate (1) genetic parameters for 2 methane traits (methane concentration, **MeC**; and methane production, **MeP**) at 2 parity levels in Danish Holstein dairy cows across the entire lactation using random regression models; (2) genetic correlations within and between the methane traits across the entire lactation; and (3) genetic correlations between the methane traits and other traits along first lactation.

MATERIALS AND METHODS

The phenotypic records in the present study were collected on Danish Holstein cows from the Danish Cattle Research Center (**DCRC**, Tjele, Denmark); DCRC has collected DMI, ECM, and BW data since its inception in 2001, and "sniffer" equipment was installed at DCRC in 2013 for the recording of MeC. The number of cows, phenotype recording, and data editing steps are described sequentially below for the methane database and for the intake and production database. Ethical approval was not needed for this study because no animal procedures were performed, as only existing data were used.

Methane Data Collection and Editing

Methane concentration records from 649 Holstein cows between 2013 and 2020 from DCRC were available. Data are described in part by Zetouni et al. (2018), Difford et al. (2020), and Manzanilla-Pech et al. (2020). Methane concentration was measured using a nondispersive infrared CH₄ sensor (Guardian NG, Edinburgh Instruments Ltd.) and, in parallel, CO₂ was measured using same technique (Gascard, Edinburgh Instruments Ltd.). More than 200,000 daily MeC records on 649 cows were available; however, weekly (average) MeC records were calculated to match the weekly records of ECM and BW available, which were used to calculate MeP (described below). Data included weekly averages in which up to 3 d of data were allowed to be missing within a week, and individual cows required a minimum of 3 weekly measurements to be retained for further analysis. After editing, only first and second lactations were used, resulting in 19,639 weekly MeC records from 575 Danish Holstein cows and 13,866 MeP records from 504 cows being analyzed. This reduction from MeC records to MeP records is due to the lack

of ECM or BW, traits that are needed in the calculation of MeP. Methane concentration distribution per lactation is shown in Table 1. Methane concentration (CH_4 in parts per million, ppm; MeC) was transformed using natural logarithm (\ln) to achieve normality and then multiplied by 100 to avoid problems with the scale of the other traits. Methane production (CH_4 in g/d; MeP) was calculated as follows. First, CH_4 in liters/day was computed using the formula of Madsen et al. (2010) based on heat-producing units (HPU):

$$\text{CH}_4 \text{ (L/d)} = (\text{CH}_4/\text{CO}_2) \times 180 \times 24 \times \text{HPU}, \quad [1]$$

where

$$\begin{aligned} \text{HPU} = & 5.6 \text{ metabolic BW} + 22 \text{ ECM} + 1.6 \\ & \times 10^{-5} \times (\text{days carried calf})^3. \end{aligned} \quad [2]$$

Second, CH_4 in liters per day was converted to CH_4 in grams per day using the formula

$$\text{MeP (CH}_4 \text{ g/d)} = \text{density} \times \text{CH}_4 \text{ (L/d)}, \quad [3]$$

where the density of CH_4 at $20^\circ\text{C} = 0.668 \text{ g/L}$.

Given that the traits would be analyzed by random regression, the analyses were performed per trait per lactation (L1 and L2), resulting in the following traits: **MeC_L1**, **MeP_L1**, **MeC_L2**, and **MeP_L2**.

Production, Maintenance, and Intake Data Collection and Editing

Records on ECM, BW, and DMI from 960 primiparous cows belonging to the DCRC research farm (Table 2) from 2003 to 2019 were available. Cows were fed with automated feeders (Insentec, RIC system). Cows were part of numerous nutritional experiments, and diets included primarily rolled barley, corn silage, grass clover silage, rapeseed meal, and soybean meal. Body weight was measured automatically at each milking, and averaged per week (Li et al., 2017). The barn was a loose housing system with access to automatic milking stations (DeLaval International AB). Each milking system

was fitted with a weighing platform (Danvaegt) that recorded BW at each milking. Energy-corrected milk was calculated using the following formula (Sjaunja et al., 1991):

$$\begin{aligned} \text{ECM (kg)} = & 0.25 \text{ milk (kg)} + 12.2 \text{ fat content (kg)} \\ & + 7.7 \text{ protein content (kg)}. \end{aligned} \quad [4]$$

Variance Components Estimation

Variance components for the 4 methane traits (MeC_L1, MeC_L2, MeP_L1, MeP_L2) were estimated using a single-trait model with the average information (AI)-REML algorithm in DMU software (Version 6, Release 5.4; Madsen and Jensen, 2014) using a pedigree relationship matrix. A pedigree containing the identification of the cow, sire, and dam with 11,778 animals (after pruning) in the relationship matrix was used, with an average of 10 generations deep. The pedigree included 152 sires with an average of 4.3 daughters per sire. The relationship matrix for animals with methane phenotypes is shown in Supplemental Figure S1 (<https://dataverse.harvard.edu/dataverse/supplementals1>; Manzanilla-Pech, 2022).

