Genetic parameters for cheese-making properties and milk composition predicted from mid-infrared spectra in a large data set of Montbéliarde cows

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ABSTRACT

Cheese-making properties of pressed cooked cheeses (PCC) and soft cheeses (SC) were predicted from mid-infrared (MIR) spectra. The traits that were best predicted by MIR spectra (as determined by comparison with reference measurements) were 3 measures of laboratory cheese yield, 5 coagulation traits, and 1 acidification trait for PCC (initial pH; pH₀ PPC). Coefficients of determination of these traits ranged between 0.54 and 0.89. These 9 traits as well as milk composition traits (fatty acid, protein, mineral, lactose, and citrate content) were then predicted from 1,100,238 MIR spectra from 126,873 primiparous Montbéliarde cows. Using this data set, we estimated the corresponding genetic parameters of these traits by REML procedures. A univariate or bivariate repeatability animal model was used that included the fixed effects of herd × test day × spectrometer, stage of lactation, and year × month of calving as well as the random additive genetic, permanent environmental, and residual effects. Heritability estimates varied between 0.37 and 0.48 for the 9 cheese-making property traits analyzed. Coagulation traits were the ones with the highest heritability (0.42 to 0.48), whereas cheese yields and pH₀ PPC had the lowest heritability (0.37 to 0.39). Strong favorable genetic correlations, with absolute values between 0.64 and 0.97, were found between different measures of cheese yield, between coagulation traits, between cheese yields and coagulation traits, and between coagulation traits measured for PCC and SC. In contrast, the genetic correlations between milk pH₀ PPC and CY or coagulation traits were weak (−0.08 to 0.09). The genetic relationships between cheese-making property traits and

milk composition were moderate to high. In particular, high levels of proteins, fatty acids, Ca, P, and Mg in milk were associated with better cheese yields and improved coagulation. Proteins in milk were strongly genetically correlated with coagulation traits and, to a lesser extent, with cheese yields, whereas fatty acids in milk were more genetically correlated with cheese yields than with coagulation traits. This study, carried out on a large scale in Montbéliarde cows, shows that MIR predictions of cheese yields and milk coagulation properties are sufficiently accurate to be used for genetic analyses. Cheese-making traits, as predicted from MIR spectra, are moderately heritable and could be integrated into breeding objectives without additional phenotyping cost, thus creating an opportunity for efficient improvement via selection.

Key words: Montbéliarde, cheese-making property, mid-infrared spectrometry, genetic parameter

INTRODUCTION

More than 36% of total cow milk is processed into cheese products (International Dairy Federation, 2016), and this proportion has increased by 23% during the last decade. The milk processing industry thus stands to gain a great deal economically from the improvement of milk cheese-making properties (**CMP**). To assess CMP, different laboratory methods have been developed (reviewed in Bittante et al., 2012), but they are costly and time consuming and thus difficult to implement on a large scale. Mid-infrared (**MIR**) spectrometry has been proposed as an alternative method for prediction of various milk characteristics, including fractions of proteins, fatty acids, or minerals as well as cheese yield or coagulation properties (De Marchi et al., 2014). Mid-infrared technology is cheap and routinely used. Consequently, CMP can be measured on a large scale and, therefore, included in breeding goals for dairy cattle. However, before this approach is

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generalized, it is necessary to better understand the genetic background of these traits. During the last 10 yr, several studies have estimated the genetic parameters of CMP, with data sets comprising from 892 to 17,577 reference measurements (Vallas et al., 2010; Cecchinato et al., 2011, 2015; Bittante et al., 2013; Poulsen et al., 2015) or 136,807 to 311,354 MIR predictions (Cecchinato et al., 2015; Bonfatti et al., 2017; Visentin et al., 2017). Using a micro-cheese-making procedure, some Italian studies reported low to moderate heritability for cheese yields (0.09 to 0.41; Bittante et al., 2013; Cecchinato et al., 2015; Cecchinato and Bittante, 2016; Bonfatti et al., 2017). In most other studies, coagulation properties were quantified with mechanical or optical lactodynamograph measurements after the addition of rennet. The traits most commonly analyzed were rennet coagulation time (**RCT**), time to curd firmness of 20 mm, and curd firmness 30, 45, and 60 min after chymosin addition. The heritability of some of these traits was found to be high, whereas it was low for others (heritabilities from 0.12 to 0.75). Heritability estimates of milk acidification, as assessed by milk pH measurements, were low to moderate (0.06 to 0.37). Most of these studies investigated the genetic correlations between various CMP traits as well as between CMP traits and total milk protein and fat content, but so far none have examined the genetic relationships between fine-scale milk composition traits (e.g., levels of individual proteins, fatty acids, minerals) and CMP.

