

Consequences of genetic selection for environmental impact traits on economically important traits in dairy cows

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Abstract. Methane (CH₄) emission is an important environmental trait in dairy cows. Breeding aiming to mitigate CH₄ emissions require the estimation of genetic correlations with other economically important traits and the prediction of their selection response. In this study, test-day CH₄ emissions were predicted from milk mid-infrared spectra of Holstein cows. Predicted CH₄ emissions (PME) and log-transformed CH₄ intensity (LMI) computed as the natural logarithm of PME divided by milk yield (MY). Genetic correlations of PME and LMI with traits used currently were approximated from correlations between estimated breeding values of sires. Values were for PME with MY 0.06, fat yield (FY) 0.09, protein yield (PY) 0.13, fertility 0.17; body condition score (BCS) -0.02; udder health (UDH) 0.22; and longevity 0.22. As expected by its definition, values were negative for LMI with production traits (MY -0.61; FY -0.15 and PY -0.40) and positive with fertility (0.36); BCS (0.20); UDH (0.08) and longevity (0.06). The genetic correlations of 33 type traits with PME ranged from -0.12 to 0.25 and for LMI ranged from -0.22 to 0.18. Without selecting PME and LMI (*status quo*) the relative genetic change through correlated responses of other traits were in PME by 2% and in LMI by -15%, but only due to the correlated response to MY. Results showed for PME that direct selection of this environmental trait would reduce milk carbon footprint but would also affect negatively fertility. Therefore, more profound changes in current indexes will be required than simply adding environmental traits as these traits also affect the expected progress of other traits.

Additional keywords: dairy cows, genetic correlation, methane intensity, predicted methane emissions, selection response.

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Introduction

The breeding goal in dairy cattle should support the profitability of milk production. Genetic correlations between milk yield (MY) and reproduction, health and fitness traits are negative, and a decline in many functional traits was reported by many studies (Egger-Danner *et al.* 2015). Accordingly reproduction, health and fitness traits have been included in breeding goal and also selection indices over the past decade. This has resulted in improvement in these traits (Egger-Danner *et al.* 2015). However, a novel class of traits will need to be considered in the future, those linked to environment concerns. There are at least two major reasons why they are not yet addressed. First direct accurate measurements of these traits on a large scale are difficult to impossible, making their use as selection index traits difficult. Second introduction of environment concerns into breeding goal is also very difficult due to the knowledge gap on how to improve them most efficiently without putting profitability into jeopardy. A major source of the environmental footprint from dairy system is methane (CH₄) emissions, which is responsible for 4% of the anthropogenic CH₄ emission (FAO 2010). The enteric fermentation in the rumen accounts for a major part of total

CH₄ emitted from dairy cows. In addition to the environmental impact, CH₄ is associated in the literature to a loss of 2–12% of gross energy intake (Johnson and Johnson 1995). Therefore, reducing the CH₄ emitted by dairy cows is of both, economic and environmental, interests. Genetic gains are cumulative and small improvements per generation can build over time. To select any new trait, it must have genetic variation and show heritability. Even with currently only limited research available, CH₄ traits predicted from milk fatty acids (Kandel *et al.* 2015) and measured through non-invasive method (Lassen and L ovendahl 2016) have shown sufficient heritability. Previous studies have shown that mid-infrared (MIR) spectroscopy can be used to predict milk fatty acids (Soyeurt *et al.* 2011) and that milk fatty acids are indirectly related to CH₄ emission (Chilliard *et al.* 2009; Dijkstra *et al.* 2011). Also, the heritability of MIR milk fatty acids predicted CH₄ emission was estimated between 0.21 and 0.40 (Kandel *et al.* 2015). Moreover, direct prediction of CH₄ from MIR spectra without the use of milk fatty acids would be a step forward because by avoiding intermediate steps, prediction errors could be minimised (Gengler *et al.* 2016). Dehareng *et al.* (2012) and Vanlierde *et al.* (2015, 2016) demonstrated that quantification of

CH₄ emission directly by MIR spectroscopy from milk samples was feasible and can be useful to generate a large number of indirect CH₄ phenotypes. Vanlierde *et al.* (2015) supported by results from Vanrobays *et al.* (2016) showed that links between CH₄ and milk composition are lactation stage specific.

Genetic selection of CH₄ emission traits predicted from MIR spectra of milk samples can be imagined because recent research demonstrated genetic variance and sufficient heritability (Kandel *et al.* 2017). However, the addition of environmental impact traits into the selection goal needs the careful consideration of its impact on other traits in this goal. Before adding any novel traits, additional information about genetic correlations with other objective traits that are already in place and their predicted response are needed. Amongst the correlations needed are those with milk production traits, with functional traits like fertility and with health traits. Udder health (UDH) was represented by somatic cell score (SCS) on a reversed scale. Even if they are not in the breeding objective, correlations to type and body condition scores (BCS), will allow assessing the impact on these traits too.