The model used to estimate the variance components was

$$\begin{aligned} y_{ijklm} = & TYS_j + ACC_l + LACW_t + \sum_{k=0}^{n-2} a_{ik} \Phi_{itk} \\ & + \sum_{k=0}^{n-2} p e_{ik} \Phi_{itk} + e_{ijklm}, \end{aligned} \quad [5]$$

where y_{ijklm} is the phenotype for MeC_L1, MeC_L2, MeP_L1, and MeP_L2; TYS is the fixed effect j for trial-year-season (98 classes); ACC is the l effect of age of cow at calving in months as a covariate (10 classes for L1 and 17 for L2); and $LACW$ is the fixed effect of time t for lactation week (1 to 45 weeks). Random effects are as follows: a_{ik} is the k th regression coefficient of Legendre polynomial for the additive genetic effect of the i th cow, Φ_{itk} is the term of the second-order Legendre polynomial for cow i measured at $LACW$ t , $p e_{ik}$ is the k th regression coefficient of Legendre polynomial for the permanent environmental effect of the i th cow,

Table 1. Descriptive statistics for methane concentration (MeC) and methane production (MeP) at first (MeC_L1, MeP_L1) and second lactation (MeC_L2, MeP_L2)

Trait	Unit	No. of cows	No. of records	Mean	SD	Minimum	Maximum	CV (%)
MeC_L1	$\text{Log}(\text{ppm}) \times 100$	489	11,243	575.7	53.9	414.2	731.5	9.4
MeC_L2		368	8,405	573.4	50.5	414.3	714.2	8.8
MeP_L1	g/d	425	8,065	306.6	77.6	77.3	588.0	25.3
MeP_L2		318	5,801	354.5	81.5	88.9	598.2	22.9

Table 2. Descriptive statistics for ECM, BW, and DMI for first-lactation cows (ECM_L1, BW_L1, and DMI_L1)

Trait	Unit	No. of cows	No. of records	Mean	SD	Minimum	Maximum	CV (%)
ECM_L1	kg/d	921	30,498	30.2	5.7	8.7	57.9	18.9
BW_L1	kg	963	32,038	617.0	66.5	421.7	893.0	10.7
DMI_L1	kg/d	958	32,275	19.4	2.9	9.8	33.0	14.9

and e is the residual error of y_{ijklm} . Residual errors were assumed to have heterogeneous variances and were divided into 11 classes according to lactation month (1 to 11). Residual covariances within the same trait at different lactation month were assumed to be zero. Genetic correlations were estimated through pairwise bivariate analyses between the traits without heterogeneous residual variances to avoid over-parametrization of the model. The (co)variance structure for a is $\text{Var}(a) = \mathbf{A} \otimes \mathbf{G}$, where \mathbf{A} = additive genetic relationship matrix, \otimes = Kronecker product function, and \mathbf{G} = additive genetic covariance matrix of the genetic random regression coefficients. Similarly, $\text{Var}(pe) = \mathbf{I} \otimes \mathbf{PE}$, where \mathbf{I} = identity matrix and \mathbf{PE} = permanent environmental covariance matrix of the random regression coefficients (description below) and describes the permanent environmental component of a lactation for a cow. The residual variance structure $[\text{Var}(e)]$ was assumed diagonal and constant over lactation month.

Estimated (co)variance components of the random regression were used together with Legendre polynomial coefficients to calculate genetic and permanent environmental variances and covariances for each lactation month using the methodology of Fischer et al. (2004):

$$\mathbf{G} = \mathbf{\Phi} \mathbf{K} \mathbf{\Phi}' \text{ and}$$

$$\mathbf{PE} = \mathbf{\Phi} \mathbf{KPE} \mathbf{\Phi}' \quad [6]$$

where \mathbf{G} is the genetic variance-covariance matrix within trait per lactation week (matrix $n \times n$), $\mathbf{\Phi}$ is a matrix of order $t \times n$ ($t = 3$ and $n = 45$), which contains 3 orthogonal polynomial coefficients for each of the traits through 45 lactation weeks; \mathbf{K} is a matrix of order $t \times t$, which contains the estimated covariance function describing the genetic variance components for the random regression coefficients. Likewise, \mathbf{PE} is the permanent environmental variance-covariance matrix and \mathbf{KPE} is a matrix of order $t \times t$, which contains the covariance function for the permanent environmental variance components. For bivariate analyses, \mathbf{G} and \mathbf{PE} were across traits and lactation week, being of size $2n$ ($= 90$), where \mathbf{K} and \mathbf{KPE} were size $2t$ ($= 6$).