The FROMMIR project, initiated in 2015, aims to analyze CMP and milk composition traits predicted from MIR spectra in Montbéliarde cows from the Franche-Comté region; the milk from these cows is used to produce several cheeses that bear appellations of a protected designation of origin or a protected geographical indication. A set of 24 CMP was measured on 416 milk samples in which milk had been coagulated and then processed for making either soft cheese (**SC**) or pressed cooked cheese (**PCC**). Cheese-making traits included 3 laboratory cheese yields, 13 coagulation traits measured with a Formoptic instrument adapted from a mechanical Formagraph (Foss Electric, Hillerød, Denmark) by Chr. Hansen (Horsholm, Denmark) and ENILBio (Poligny, France), and 8 acidification traits measured with the Cinac system (Corrieu et al., 1988). Prediction equations were developed (El Jabri et al., 2017; Laithier et al., 2017) and applied to more than 6 million MIR spectra obtained from more than 400,000 Montbéliarde cows. To estimate the genetic relationships between CMP and milk composition, the content in proteins, fatty acids, minerals, citrate, and lactose was also predicted from MIR spectra using equations developed in previous projects—namely the French PhénoFinlait project (Ferrand et al., 2012; Ferrand-

Calmels et al., 2014) and the European Optimir project (Gengler et al., 2016).

The objectives of the present study were to estimate the heritability and repeatability of the 9 CMP traits that were best predicted by MIR spectra (3 cheese yields, 5 coagulation traits, and 1 acidification trait) as well as that of milk composition traits (proteins, fatty acids, minerals, citrate, and lactose). Furthermore, we investigated the genetic relationships among different CMP and milk composition traits.

MATERIALS AND METHODS

Reference Analyses

The reference data set included 420 milk samples corresponding to 250 individual Montbéliarde cows, 100 herd tanks, and 70 dairy vats. The sampling was designed to maximize genetic diversity as well as variation in milk composition. To this end, herd and dairy vat milks were obtained from dairy farms that varied in geographical location, calving season, average annual herd protein content of the previous milking campaign, and herd size; samples were collected in February to March 2015 and May to June 2015. Individual milk samples were collected between January and June 2016 from cows at different stages of lactation, which represented a wide range of lactoprotein phenotypes (Fang et al., 2016). Of the 250 individual milk samples that were retained, 98 came from the morning milking, 99 came from the evening milking, and 53 were a mixture of 2 successive milkings in relative proportions. Milk samples were excluded if SCC were greater than 10^6 or if more than 10^5 cfu were present. Four individual samples were excluded. In total, 416 milk samples (246 from individual cows, 100 from herd tanks, and 70 from dairy vats) were included in reference analyses.

Whole fresh raw milk samples were collected under strict hygienic conditions, immediately cooled to 4°C, and analyzed within 24 h. Each sample was divided into 2 aliquots: one was preserved by bronopol and analyzed by MIR spectrometry, and the other was analyzed by reference methods of measuring milk coagulation, acidification, and curd yield.