Therefore, the objective of this study was 2-fold, first to estimate the genetic correlations between environmental impact traits and other traits of interest, and second to quantify their predicted selection response in simple scenarios.

Materials and methods

Genetic valuation of environmental impact traits

Currently no routine genetic evaluation exists in the Walloon region of Belgium for environmental impact traits linked to CH₄ emissions. However, in order to approximate genetic correlations among traits, preliminary evaluations were necessary.

Milk samples and prediction of environmental traits

Milk samples were collected from Holstein cows in their first three lactations from January 2010 and March 2014 as routine Walloon milk recording. All milk samples were analysed using a Milkoscan FT6000 spectrometer (Foss, Hillerød, Denmark) by the milk laboratory 'Comité du Lait' (Battice, Belgium) to quantify the contents of fat and protein and to record the spectral data. Production records ranged between 5 and 365 days in milk (DIM). Official International Committee of Animal Recording (ICAR) norms were applied. Therefore, observations outside of ranges of 3–99 kg MY, 1–7% protein content and 1.5–9% fat content were not used for the calculations as suggested in these norms (ICAR 2016).

The CH₄ emission (PME; g/day) was predicted from the recorded and standardised (Grelet *et al.* 2015) milk MIR spectral database of Walloon milk recording using the equation developed by Vanlierde *et al.* (2015). The predicted CH₄ intensity (PMI; g/kg of milk) was defined as the ratio of PME divided by the total milk MY recorded for the considered test-day. The distribution of PMI was non-normal and skewed therefore (Fig. 1) presenting a log-normal aspect. Therefore, PMI was log-transformed and called log-transformed CH₄ intensity (LMI) using the natural logarithm. The datasets of predicted environmental traits had 700 505 test-day records from 58 412 first three parity cows sired by 2455 bulls. The heritabilities of PME and LMI were estimated to be 0.25 and 0.18 respectively

(Kandel *et al.* 2017). Within cow, if parity 3 was present, parities 1 and 2 had to be present, and if parity 2 was present, parity 1 had to be present. Animals which had, based on their pedigree, at least 75% of confirm Holstein genetics in their breed composition were kept for this study. Pedigree data were extracted from pedigree used for routine Walloon genetic evaluation and contained 119 068 animals born after 1990, which permitted pedigree up to three generations back.

Model

A single trait multiple lactation random regression test-day model was used to estimate the genetic parameters and breeding values of each of PME and LMI. The model can be presented as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Q}(\mathbf{H}\mathbf{h} + \mathbf{Z}\mathbf{p} + \mathbf{Z}\mathbf{u}) + \mathbf{e}$$

where \mathbf{y} was the vector of observations for each trait (PME or LMI), $\boldsymbol{\beta}$ was the vector of fixed effects (herd \times test-day, days in milk (24 classes of 15 days' interval), and age at calving (9 classes: 21–28 months, 29 to 32 months, and 33 months and more for first lactation; 31–44 months, 44–48 months, and 49 months and more for second lactation and 41–57 months, 57–60 months, and 60 months and more for third lactation), \mathbf{h} was the vector of random within-herd lactation curve effects, \mathbf{p} was the vector of permanent environmental (PE) random effects, \mathbf{u} was the vector of additive genetic effects; \mathbf{Q} was the matrix containing the coefficients of 2nd order Legendre polynomial regressors; \mathbf{e} was the vector of residuals; \mathbf{X} was an incidence matrix assigning observations to levels of fixed effects., \mathbf{H} and \mathbf{Z} were incidence matrices assigning regressors to random regression coefficients.

Variance components and solutions of mixed model equations

The variance components were estimated by Bayesian method with Gibbs sampling. Priors of variance components were estimated using univariate models using the average information REML. Posterior means of (co)variance components were calculated using 90 000 samples after a burn-in of 10 000 samples. The estimated breeding values (EBV) were calculated using a BLUP approach using obtained variance components.