Finally, to disentangle the relationship (genetic correlation) of both methane traits with production, maintenance, and intake traits, bivariate analyses were performed between MeC_L1 and MeP_L1 with ECM, DMI, and BW for first lactation. The model for ECM, DMI, and BW used in the bivariate analyses with methane traits was the same model as in Eq. [5]. Second-lactation data were excluded from this analysis due to an insufficient number of cows and records available across these traits, particularly for methane production (MeP_L2). Heritabilities, permanent environmental ratio, repeatabilities, and genetic correlations between traits were calculated for each week of lactation. Standard errors (**SE**) were calculated per lactation week based on the methodology of Fischer et al. (2004) and reported by quartile (**Q2**, **Q3**), where Q2 is the median and Q3 (upper quartile) is the value under which 75% of data points are found when arranged in increasing order.

RESULTS AND DISCUSSION

Descriptive Statistics

Descriptive statistics of the 4 methane traits (MeP_L1, MeP_L2, MeC_L1, MeC_L2) are shown in Table 1. The average for MeP_L1 (first lactation) was 307 g/d and for MeP_L2 (second lactation) was 355 g/d. Averages for MeP were lower than reported (396–503 g/d) by Sypniewski et al. (2021) in multiparous Polish Holsteins (in 2 farms) and Richardson et al. (2021; 469 g/d) in multiparous Australian Holsteins. However, our averages for MeP in both lactations were higher than those presented by López-Paredes et al. (2020; 183 g/d) in Spanish Holstein cows. As expected, methane production showed a lower average for first-lactation cows than for second-lactation cows (307 g/d), as they are lighter animals with lower intake and production (Table 2). The average for MeC_L1 was 576 and that for MeP_L2 was 574, which were higher than reported (505–517) by Sypniewski et al. (2021). Descriptive statistics for ECM, BW, and DMI for first lactation are presented in Table 2. The average for ECM was 30.2 kg/d, whereas that for BW was 617 kg, and for DMI was 19.4 kg/d. Averages for ECM, BW, and DMI were

within the range of values previously reported for primiparous Holstein cows (Manzanilla-Pech et al., 2014; Li et al., 2017; Difford et al., 2020).

Heritabilities, Permanent Environmental Ratio, and Repeatabilities Across Lactation(s)

Estimated heritabilities (h^2) per lactation week for MeP_L1, MeP_L2, MeC_L1, and MeC_L2 are reported in Figure 1. Heritabilities for MeP were higher than those for MeC for both lactations. Methane concentration (MeC_L1, and MeC_L2) heritabilities were more similar to each other along lactation compared with MeP heritabilities, which showed a higher heritability for first lactation than for second lactation. Estimated heritabilities for MeC traits varied from 0.10 to 0.20 at the beginning of the lactation, from 0.25 to 0.53 in mid lactation, and from 0.11 to 0.24 at the end of lactation (Q2–Q3 SE = 0.05–0.06); for MeP, estimated heritabilities varied from 0.14 to 0.25 at the beginning of the lactation, from 0.28 to 0.47 in mid lactation, and from 0.11 to 0.29 at the end of lactation (Q2–Q3 SE = 0.07–0.13). Sypniewski et al. (2021) reported a similar pattern of heritability along lactation and similar values (from 0.13 to 0.26) for MeP in Holstein cows, including different lactations. Breider et al. (2019) presented heritabilities ranging from 0.12 to 0.45 along the lactation (until wk 52) in multiparous Holstein cows; however, their heritability values showed a very different pattern across lactation, with the lowest point occurring at wk 20. Furthermore, Sypniewski et al. (2021) presented different patterns of heritability for MeC across lactation, with low heritabilities close to zero at the beginning of lactation and a constant increase toward end of the lactation (up to 0.14). Even though Breider et al. (2019) and Sypniewski et al. (2021) used the same method (sniffer) to measure methane, there are differences in their results compared with the current study. These differences could be due to the inclusion of several lactations (4 and 8, respectively) in the analyses, whereas, in the current study, we analyzed traits separately per lactation and only for the first and second lactations. Furthermore, it is interesting to observe that the distribution of heritability estimates across lactation for MeP is similar to the ECM and DMI curves previously reported by Manzanilla-Pech et al. (2014) and Li et al. (2017) in primiparous Holstein cows. This further supports the notion that heritability estimates for MeP are influenced by the genetic architecture of ECM heritabilities along lactation. This makes it complicated to disentangle which part of the genetic variation of MeP

is due to MeC and which is due to addition of ECM in the calculation of MeP. To summarize, estimates of heritability for MeP vary along the lactation from low to moderate; however, there is no clear consensus on the shape of changes during lactation across the few studies that have reported heritabilities along the lactation.