Milk samples (10 mL) were standardized in pH with lactic acid and coagulated with rennet according to 1 of 2 protocols for SC or PCC. For SC, rennet was added at pH 6.45 at a dose of 25 mL/100 L of milk (equivalent to 520 mg of chymosin/L). For PCC, rennet was added at pH 6.60 at a dose of 14 mL/100 L of milk (810 mg of chymosin/L of milk). After 30 min at 32°C, coagulation properties were measured with a Formoptic device, which was adapted from a mechanical Formagraph (Foss Electric) by Chr. Hansen

and ENILBio to improve data computerization. As a Formagraph, the Formoptic registers the position of a pendulum immersed in milk to which rennet has been added. Only the way of recording the position of the pendulum axis is modified. With Formagraph, the position is recorded on a photosensitive piece of paper (the firmness measurements are made manually using a ruler) and is expressed in millimeters. In the case of the Formoptic, the position is automatically recorded via optical transmitters and receivers that convert the physical positions of the pendulum into voltages that are computerized and expressed as a firmness index (**FI**; $FI = 10 \times \text{volts}$). The following coagulation traits were calculated:

1. RCT to 0.5 FI (in min) for SC (**RCT_{SC}**) and PCC (**RCT_{PCC}**),
2. curd firmness at RCT (in FI units) for SC (**a_{SC}**) and PCC (**a_{PCC}**),
3. curd firmness at 2 times RCT (in FI units) for SC (**a2_{SC}**),
4. time to obtain 10 FI from RCT (in min) for SC (**K10_{SC}**) and PCC (**K10_{PCC}**),
5. ratio of K10 to RCT for SC (**K10/RCT_{SC}**) and PCC (**K10/RCT_{PCC}**),
6. curd organization speed (slope of the curve at 10 FI) for SC (**TG10_{SC}**) and PCC (**TG10_{PCC}**), and
7. ratio of TG10 to RCT for SC (**TG10/RCT_{SC}**) and PCC (**TG10/RCT_{PCC}**).

Laboratory curd yields (**CY**) were measured in duplicate using the method of Hurtaud et al. (1995). Coagulated milk (50 mL at pH 6.6 and 32°C) was centrifuged ($2,700 \times g$, 15 min), curd and whey were weighed, and DM of whey and milk was measured. The following CY were calculated:

1. fresh CY (**CY_{FRESH}**; %): $CY_{FRESH} = 100 \times (\text{g of curd} / \text{g of milk})$.
2. CY in DM (**CY_{DM}**; %): $CY_{DM} = 100 \times (1 - \text{g of DM whey} / \text{g of DM milk})$.
3. CY in protein and fat (**CY_{FAT-PROT}**; g/kg): $CY_{FAT-PROT} = (PC + FC) \times (\text{g of milk} / \text{g of curd})$, where **PC** = protein content and **FC** = fat content.

Note that **CY_{FRESH}** and **CY_{DM}** are expressed as a ratio of curd to processed milk, whereas **CY_{FAT-PROT}** is expressed as a ratio of processed milk to curd. Therefore, these traits are expected to be inversely correlated.

Finally, acidification properties were assessed along a temperature gradient using the Cinac system (Corrieu et al., 1988). The decrease in pH was measured for 20 h after the addition of lactic bacteria (mesophilic

or thermophilic strains for SC and PCC, respectively). Different cheese-specific traits were measured:

1. initial pH (in pH units; **upH**) for SC (**pH_{0 SC}**) and PCC (**pH_{0 PCC}**),
2. acidification rate from 170 to 230 min (in upH/h),
3. pH at 10 h (in upH),
4. time to decrease by 0.08 upH from pH₀ (in h),
5. time from pH 6 to pH 4.8 (in h),
6. decrease in pH from 16 h to 20 h (in upH), and
7. pH at 20 h (in upH).

Mid-infrared spectra of the 416 milk samples were standardized by piecewise direct standardization, which matches slave-instrument spectra to master-instrument spectra (Grelet et al., 2015). Only the wavelengths not absorbed by water molecules were used (i.e., absorption was measured for 446 wavelengths following the recommendations of the manufacturer of the MilkoScan FT6000). El Jabri et al. (2017) and Laithier et al. (2017) compared different approaches [Bayesian or partial least squares (**PLS**) using random forest or uninformative variable elimination] for different data sets. They found the highest accuracy with PLS applied to the largest composite data set including individual, herd, and vat samples. An optimal number of latent variables was selected for each equation by minimizing the root mean squared error (**RMSE**) in cross-validation using 10 random segments. Coefficient of determination (**R²**) and RMSE were calculated in both calibration (70%) and validation (30%) sets randomly selected (Table 1). For all 24 CMP traits, these PLS equations were used for all further analyses, and all CMP traits had a relatively normal distribution. The accuracies of MIR predictions were estimated using the **R²** in the validation set. These values ranged from 0.04 to 0.89 depending on the CMP trait (Table 1). Of the 24 CMP traits, only 9 were predicted with relatively good accuracy (**R²** value >0.50): 3 CY traits; 5 coagulation traits, which included measurements of curd-firming time (K10/RCT for PCC and SC) and curd firmness (a for PCC and SC and a2 for SC); and 1 acidification trait for PCC (pH_{0 PCC}). These 9 traits were thus retained for genetic parameter estimations, whereas all others were excluded from further analysis. It should be noted that MIR analysis generally failed to accurately predict the acidification process and succeeded only in predicting the initial pH.