Economically important traits

The Walloon Breeding Association (Ciney, Belgium) uses for Holstein dairy cows a selection index called V€G (Vanderick *et al.* 2015). Table 1 gives the relative importance of the different traits used in the current index. This index was obtained to select for a breeding goal that was derived based on a lifetime economic function including production and functional traits (N. Gengler, pers. comm.). The three categories of traits under routine genetic evaluation in Wallonia and included in the selection index are production, functional traits and type traits. The later were not considered having an economic value on their own, but contributing to the traits in the breeding goal (N. Gengler, pers. comm.). Production traits included MY, fat yield (FY) and protein yield (PY), functional traits were UDH and longevity and more recently fertility and calving traits. These traits were (a) combined female fertility (CFF), (b) direct calving

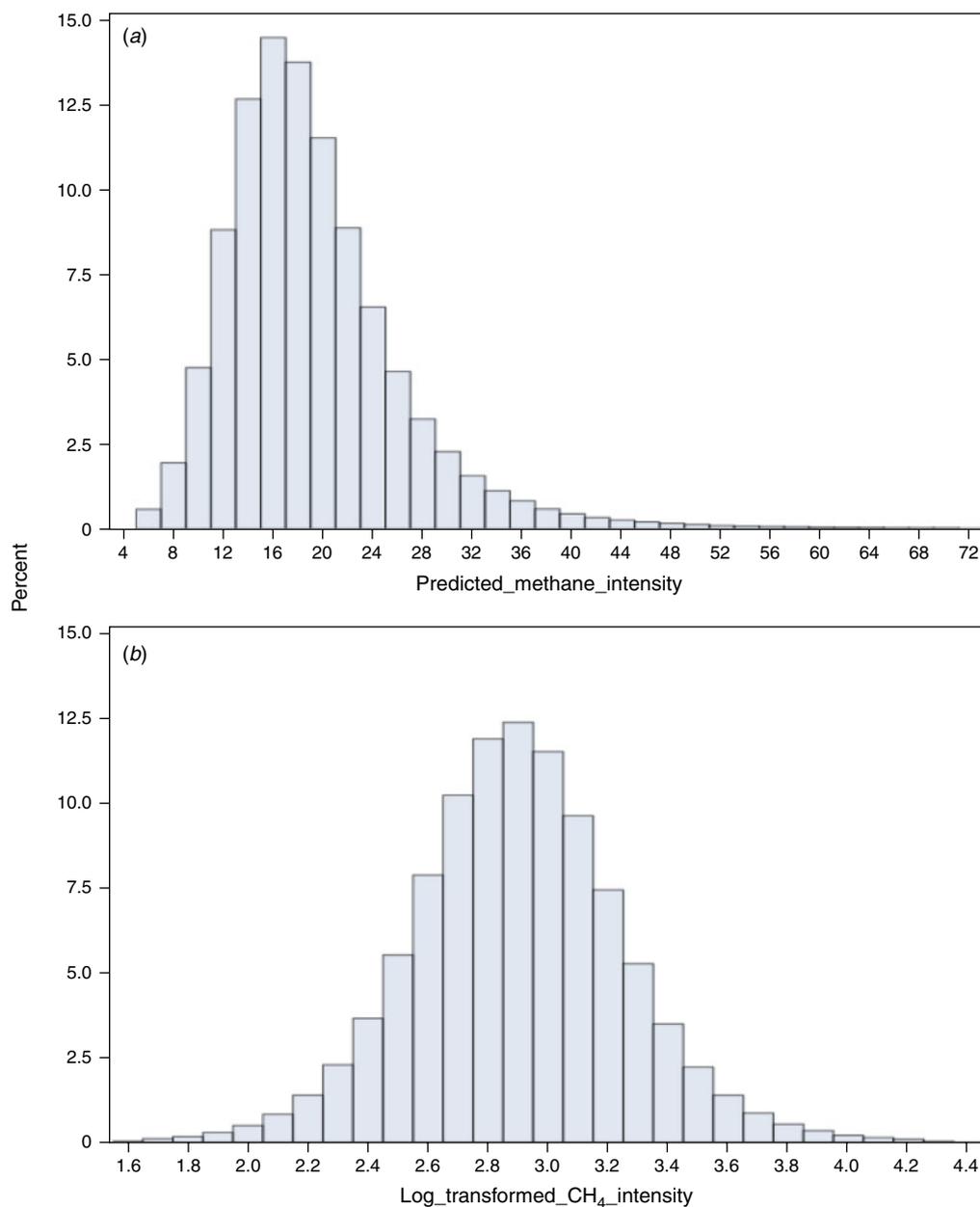


Fig. 1. Frequency distribution of 700 505 records of (a) predicted methane intensity (g/kg of milk) and (b) log-transformed methane intensity for 58 412 Holstein cows.