Estimated permanent environmental ratio (pe^2 , Figure 1) per lactation week for MeP_L1, MeP_L2, MeC_L1, and MeC_L2 were lower for MeP than for MeC. Estimated pe^2 for MeC traits varied from 0.49 to 0.62 at the beginning of the lactation, from 0.50 to 0.58 in mid lactation and from 0.45 to 0.63 at the end of lactation (Q2–Q3 SE = 0.02–0.05); for MeP, estimated pe^2 varied from 0.26 to 0.44 at the beginning of the lactation, from 0.23 to 0.28 in mid lactation, and from 0.26 to 0.68 at the end of lactation (Q2–Q3 SE = 0.11–0.18). Additionally, repeatability estimates (t) per lactation week for MeP_L1, MeP_L2, MeC_L1, and MeC_L2 are reported in Supplemental Figure S2 (<https://dataverse.harvard.edu/dataverse/supplementals1>; Manzanilla-Pech, 2022). Estimated repeatabilities ranged from moderate to high for all traits: 0.63 to 0.86 for MeC_L1, 0.64 to 0.79 for MeC_L1, 0.62 to 0.82 for MeC_L2, and 0.53 to 0.82 for MeC_L2, with Q2–Q3 SE between 0.03 and 0.09.

Genetic Correlations Within Trait and Lactation

Estimated genetic correlations (r_g) per lactation week for MeC_L1, MeC_L2, MeP_L1, and MeP_L2 are shown in Figure 2. Genetic correlations within lactation were, as expected, highest between weeks close to each other in time and decreased as the time between measurements increased. First-lactation traits (MeC_L1 and MeP_L1) showed similar patterns of correlations, with predominantly high correlations within trait and the weakest correlations between early and late lactation (as low as 0.4). However, MeP_L1 was marginally more strongly correlated between early and mid lactation. In contrast, the second-lactation traits (MeC_L2 and MeP_L2) showed differential correlation patterns along lactation weeks, with r_g for MeC_L2 being mostly high and positive (>0.8) during the entire lactation, and MeP_L2 having lower r_g between early and mid lactation for MeP_L2 (as low as 0.3). Similar genetic correlations at different lactation weeks have been reported by Manzanilla-Pech et al. (2014) and Li et al. (2018) for ECM, DMI, and BW in primiparous Holstein cows. For MeP_L2, it is not clear whether these lower correlations between mid and late lactation are related to the use of ECM in the calculation of MeP.