MIR Spectra Predictions

The original data set of the present study comprised 6,670,769 milk samples from 410,622 Montbéliarde

Table 1. Descriptive statistics of mid-infrared (MIR) predictions and performance of prediction equations in the calibration (n = 291) and validation (n = 125) sets for cheese-making properties

Item	Trait ¹	MIR predictions				Prediction equations ²					
		No.	Mean	SD	CV	LV	R ² _{cal}	RMSE _{cal}	R ² _{val}	RMSE _{val}	
Cheese yields	CY _{FRESH} , %	1,098,841	38.3	6.8	17.8	13	0.85	2.96	0.86	2.78	
	CY _{DM} , %	1,099,179	67.2	4.6	6.8	13	0.90	1.68	0.89	1.67	
	CY _{FAT-PROT} , %	1,097,248	185.5	20.3	10.9	18	0.64	13.49	0.54	14.50	
Coagulation traits for pressed cooked cheese	RCT, min	1,095,809	34.33	5.10	14.9	13	0.47	3.74	0.23	5.53	
	K10, min	1,097,657	12.11	2.76	22.8	10	0.51	2.64	0.37	3.05	
	K10/RCT	1,100,235	0.37	0.09	24.3	12	0.74	0.052	0.62	0.06	
	a, FI	1,099,010	18.94	2.43	12.8	12	0.79	1.16	0.72	1.44	
	TG10	1,097,904	7.49	1.89	25.2	10	0.51	1.66	0.32	2.01	
	TG10/RCT	1,100,235	0.22	0.08	36.4	13	0.52	0.067	0.14	0.10	
Coagulation traits for soft cheese	RCT, min	1,096,665	18.12	2.05	11.3	10	0.37	2.33	0.22	2.47	
	K10, min	1,096,525	6.50	1.36	20.9	13	0.50	1.24	0.35	1.37	
	K10/RCT	1,100,235	0.36	0.10	27.8	14	0.76	0.051	0.62	0.071	
	a, FI	1,098,890	19.18	2.58	13.5	13	0.80	1.14	0.73	1.52	
	a2, FI	1,098,766	23.04	2.03	8.8	13	0.76	1.01	0.64	1.37	
	TG10	1,097,899	13.72	3.60	26.2	11	0.51	3.08	0.44	3.21	
	TG10/RCT	1,095,689	0.81	0.27	33.3	16	0.49	0.23	0.26	0.26	
Acidification traits for pressed cooked cheese	pH ₀	1,098,925	6.52	0.07	1.1	17	0.68	0.030	0.65	0.035	
	Acidification rate from 170 to 230 min, upH/h	1,099,954	0.11	0.03	27.3	15	0.56	0.024	0.30	0.031	
	pH at 10h	1,095,145	5.52	0.12	2.2	14	0.41	0.13	0.38	0.16	
Acidification traits for soft cheese	pH ₀	1,098,563	6.57	0.07	1.1	16	0.60	0.041	0.46	0.059	
	Time to reach a decrease of 0.08 upH, h	1,093,320	3.39	0.15	4.4	9	0.15	0.29	0.17	0.29	
	Decrease of pH from 16 h to 20 h	1,098,757	0.17	0.11	64.7	17	0.42	0.10	0.18	0.11	
	pH at 20 h	1,100,236	4.49	0.03	0.67	6	0.17	0.075	0.04	0.074	
	Time from pH 6 to pH 4.8, h	1,098,099	5.84	1.29	22.1	18	0.51	1.01	0.27	1.21	

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat; RCT = rennet coagulation time at 0.5 firmness index (FI); optical sensors convert positions into voltages that are computerized and expressed as units of an FI; FI = 10 × volts; K10 = time to obtain 10 FI from RCT; a = curd firmness at RCT; TG10 = curd organization speed; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria; upH = pH units.