ease (DCE) and (c) maternal calving ease (MCE). The genetic correlations were calculated for all fertility-related traits however response to selection was only calculated for combined female fertility. CFF representing pregnancy rate and higher values are better. Direct calving ease and maternal calving ease were just recently added in selection index; therefore, the responses were not calculated in this study however genetic correlations were calculated. The trait BCS is currently used in computations of EBV for combined fertility and not directly in the index or even breeding goal. However, there are indications (e.g. Vanrobays *et al.* 2016) that CH_4 production through its links to fatty acids and intake interacts with body fat mobilisation. Effects of selection on

CH_4 were also computed for BCS, an indicator of body fat mobilisation and, indirectly, an important element for a long-term effect on fertility. Longevity was also calculated from direct longevity trait plus genetically correlated type traits. In addition to production and functional traits, a total of 33 type traits (recorded and derived) are also part of Walloon animal genetic evaluation system. Type traits were broadly classified as body capacity, udder and feet and leg traits. Details of all these traits definitions, their genetic model for parameter estimations are described in Vanderick *et al.* (2015) and Croquet *et al.* (2006). The EBV of sires for production, functional and type traits were extracted from the database containing the EBV computed for the official

Table 1. Current Walloon selection index V€G for dairy cows (Scenario I) and selection scenarios for environmental traits (II-V)
V€M, feet and leg economic index; V€C, capacity economic index; V€P, udder economic index; PME, predicted methane emission (g/day); LMI, log-transformed methane intensity

Sub-index	2nd order sub-index	Traits	Weight	Selection scenarios				
				I (= V€G)	II	III	IV	V
Production (V€L)	–		48	48	45.60	42	36	24
	–	Milk (kg)	–	10	9.50	8.75	7.50	5
	–	Fat (kg)	–	9	8.55	7.87	6.75	4.50
Functional (V€F)	–	Protein (kg)	–	29	27.55	25.37	21.75	14.50
	–		28	28	26.60	24.5	21	14
	–	Udder health	–	3.36	3.19	2.94	2.52	1.68
	–	Longevity	–	20.72	19.68	18.13	15.54	10.36
	–	Total fertility	–	1.96	1.86	1.71	1.47	0.98
Type (V€T)	–	Direct calving ease	–	0.84	0.79	0.73	0.63	0.42
	–	Maternal calving ease	–	1.12	1.06	0.98	0.84	0.56
	–		24	24	22.8	21	18	12
	V€M	Rear leg set	–	1.40	1.33	1.22	1.05	0.70
	–	Rear leg rear view	–	0.70	0.66	0.61	0.52	0.35
	–	Bone quality	–	3.70	3.51	3.23	2.77	1.85
	–	Feet and legs	–	3.20	3.04	2.80	2.4	1.60
	V€C	Overall development	–	0.30	0.28	0.26	0.22	0.15
	–	Final conformation	–	0.50	0.47	0.43	0.37	0.25
	–	Overall udder	–	0.20	0.19	0.17	0.15	0.10
V€P	Fore udder	–	2.00	1.90	1.75	1.50	1	
–	Rear udder height	–	3.20	3.04	2.80	2.40	1.60	
–	Udder support	–	1.30	1.23	1.13	0.97	0.65	
–	Udder depth	–	3.20	3.04	2.80	2.40	1.60	
–	Front teat placement	–	0.50	0.47	0.43	0.37	0.25	
–	Rear teat placement	–	2.50	2.37	2.18	1.87	1.25	
–	Teat length	–	1.30	1.23	1.13	0.97	0.65	
Environment		PME or LMI	–	–	5	12.50	25	50
Total (V€G)				100	100	100	100	100

Walloon genetic evaluation 2016 March run. These EBV were of domestic, but more often of Multiple Across Country Evaluation (MACE) origin, provided by the INTERBULL Center (Uppsala, Sweden).

Approximated genetic correlations

Very few genetic evaluation systems are completely multivariate across all the index traits. An implication of this is also that genetic correlations amongst these traits are not known. In order to achieve the objective of this study approximated values were needed. Pearson's correlations among EBV of sires were computed in order to get lower-bound estimates of genetic correlations. The productive life of higher yielding cows goes over 2.5 to 3.2 parities before being culled (e.g. Hare *et al.* 2006). As life (3 parities) genetic correlations and selection response is easy to understand and interpret, therefore in this study we studied all traits cumulated over life time (at least 3 parities). A total of 2455 bulls had daughters with environmental records and subsequently EBV. These EBV were centred and expressed as average daily values but based on cumulative 305-day emissions over the three lactations (Table 2). For this 2455 sires the corresponding sire EBV for current official genetic evaluations were selected when they showed sufficient reliability (limits depending upon the traits: 50–99% for production traits and 25–99% for functional and type traits). Table 2 gives the figures of selected bulls ranging from 1369 to 1427 for

production and functional traits. The equivalent figure was 1422 sires for type traits.