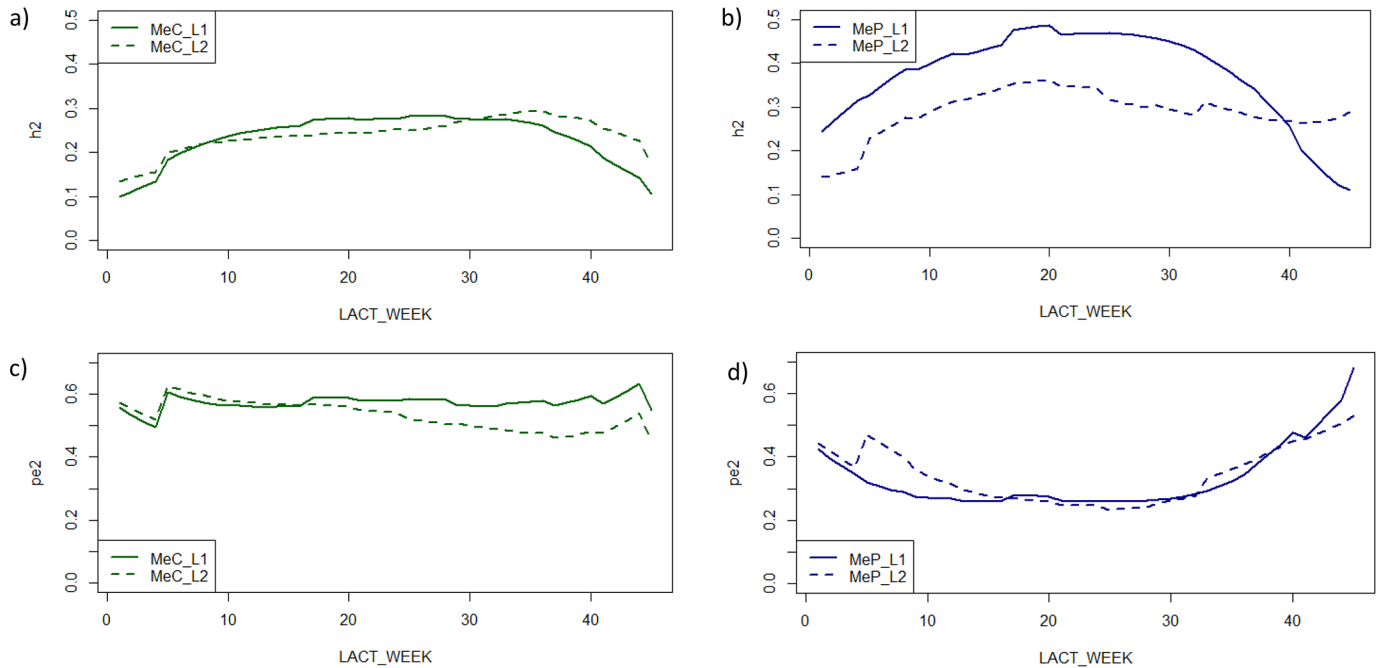


Figure 1. Estimated heritabilities (h^2) per lactation week (LACT_WEEK) for (a) methane concentration (MeC) for first lactation (MeC_L1; Q2–Q3 SE = 0.06) and MeC for second lactation (MeC_L2; Q2–Q3 SE = 0.05); (b) methane production (MeP) for first lactation (MeP_L1; Q2–Q3 SE = 0.11–0.13) and MeP for second lactation (MeP_L2; Q2–Q3 SE = 0.07–0.08); and permanent environmental ratio (pe^2) per lactation week for (c) MeC_L1 (Q2–Q3 SE = 0.02) and MeC_L2 (Q2–Q3 SE = 0.05), and (d) MeP_L1 (Q2–Q3 SE = 0.11–0.13), and MeP_L2 (Q2–Q3 SE = 0.17–0.18). Quartile (Q)2 is the median and Q3 (upper quartile) is the value under which 75% of data points are found when arranged in increasing order.

Genetic Correlation Between Traits in the Same Lactation Week

Estimated r_g at the same lactation week for the 4 traits are shown in Figure 3. All 4 pairwise r_g followed the same pattern, with moderate to high correlations (up to 0.9) during early and mid lactation, with a peak around wk 32, falling after this point until the end of the lactation (as low as 0.45). The highest r_g was for the MeP_L1–MeP_L2, which was close to 0.8 during most of the lactation, followed closely by MeC_L1–MeP_L1 and MeC_L2–MeP_L2, meaning that the highest r_g was for the same trait (MeP) across lactations (L1–L2) followed by r_g at the same lactation between traits. Finally, the lowest r_g was for MeC_L1–MeC_L2, with r_g from 0.45 at the beginning of lactation increasing steeply toward a peak at wk 32 and decreasing after this point. Standard errors (Q2–Q3) between traits at the same parity ranged between 0.11 and 0.15, whereas those for same trait at different parity were considerably larger (Q2–Q3 = 0.20–0.30). Based on these results, MeC could be genetically more stable across lactations than MeP; however, due to the large SE, we cannot draw firm conclusions. Analysis including more data and (possibly) further lactations is recommended

to verify the trends reported in this study. These results are important because it could be assumed that methane is the same trait across lactations; however, this might not be always the case, as genetic correlation varies across lactations (as we can see in MeP and MeC, where the genetic correlation between lactations is not unity). It is important to mention that we did not find additional studies that analyze methane traits across and along lactation, given the global scarcity of recording schemes for CH_4 emissions. This study is the first of its kind to estimate genetic correlations for methane traits across and between lactations. Another key finding of this study was the high genetic correlations between MeC and MeP (>0.7 for most of the lactation), showing that MeC could be used as a proxy for methane production, especially when the measuring method is a sniffer, avoiding the need to calculate MeP using ECM.

Genetic Correlations Between Methane Traits and Production, Maintenance, and Intake Traits Along First Lactation

Estimated r_g at the same lactation week between methane concentration and methane production during