²Number of latent variables (LV), coefficients of determination (R²), and root mean squared error (RMSE) in the calibration (cal) and validation (val) sets; R² values of cheese-making traits retained for genetic parameter estimations are in *italics*.

Table 2. Heritability (h^2), proportion of phenotypic variance explained by permanent environmental (PE) effect, repeatability (t), and coefficient of genetic variation (CV_{gen}) of cheese-making properties

Trait ¹	h^2	SE h^2	PE	SE PE	t	CV_{gen} , %
Cheese yield						
CY _{FRESH}	0.38	0.006	0.08	0.005	0.46	8.2
CY _{DM}	0.39	0.006	0.08	0.005	0.47	3.3
CY _{FAT-PROT}	0.37	0.006	0.06	0.004	0.43	4.4
Coagulation trait						
K10/RCT _{PCC}	0.42	0.009	0.21	0.007	0.63	12.0
a _{PCC}	0.47	0.007	0.13	0.006	0.60	6.3
K10/RCT _{SC}	0.45	0.008	0.19	0.007	0.64	13.8
a _{SC}	0.48	0.007	0.13	0.006	0.61	6.6
a2 _{SC}	0.47	0.007	0.13	0.006	0.60	4.3
Acidification trait						
pH _{0 PCC}	0.37	0.011	0.31	0.010	0.68	0.5

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat. Coagulation and acidification traits were measured for soft cheese (SC) and pressed cooked cheese (PCC): K10 = time to obtain 10 firmness index units (FI) from rennet coagulation time (RCT); a = curd firmness at RCT; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria.

cows. Milk samples were collected between January 2012 and June 2017 and analyzed by MIR spectrometry using a MilkoScan FT6000 (Foss Electric). Cows originated from 3,246 commercial herds in the Franche-Comté region in Eastern France. The MIR spectra of these samples were obtained from 10 spectrometers and standardized according to the method of Grelet et al. (2015).

Cheese-making traits were predicted by applying equations developed in the FROM'MIR project (El Jabri et al., 2017; Laithier et al., 2017). Proteins ($0.54 < R^2 < 1$; Ferrand et al., 2012; Sanchez et al., 2017) and fatty acids ($0.84 < R^2 < 1$; Ferrand-Calmels et al., 2014) were predicted with the equations developed in the PhénoFinlait project, whereas minerals, citrate, and lactose ($0.44 < R^2 < 0.90$) used the equations of the Optimir project (Gengler et al., 2016). Nine CMP (Table 2) and 45 milk composition traits (Appendix Tables A1, A2, and A3) were included in our analyses.

Test-day records before 7 or after 350 DIM were excluded. We selected test-day records from complete lactations or from ongoing lactations with at least 7 test-day records. Lactations that started after December 2016 were excluded. For each trait, outlier values (outside the mean ± 3 SD) were discarded. Furthermore, test-day records that had outlier values for PC or FC were removed from the analyses. After data editing, 4,100,261 test-day records from 237,661 cows remained.

For estimations of variance components, we retained only the first-lactation records. Age at calving of the cows ranged from 24 to 42 mo. Contemporary groups were defined as the combination of test day $\times$ herd $\times$ spectrometer, and season of calving was defined as the month $\times$ year of calving combination. Thirty classes of stage of lactation were defined as follows: one stage for 7 to 10 DIM, twenty-four 10-d stages between 10 and 250

DIM (11 to 20 DIM, 21 to 30 DIM, and so on), and five 20-d stages between 250 and 350 DIM (251 to 270 DIM, 271 to 290 DIM, and so on). The minimum number of records per class was 5, 1,000, and 500 for contemporary groups, season, and lactation stage, respectively. The final data set included 1,100,238 test-day records (7 to 13 test-day records per cow, with an average of 8.7) from 126,873 cows born between 2008 and 2014. Data were distributed among 3,086 commercial herds, 89,129 contemporary groups, 58 seasons of calving, and 30 stages of lactation.