Selection scenarios and predicted responses

Five selection scenarios were proposed to calculate the selection response. Scenario I was the current Walloon selection index V€G (*status quo*), and from second to fifth selection scenarios were 5%, 12.5% and 25% and 50% addition of CH₄ emission traits (PME respectively LMI) and proportional reduction on other traits present in current index (Table 1). The weight of CH₄ traits were put negative because we were interested to reduce the CH₄ emission from our dairy production. Relative genetic changes for each trait from selection based on these alternative total indexes were estimated as $\mathbf{r} = \mathbf{b}'\mathbf{G}$ where \mathbf{r} = vector of relative genetic gain on all traits; and \mathbf{b} = vector of proportional index weights; \mathbf{G} = matrix of genetic correlations between index traits and goal traits. As only relative changes were relevant for this study, selection intensity was set to 1 and response was calculated for one generation.

Results

Environmental traits and economic important traits descriptions

The average \pm s.d. PME was 443.86 ± 77.04 (g/day) and LMI was 2.87 ± 0.36 for first three lactations. The sire EBV of

Table 2. Sire estimated breeding values (EBV) of environmental impact, production and functional traits in the Walloon Holstein dairy population used in this study, all traits except environmental traits are from official genetic evaluation of March 2016 (domestic and MACE EBV)

Estimated breeding values for predicted methane emission (PME) and log-transformed methane intensity (LMI) were computed in this study. PME and LMI were centred for the 2455 sires, all other traits expressed in their original scales

Traits	Sires	Mean	s.d.	Minimum	Maximum	Average reliability
PME (g/day)	2455	0.00	9.57	-31.80	33.67	-
LMI	2455	0.00	0.46	-2.17	2.04	-
Milk yield (kg/lactation)	1427	331.97	492.74	-1988	1995	86
Fat yield (kg/lactation)	1427	11.99	19.43	-50	77	86
Protein Yield (kg/lactation)	1427	9.92	15.30	-58	56	86
Combined female fertility (mean = 100, s.d. = 10)	1425	97.94	10.20	65	141	81
Direct calving ease (mean = 100, s.d. = 10)	1406	93.42	15.29	34	144	67
Maternal calving ease (mean = 100, s.d. = 10)	1369	96.55	15.19	41	150	61
Body condition score (mean = 0; s.d. = 1)	1392	-0.27	0.91	-2.94	3.49	71
Udder health (mean = 100, s.d. = 10)	1426	96.19	13.24	48	134	91
Longevity (mean = 100, s.d. = 10)	1425	93.41	17.45	29	147	78

CH₄ emissions traits that had daughters in production were accumulated over three parities, expressed on a daily basis and presented in Table 2. Similarly the corresponding sire EBV obtained from official Walloon genetic evaluation for production (MY, FY and PY) and functional traits (Fertility, BCS, UDH and longevity) were also presented in Table 2. Average reliabilities of selected groups ranged between 61 (for maternal calving ease) and 91 (for UDH). The selected sire EBV for type traits are presented in Table 3 with average reliabilities between 74 and 91.

Genetic correlations between environmental traits and economic important traits

The approximate genetic correlations based on correlation between sire EBV, hereafter called for simplicity genetic correlation, between PME and LMI and production and functional traits are presented in Table 4. The genetic correlation between PME and LMI was estimated 0.33. PME had small positive genetic correlations with milk production traits i.e. 0.06 with MY, 0.09 with FY and 0.13 with PY. However, the genetic correlations between LMI and milk production traits were negative and in case with MY was highly negative (-0.61) and moderate negative with PY (-0.40) and low negative (-0.15) with FY. The genetic correlation of combined female fertility with both CH₄ traits was positive but higher in case of LMI (0.36 vs 0.17). Other reproductive traits (DCE and MCE) also had positive genetic correlation with PME however negative correlation were observed between LMI and MCE. The correlation between PME and BCS was very close to zero but 0.20 between LMI and BCS. UDH had positive genetic correlation with both CH₄ traits. Finally, longevity had positive genetic correlation with both CH₄ traits (Table 4).

The genetic correlations between CH₄ traits and type traits are reported in Table 3. The genetic correlation between PME and 33 type traits ranged from -0.12 to 0.25 and between LMI and 33 type traits ranged from -0.22 to 0.18. The body capacity traits also had in general positive genetic correlations with PME and negative genetic correlations with LMI. The bodyweight related traits like stature and angularity had positive genetic correlations with PME and negative genetic correlations with LMI. The udder capacity traits also had in general

positive genetic correlation with PME and negative genetic correlations with LMI.