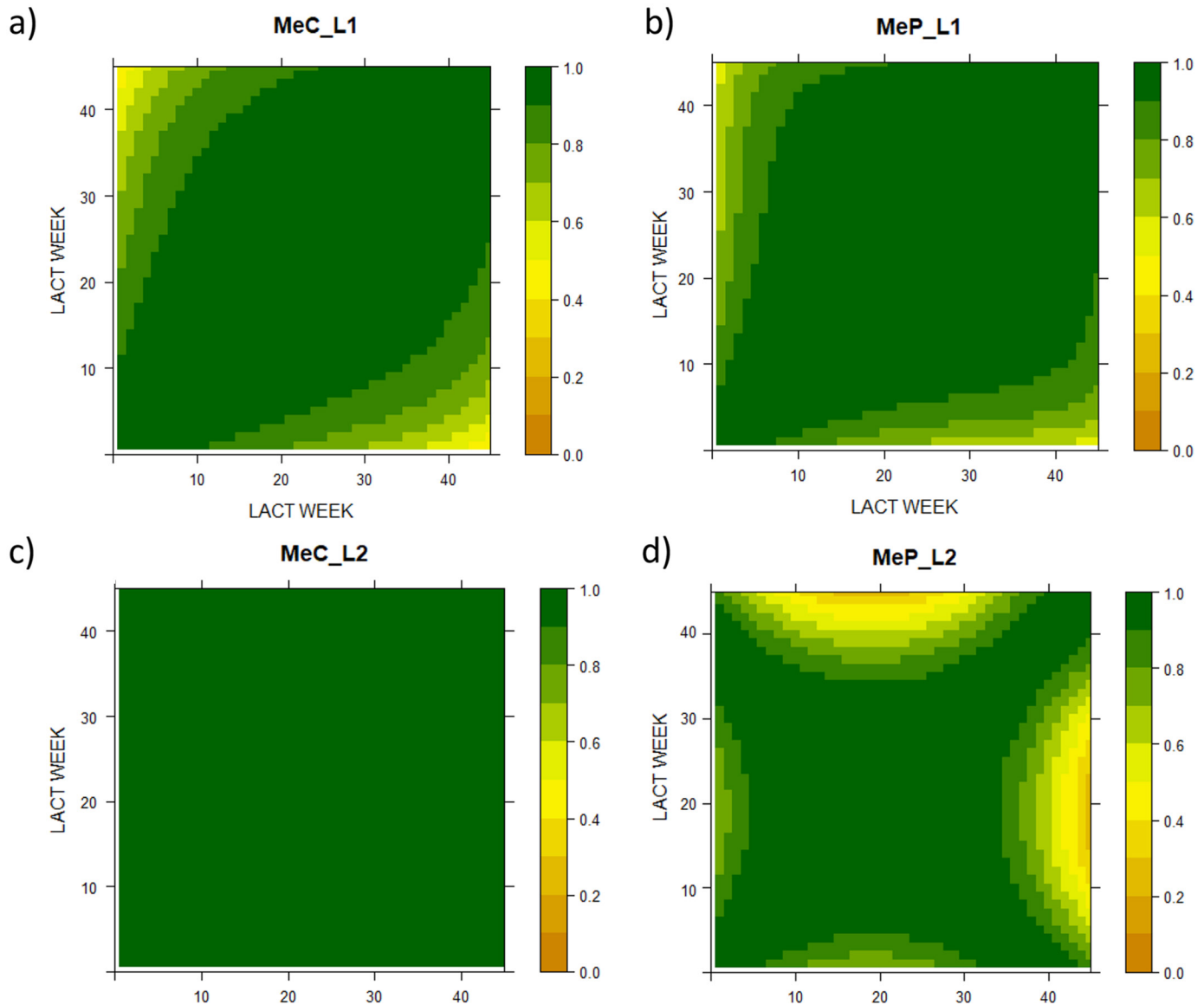


Figure 2. Estimated genetic correlations (r_g) per lactation week (LACT WEEK) for (a) methane concentration (MeC) for first lactation (MeC_L1), (b) methane production (MeP) for first lactation (MeP_L1), (c) MeC for second lactation (MeC_L2), and (d) MeP for second lactation (MeP_L2).

first lactation (MeC_L1, MeP_L1) with ECM, BW, and DMI at first lactation (ECM_L1, BW_L1, DMI_L1) are presented in Figure 4. Due to the restrictive size of the databases, SE of the r_g between MeC and MeP with ECM, BW, and DMI were large (Q2–Q3 = 0.30–0.42). Genetic correlations between MeC and ECM, BW, and DMI at first lactation were mostly positive during early and mid lactation and became negative for late lactation (after wk 30). All 3 genetic correlations following the same sigmoidal pattern throughout first lactation, with MeC_L1–DMI_L1 having the highest positive correlation (up to 0.55) and MeC_L1–BW_L1 having

the highest negative correlation (as low as -0.4). The estimated genetic correlations between MeC_L1 and ECM_L1 ranged from low–moderate positive (up to 0.44) during early and mid lactation to low–moderate negative in late lactation (as low as -0.25). Difford et al. (2020) reported moderate positive genetic correlations between MeC and ECM (0.37) and between MeC and DMI (0.60) in Danish Holstein cows using a repeatability model. Genetic correlations between MeP_L1 and ECM_L1 and DMI_L1 were moderately positive (>0.5) for most of the lactation, whereas those between MeP_L1 and BW_L1 were close to zero for