Estimations of (Co)variance Components and Genetic Parameters

First-lactation data were analyzed using univariate and bivariate repeatability animal models. In the case of the univariate model, variance components were estimated using the AI-REML algorithm as implemented in Wombat software (Meyer, 2007) with the following linear animal model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{p} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of test-day observations, $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ is the vector of random additive genetic effects, $\mathbf{p} \sim N(\mathbf{0}, \mathbf{I}\sigma_p^2)$ is the vector of random permanent environmental (PE) effects, and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ is the vector of random residual effects. $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are incidence matrices; $\mathbf{A}$ is the relationship matrix among individuals; $\mathbf{I}$ is the identity matrix; and σ_a^2 , σ_p^2 , and σ_e^2 are the additive genetic, PE, and residual variances, respectively. The $\boldsymbol{\beta}$ vector included the fixed effects of herd $\times$ test day $\times$ spectrometer, stage of lactation, and

season of calving. The relationship matrix was calculated from the pedigree, which was traced over 4 generations and contained 315,661 animals. Covariances were estimated with a similar bivariate model, with the genetic, PE, and residual variances as 2×2 matrices.

Heritability $\left(h^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2} \right)$ and repeatability $\left(t = \frac{\hat{\sigma}_a^2 + \hat{\sigma}_p^2}{\hat{\sigma}_a^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2} \right)$ were calculated from the additive genetic $\left(\hat{\sigma}_a^2 \right)$, PE $\left(\hat{\sigma}_p^2 \right)$, and residual $\left(\hat{\sigma}_e^2 \right)$ variance estimates for the 9 best-predicted CMP traits and 45 milk composition traits. The additive genetic correlations (r_a) were computed between CMP traits and between CMP and milk composition traits in bivariate models, $\left(r_a = \frac{\hat{\sigma}_{a1,a2}}{\hat{\sigma}_{a1}\hat{\sigma}_{a2}} \right)$, with $\hat{\sigma}_{a1,a2}$ being the estimate of additive genetic covariance between trait 1 and trait 2 and $\hat{\sigma}_{a1}$ and $\hat{\sigma}_{a2}$ being the additive genetic standard deviation estimates for traits 1 and 2, respectively.

RESULTS

CMP

Descriptive statistics and accuracy of MIR predictions for the 24 CMP are reported in Table 1. The accuracy of MIR predictions, as estimated by the R^2 in the validation set, was high for 2 measures of cheese yield (CY_{FRESH} : 0.86; CY_{DM} : 0.89) and 2 coagulation traits (0.73 for a_{SC} ; 0.72 for a_{PCC}). Mid-infrared-based predictions were moderately accurate for $a_{2\text{SC}}$ (0.64), $K10/RCT_{\text{PCC}}$ (0.62), $K10/RCT_{\text{SC}}$ (0.62), $pH_{0\text{PCC}}$ (0.65), and $CY_{\text{FAT-PROT}}$ (0.54). Predictions of all other CMP—8 coagulation traits, including RCT measured for both SC ($R^2 = 0.22$) and PCC ($R^2 = 0.23$), and 7 acidification traits ($0.04 < R^2 < 0.46$)—had low accuracy and consequently were not included in genetic analyses. The 9 traits best predicted by MIR spectra analysis (CY_{FRESH} , CY_{DM} , $CY_{\text{FAT-PROT}}$, a_{PCC} , a_{SC} , $a_{2\text{SC}}$, $K10/RCT_{\text{SC}}$, $K10/RCT_{\text{PCC}}$, and $pH_{0\text{PCC}}$) were used for further investigations of the genetic determinism of CMP.