Expected genetic changes under selection scenarios

The selection response to each scenario of selecting PME is reported in Table 5. The PME would be increased by 2% without selecting this trait but through correlated responses of other traits. A relative weight of 12.5% on PME (selection scenario III) was necessary to decrease PME. A relative weight of 25% of PME (selection scenario IV) generated a response of PME by -6%, MY by 15%, FY by 6%, PY by 11%, fertility by -4%, BCS by -11%, UDH by -13% and longevity by 22%. In all scenarios MY, FY and PY also increased except with the extreme selection scenario V (50% weight on PME), which decreased FY and PY. In all PME reduction scenarios, fertility, BCS and UDH would decrease. Given that the longevity has currently a very high weight in Walloon index (~21%) longevity has a very positive response in selection scenario I, however the progress would be reduced with each scenario selecting for lower PME.

The favourable genetic gain would be achieved for LMI in all selection scenarios (Table 6). The expected response of LMI would range from -15% to -33% from selection scenario I to selection scenario V. MY, FY and PY would increase in each scenario. For example by the addition of 25% of LMI, the resulting response would be for LMI by -24%, MY by 29%, FY by 16%, PY by 28%, fertility by -10%, BCS by -13%, UDH by -13% and longevity by 23%.

Discussion

The final objective of this study was to assess the response of selection for environmental traits by selecting them directly as well as the correlated responses of other economic important traits. Similarly, the motivation was also to improve the understanding of the genetic influence and their correlations on CH₄ emission by dairy cows. Currently, there is no direct economic incentive for a dairy producer to develop a program which reduces CH₄ emissions. Given that increasing significance of climate change, in national agendas but also for the dairy industry, environmental traits would need to be included in dairy cattle breeding. Similarly, societal demands are changing from

Table 3. Sire estimated relative breeding values (RBV) of type traits (mean = 0; s.d. = 1) in the Walloon Holstein dairy population for the genetic evaluations of March 2016 (domestic and MACE RBV) used and their genetic correlations with environmental impact traits (PME and LMI)
PME, predicted methane emissions (g/day); LMI, log-transformed methane intensity

Traits	Mean	s.d.	Minimum	Maximum	Average reliability	Genetic correlations	
						PME	LMI
Stature	0.18	0.96	-3.11	3.22	90	0.15	-0.06
Chest width	0.12	1.34	-4.42	4.52	82	0.01	-0.11
Body depth	0.16	1.15	-3.98	4.40	86	0.00	-0.10
Chest depth	0.14	1.14	-3.85	3.65	86	0.04	-0.12
Loin strength	-0.03	1.08	-3.93	3.72	87	0.00	-0.01
Rump length	0.21	1.13	-3.61	4.02	89	0.17	-0.07
Rump angle	-0.14	1.42	-5.75	5.28	91	0.01	-0.09
Hips width	0.17	1.08	-3.50	3.74	89	0.03	-0.16
Rump width	0.10	1.29	-4.81	4.85	89	-0.01	-0.10
Foot angle	0.14	1.45	-4.47	4.79	75	0.06	-0.04
Rear leg set	0.08	1.38	-3.92	5.04	87	0.00	0.05
Bone quality	0.13	1.03	-3.40	3.34	87	0.10	0.10
Rear leg rear view	-0.04	1.55	-5.12	5.64	81	0.04	-0.03
Udder balance	0.13	1.01	-3.99	3.05	89	0.06	-0.08
Udder depth	0.09	1.29	-4.16	4.47	91	0.25	0.18
Teat placement side	0.06	1.17	-4.18	3.67	85	-0.09	-0.02
Udder support	0.28	1.23	-4.61	3.91	79	0.02	-0.13
Udder texture	0.23	0.99	-3.29	3.37	84	0.07	-0.13
Fore udder	0.14	1.25	-4.25	3.30	80	0.11	0.07
Front teat placement	0.17	1.23	-3.72	4.03	90	0.07	-0.11
Teat length	-0.01	1.30	-5.39	4.97	92	-0.12	-0.13
Rear udder height	0.21	1.12	-3.85	3.79	83	0.13	-0.13
Rear udder width	0.16	0.91	-3.38	2.91	86	0.02	-0.22
Rear teat placement	0.29	1.21	-3.99	4.03	90	0.02	-0.12
Angularity	0.19	0.90	-3.21	3.11	76	0.12	-0.11
Overall development	0.14	1.24	-4.19	4.05	87	0.09	-0.10
Overall rump	0.03	1.29	-4.23	4.85	86	0.01	-0.17
Overall feet and leg score	0.10	1.24	-4.73	4.03	75	0.07	-0.03
Overall udder score	0.18	1.00	-3.59	3.39	78	0.16	0.02
Overall fore udder	0.20	1.16	-4.33	3.56	85	0.17	0.06
Overall rear udder	0.10	1.09	-4.11	3.30	85	0.13	-0.05
Overall dairy trait	0.13	0.95	-3.51	3.07	83	0.12	-0.09
Overall conformation score	0.19	0.89	-3.29	2.89	74	0.15	-0.06