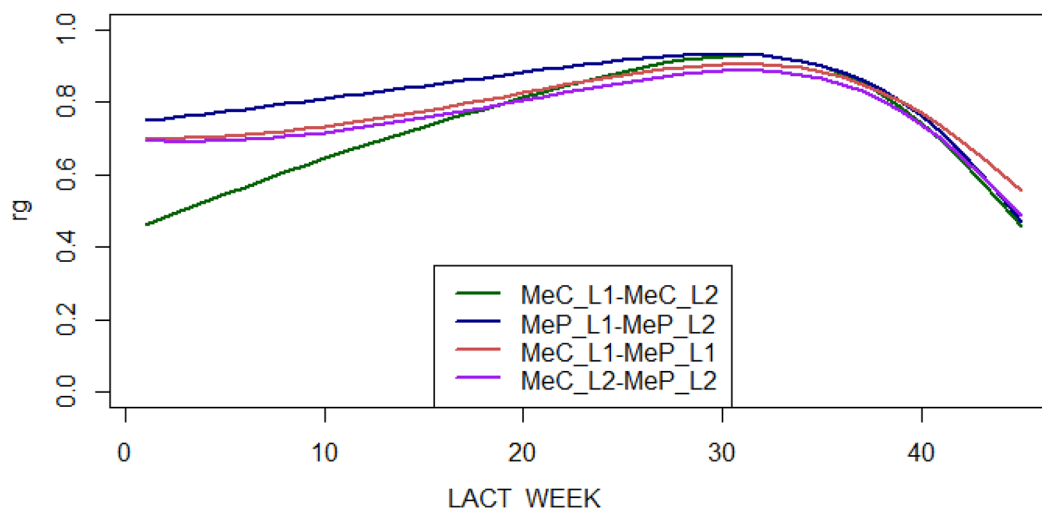


Figure 3. Estimated genetic correlations (r_g) at the same lactation week (LACT_WEEK) between methane concentration (MeC) at first lactation and MeC at second lactation (MeC_L1-MeC_L2, Q2-Q3 SE = 0.20–0.25), methane production (MeP) at first lactation and MeP at second lactation (MeP_L1-MeP_L2, Q2-Q3 SE = 0.24–0.30), MeC at first lactation and MeP at first lactation (MeC_L1-MeP_L1, Q2-Q3, SE = 0.10–0.11), and MeC at second lactation and MeP at second lactation (MeC_L2-MeP_L2, Q2-Q3 SE = 0.15). Quartile (Q)2 is the median and Q3 (upper quartile) is the value under which 75% of data points are found when arranged in increasing order.

most of the lactation, with a slight increase toward wk 30 followed by a decrease, becoming negative at the end of the lactation. Only a single study has estimated genetic correlations between methane and production and maintenance traits in Holstein cows along lactation using random regression models (Breider et al., 2019). Breider et al. (2019) presented moderate (0.38–0.57) genetic correlations between MeP and milk yield during the entire lactation, with a maximum at mid lactation (20–30 wk) in multiparous UK Holstein cows. Likewise, they reported genetic correlations between MeP and BW close to zero along the lactation. As methane is derived from fermentation of the feed, it is not surprising that the genetic correlations across lactation between MeP and DMI follow a similar pattern as the feed intake curve across lactation, with sharp increases from early to mid lactation and a steady decline toward the end of lactation (Harder et al., 2019).

Previous studies using single CH_4 phenotypes per lactation in multiparous cows have reported (using linear animal models) a wide range of genetic correlations between MeP and ECM, ranging from -0.08 to 0.74 (Breider et al., 2018; Richardson et al., 2021) in Holstein cows from the UK and Australia. However, Richardson et al. (2021) used a different method to measure CH_4 , the SF_6 tracer method previously described by Deighton et al. (2013), which could explain some of the differences in results. Furthermore, previous studies in Danish cows have reported genetic correlations between MeP and ECM from 0.45 to 0.6 (Lassen and Løvendahl, 2016; Manzanilla-Pech et al., 2020) with a popula-

tion that includes part of the population used in this study. To summarize, MeP has shown higher genetic correlations with ECM and DMI compared with MeC. These analyses were performed in an attempt to better elucidate the similarities between the studied methane traits, genetic correlations between the methane traits and with production, maintenance, and intake traits in the first lactation. As we have explained before, we incorporate ECM and BW when we transform MeC into MeP, with the aim of accounting for the size and production of the animal. However, this incorporation could lead to induced higher correlations between MeP and ECM and BW. This is particularly true for the higher correlation between MeP and ECM compared with that between MeC and ECM. However, more important is the genetic correlation of MeC with ECM and DMI, as MeC is the raw unadulterated trait and that correlation is the true genetic correlation between methane and production and intake.

Implications

One of the methods used to measure methane, given its large scale and low cost, are the sniffers installed in automated milking systems (Garnsworthy et al., 2012; Pszczola et al., 2017; Lassen and Difford, 2020; López-Paredes et al., 2020). However, the output of this method is methane concentration and, to calculate methane production (in g/d), the ratio of recorded $\text{CH}_4:\text{CO}_2$ and ECM and BW are required (Madsen et al., 2010), which evidently cause high correlations with ECM and