Heritability estimates varied between 0.37 and 0.48 for the 9 CMP traits analyzed (Table 2). Coagulation traits were the most heritable (0.42 to 0.48): $K10/RCT$ had heritability estimates of 0.42 and 0.45 for PCC and SC, respectively, whereas all curd firmness traits presented similar values (between 0.47 and 0.48). Estimates of heritability were somewhat lower for CY (0.37 to 0.39) and for $pH_{0\text{PCC}}$ (0.37). However, all these values were relatively high considering that they come from test-day measures. Because the data set used in

our study was large, heritability estimates for all traits were highly accurate ($SE < 0.01$; Table 2).

The coefficient of genetic variation ranged from 3.3 to 13.8% for CY and coagulation traits, and it was 0.5% for $pH_{0\text{PCC}}$. For all CMP traits analyzed, the additive genetic variance was larger than the PE variance. For CY , the part of phenotypic variance due to PE ranged between 0.06 and 0.08. This part was higher for coagulation traits (0.13 to 0.21) and even higher for $pH_{0\text{PCC}}$ (0.31).

The genetic correlations calculated between CMP traits are presented in Table 3. Fresh CY and CY_{DM} were very strongly positively correlated (0.97), whereas, as expected, the genetic correlations between either of these CY and $CY_{\text{FAT-PROT}}$ (expressed as grams of fat and protein per kilogram of cheese) were highly negative (-0.84 and -0.82 , respectively). The genetic correlations between coagulation traits were also relatively high, with absolute values ranging from 0.72 to 0.80. Values of curd-firming time ($K10/RCT$) and curd firmness (a and a_2) were genetically negatively correlated, meaning that milk with longer coagulation times had softer curds. We also found strong genetic correlations between coagulation traits measured for PCC and SC: 0.80 for curd-firming time and 0.76 to 0.77 for curd firmness, which suggests that selection for improved coagulation traits for either type of cheese would be beneficial to both PCC and SC. Moreover, CY and coagulation traits were also strongly genetically correlated. Fresh CY and CY_{DM} were both positively correlated with curd firmness and negatively correlated with curd-firming time. In contrast, the genetic correlations between $pH_{0\text{PCC}}$ and CY or coagulation traits were very weak (-0.08 to 0.09).

CMP and Milk Composition

Descriptive statistics, heritability, and proportion of phenotypic variance explained by PE effect for milk protein, fatty acid, and mineral, citrate, and lactose composition are reported in Appendix Tables A1, A2, and A3, respectively. On average, the milk analyzed in this study comprised 4.96% lactose, 3.73% fat, 3.35% protein, 0.83% citrate, and 0.41% minerals.

Heritability estimates of PC and FC were 0.48 and 0.36, respectively. The heritability estimates of individual milk proteins (0.35 to 0.58) were higher than those of individual fatty acids (0.14 to 0.40). Heritability estimates of Ca, P, K, and Mg were high (0.50 to 0.56), as were the values obtained for citrate (0.48) and lactose (0.47).

As shown in Table 4, milk PC was strongly genetically correlated with coagulation traits (-0.80 and -0.81 for

Table 3. Genetic correlations between cheese-making properties for soft cheese (SC) and pressed cooked cheese (PCC)

Trait ¹	Cheese yield		Coagulation trait					Acidification
	CY _{DM}	CY _{FAT-PROT}	K10/RCT _{PCC}	a _{PCC}	K10/RCT _{SC}	a _{SC}	a2 _{SC}	pH ₀ PCC
CY _{FRESH}	0.97	−0.84	−0.73	0.78	−0.76	0.78	0.75	0.03
CY _{DM}		−0.82	−0.72	0.77	−0.74	0.76	0.72	−0.02
CY _{FAT-PROT}			0.65	−0.65	0.71	−0.67	−0.64	−0.01
K10/RCT _{PCC}				−0.76	0.80	−0.73	−0.72	0.09
a _{PCC}					−0.78	0.76	0.77	−0.08
K10/RCT _{SC}						−0.77	−0.77	0.06
a _{SC}							0.74	0.02
a2 _{SC}								0.02
pH ₀ PCC								

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat; K10 = time to obtain 10 firmness index units (FI) from rennet coagulation time (RCT); a = curd firmness at RCT; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria. SE varied between 0.001 and 0.038.