Table 4. Genetic correlation between environmental traits with production and functional traits of selection of dairy cows
LMI, log-transformed methane intensity

Traits	Predicted methane emission	Log-transformed methane intensity
LMI	0.33	/
Milk yield	0.06	-0.61
Fat yield	0.09	-0.15
Protein yield	0.13	-0.40
Fertility	0.17	0.36
Direct calving ease	0.37	0.00
Maternal calving ease	0.15	-0.11
Body condition score	-0.02	0.20
Udder health	0.22	0.08
Longevity	0.22	0.06

both environmental and economic perspectives and CH₄ emission traits could be added in the breeding goals defined for dairy cows in the near future (Hayes *et al.* 2013).

All of genetic correlations between production, functional and type traits and CH₄ emissions traits were revolving around the efficiency and inefficiency of animal from intake, digestion, production, reproduction and survival. Dairy cows seem to partition first energy for production, then for reproduction and finally for survival. More efficient dairy cows will produce more milk relative to the amount of feed ingested and less energy lost as CH₄. All production traits had small positive correlations with PME and high negative correlations with LMI, as was expected given its definition. The very negligible positive genetic correlation of PME with production traits suggested that these traits are not able to predict CH₄ emissions alone in dairy cows on a genetic level. Similarly, positive genetic correlations observed between PME and fat and protein corrected MY (0.07 ± 0.09) (Lassen and Løvendahl 2016) was similar to this study (0.06 with MY). There is ongoing debate on those figures because they appear low, but one should not forget that even if PME is also driven by intake it is also strongly related to energy lost or energy efficiency, a different mechanism *a priori* not (strongly) linked to intake. On a phenotypical level our recent research (P. Kandel, unpubl. data) showed that with increasing MY, the correlation

Table 5. Selection responses (percentage of change) of environmental, production and functional traits to PME selection scenarios

PME, predicted methane emissions; MY, milk yield; FY, fat yield; PY, protein yield; Fertility, Combined female fertility; BCS, body condition score; UDH, udder health (somatic cell score); Selection scenario 1 = current Walloon dairy cattle index (V€G), from second to fifth selection scenarios were addition of PME by 5%, 12.5%, 25% and 50% and proportional decrease on other traits respectively

Selection Scenario	PME	MY	FY	PY	Fertility	BCS	UDH	Longevity
I	1.94	16.68	17.25	22.25	-3.33	-7.97	-15.94	27.83
II	0.36	16.35	14.95	20.07	-3.44	-8.57	-15.36	26.73
III	-2.01	15.85	11.49	16.80	-3.61	-9.46	-14.48	25.09
IV	-5.95	15.02	5.73	11.35	-3.88	-10.95	-13.03	22.35
V	-13.84	13.35	-5.80	0.46	-4.44	-13.92	-10.12	16.86

Table 6. Selection responses (percentage of change) of environmental, production and functional traits to LMI selection scenarios

LMI, log-transformed methane intensity; MY, milk yield; FY, fat yield; PY, protein yield; Fertility, Combined female fertility; BCS, body condition score; UDH, udder health (somatic cell score); Selection scenario 1 = current Walloon dairy cattle selection program, from second to fifth selection scenarios were addition of PME by 5%, 12.5%, 25% and 50% and proportional decrease on other traits respectively

Selection scenario	LMI	MY	FY	PY	Fertility	BCS	UDH	Longevity
I	-14.51	16.68	17.25	22.25	-3.33	-7.97	-15.94	27.83
II	-16.38	19.24	17.06	23.48	-4.70	-8.94	-15.26	26.79
III	-19.19	23.07	16.78	25.33	-6.77	-10.40	-14.23	25.23
IV	-23.85	29.45	16.29	28.40	-10.20	-12.82	-12.53	22.63
V	-33.19	42.21	15.33	34.56	-17.08	-17.66	-9.12	17.43

with PME is decreasing and eventually inverting as always higher producing animals produce more and more from body reserve mobilisation than intake. In beef cattle, using small preliminary analysis using genomic selection, response to selection of CH₄ yield (CH₄/kg dry matter intake) was estimated to be reduction by 4% in 10 years (Hayes *et al.* 2016). In dairy cows, using prediction from feed intake, PME would at least theoretically decrease in the order of 11–26% in 10 years (de Haas *et al.* 2011). However, those predictions were totally different than prediction used in this study as they assumed that the major driving factor behind PME were only intake driven, therefore, direct comparison was difficult.