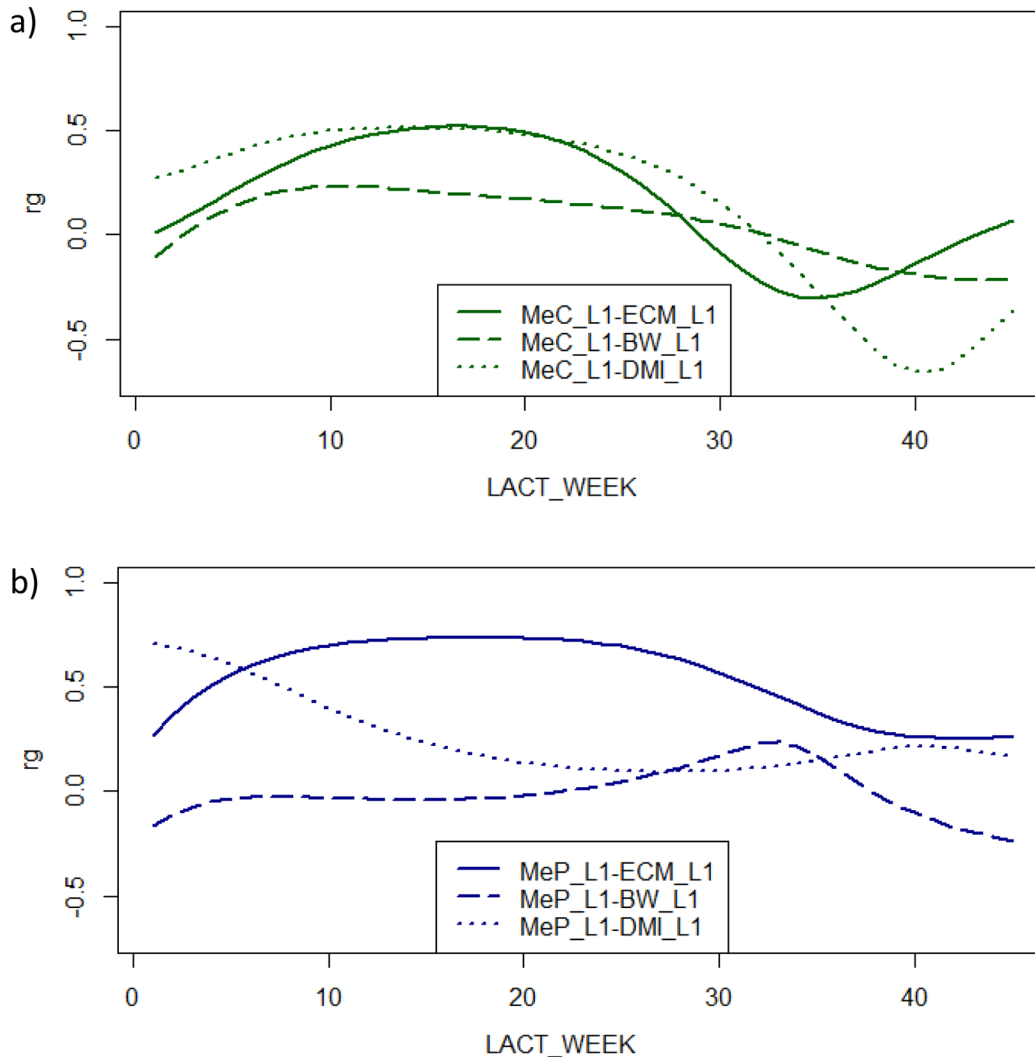


Figure 4. Estimated genetic correlations (r_g) at the same lactation week (LACT_WEEK) between (a) methane concentration at first lactation (MeC_L1) and ECM at first lactation (ECM_L1) Q2–Q3 = 0.37–0.39, BW at first lactation (BW_L1) Q2–Q3 = 0.33–0.38, and DMI at first lactation (DMI_L1) Q2–Q3 = 0.39–0.42, and between (b) methane production at first lactation (MeP_L1) with ECM_L1 Q2–Q3 = 0.30–0.33, BW_L1 Q2–Q3 = 0.29–0.30, and DMI_L1 Q2–Q3 = 0.35–0.38. Quartile (Q)2 is the median and Q3 (upper quartile) is the value under which 75% of data points are found when arranged in increasing order.

BW. For this reason, in the last couple of years, the use of methane concentration as a proxy trait for methane emissions has become more popular (Calderón-Chagoya et al., 2019; Difford et al., 2020; Manzanilla-Pech et al., 2021; Sypniewski et al., 2021). The results of this study bring to light the genetic architecture behind methane production and methane concentration and their correlations with production traits. This analysis shows the necessity of creating a phenotype independent of milk production to be able to select for methane without compromising production. One of the suggested traits is residual methane production, which could be different for first-lactation and later-lactation cows, as

it is for residual feed intake. However, given the small data sets currently available, the results are limited and should be extended for further lactations to validate this hypothesis.

CONCLUSIONS

Methane concentration traits had lower heritabilities that were more stable across lactation and between lactations than MeP traits. However, the higher heritabilities for MeP traits could be due to induced covariance from component traits such as ECM and BW, with well-documented higher heritabilities and more drastic

changes within and across lactations. Estimated genetic correlations (within trait) at different lactation weeks were similar in MeC and MeP in first lactation but different in second lactation. Most of the genetic correlations between traits (MeP and MeC) in the same lactation week were moderate to highly correlated during early and mid lactation, except between first and second parity for MeC, which were weaker than for MeP in early lactation. This suggests the possible use of MeC as a proxy for MeP without the use of ECM. Furthermore, compared with MeC, MeP (at first lactation) had stronger genetic correlations with ECM and DMI. In conclusion, both traits are different along lactation and correlate differently with production, maintenance, and intake traits, which is important to consider when including one of them in future breeding objectives. These results are useful for understanding the genetic relationship between MeC and MeP along and across lactation(s), as well as between methane traits with ECM, BW, and DMI in first lactation.

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