The reduction of LMI by 15% through the current Walloon selection index was similar to results obtained by Bell *et al.* (2011). These authors demonstrated that genetic selection for energy-corrected milk reduced CH₄/energy-corrected milk, (which is similar to LMI) by 15% for the first three lactations until mature size and maximum MY are achieved. Moreover, increasing selection pressure for reduced LMI gives a strong positive reaction of MY and associated traits. Therefore, as expected from these results, the functional traits would have negative to strongly negative correlated response. Fertility and BCS would be mostly affected but also longevity.

The genetic correlation between environmental traits and fertility could indicate that more resource inefficient cows show better female fertility and therefore simultaneous selection for both traits might be difficult. However, a breeding strategy emphasising female fertility traits would improve cow fertility and reduce within-herd replacement rates and consequently reduced replacements contribute to decreasing CH₄ emissions in herd level (Knapp *et al.* 2014) but the relationship in individual level is not known yet.

The BCS would decrease in all scenarios of selection on either PME or LMI. The substantial genetic correlation between BCS and LMI reduced BCS and positive genetic correlation between BCS and fertility (Bastin *et al.* 2012) had led to reduction in both traits. It is also well known that the early lactation period is characterised by body fat mobilisation, negative energy balance (van Knegsel *et al.* 2007), which is also related to CH₄ emissions, so test-day genetic correlations are more important than average of whole lactations.

The fact that longevity had also positive genetic correlations with emissions could indicate that the higher CH₄-producing cows might be more efficient in survival. However, like for improved fertility, by promoting longevity emissions from replacement would be diluted. In addition their effect in individual level of emission is unresolved (Grandl *et al.* 2016).

In sheep, it was demonstrated that smaller body confirmation animals had smaller rumen and shorter duration of ruminal passage, which leads to less CH₄ (Goopy *et al.* 2014). In this study, almost all capacity and body size-related traits like stature, chest width, rump length and angularity had positive genetic correlations with PME, which suggested increased body capacity and bodyweight increased also PME. However, the body capacity type traits had negative genetic correlations with LMI, suggesting that selection for LMI would preserve these traits.

Even without selection on LMI the reduction in CH₄ intensity was already substantial due to the negative correlation with production traits. The speed of reduction would be faster if we add this new trait to the selection index, however the decrease in fertility would be substantial unless fertility traits were also added or their weight increased in the selection index.

This study has some limitations. First, the analyses were only based on correlations of sire EBV. A more direct method would be

to estimate genetic correlations from the data using appropriate, e.g. bivariate, models. However, such approach would have required variance components estimation for a great number of bivariate models including complicated, e.g. random regression, models. Therefore, for this study, approximations were used and as presented by Calo *et al.* (1973), correlations between breeding values do not fully reflect the genetic relationships between two traits and they might underestimate them. Second, a better approach to create a selection index would be to put appropriate economic weights to environmental traits instead of adding a linear percentage in selection scenarios. However, even if there is an economic value of CH₄ emission in the industrial sector, this is not yet the case in agriculture. An alternative strategy would be to optimise expected gains, developing weights retrospectively. Third, the responses presented in Tables 5 and 6 assume that all breeding values for all traits have equal reliability. That might not be the case at the moment of selection. It is therefore somewhat idealised scenarios but in practice accuracy will differ due to heritability and different recording (e.g. longevity and fertility). However, this study showed practical significance of current selection and its effect on PME and LMI where PME is increasing but CH₄ intensity decreasing.

Conclusions

This study presented novel results. First, under the hypothesis to continue using the current Walloon index, without directly selection for environmental traits, PME would be increased but LMI would be decreased through correlated responses to the selection for correlated traits. This is the expected result that gains are currently only achieved per unit produced. Second, by giving direct selection pressure on environmental traits, they would respond to selection, but would also change fundamentally the responses in other traits. These responses were quantified in various scenarios. One of the scenarios –reducing all traits weight by 25% of current index and addition of 25% of PME would reduce gains in FY and PY and almost all functional traits (fertility, BCS, and longevity) would need to be protected. The addition of 25% of LMI would shift the emphasis on production traits, especially MY, and affect even stronger functional traits. In conclusion, direct selection of environmental traits would reduce milk carbon foot print but more profound changes in current indexes will be required than simply adding environmental traits, as adding these traits to the selection index would affect the equilibrium between the other traits.

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