K10/RCT_{PCC} and K10/RCT_{SC}, respectively, and 0.89 to 0.94 for curd firmness traits) and, to a lesser extent, with cheese yields (0.75, 0.74, and −0.52 for CY_{FRESH}, CY_{DM}, and CY_{FAT-PROT}, respectively). Milk FC was more genetically correlated with CY (0.87, 0.91, and −0.57 for CY_{FRESH}, CY_{DM}, and CY_{FAT-PROT}, respectively) than it was with coagulation traits (−0.53 to −0.47 for K10/RCT_{PCC} and K10/RCT_{SC}, respectively, and 0.48 to 0.55 for curd firmness traits; Table 5). In contrast, both PC and FC were only weakly genetically correlated with pH₀ PCC (−0.11 and −0.06, respectively).

For protein and fatty acid composition, we calculated genetic correlations between proteins (or fatty acids) expressed as a percentage of milk or as a percentage of total protein (or total fat). The results obtained varied greatly depending on the expression unit. It should be noted that convergence was not completely achieved for most of the genetic correlation estimates between curd-firming time and protein, fatty acid, and mineral composition. Therefore, these results have to be considered with caution. Nevertheless, CMP traits appeared to be more strongly genetically associated with protein

Table 4. Genetic correlations between cheese-making properties for soft cheese (SC) or pressed cooked cheese (PCC) and milk protein composition¹

Trait ¹	Cheese yield			Coagulation trait					Acidification
	CY _{FRESH}	CY _{DM}	CY _{FAT-PROT}	K10/RCT _{PCC}	a _{PCC}	K10/RCT _{SC}	a _{SC}	a2 _{SC}	pH ₀ PCC
Proteins, g/100 g of milk									
PC	0.75	0.74	−0.52	−0.80	0.94	−0.81	0.91	0.89	−0.11
α-LA	0.14	0.14	−0.10	−0.19	0.20	−0.15	0.20	0.20	0.04
β-LG	0.14	0.11	0.18	−0.32	0.28	−0.27	0.26	0.25	−0.04
α _{S1} -CN	0.75	0.74	−0.53	−0.78	0.81	−0.82	0.80	0.79	−0.13
α _{S2} -CN	0.34	0.33	−0.22	−0.44	0.43	−0.42	0.43	0.41	−0.05
β-CN	0.71	0.71	−0.63	−0.79	0.79	−0.79	0.77	0.77	−0.19
κ-CN	0.34	0.34	−0.25	−0.43	0.42	−0.38	0.41	0.41	0.03
ΣWP	0.26	0.23	0.09	−0.45	0.41	−0.40	0.38	0.38	−0.05
ΣCN	0.75	0.74	−0.54	−0.80	0.94	−0.81	0.90	0.90	−0.12
Proteins, g/100 g of protein									
α-LA	0.09	0.09	−0.07	−0.18	0.22	−0.17	0.28	0.31	0.32
β-LG	−0.28	−0.31	0.56	0.17	−0.19	0.20	−0.21	−0.21	0.02
α _{S1} -CN	0.04	0.11	0.04	0.17	−0.15	0.14	−0.15	−0.18	−0.14
α _{S2} -CN	0.19	0.15	−0.21	−0.41	0.41	−0.36	0.39	0.44	0.02
β-CN	−0.04	−0.02	−0.34	0.08	−0.05	0.05	−0.05	−0.02	−0.21
κ-CN	0.30	0.30	−0.22	−0.41	0.42	−0.32	0.44	0.46	0.28
ΣWP	−0.26	−0.29	0.56	0.15	−0.17	0.20	−0.18	−0.18	0.02
ΣCN	0.09	0.12	−0.17	−0.09	0.13	−0.01	0.09	0.15	−0.09

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat; K10 = time to obtain 10 firmness index units (FI) from rennet coagulation time (RCT); a = curd firmness at RCT; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria; PC = protein content; ΣWP = sum of whey proteins (α-LA + β-LG); ΣCN = sum of caseins (α_{S1}-CN + α_{S2}-CN + β-CN + κ-CN). SE varied between 0.002 and 0.022; full convergence was not achieved for values in italics.

Table 5. Genetic correlations between cheese-making properties for soft cheese (SC) or pressed cooked cheese (PCC) and milk fatty acid composition¹

Trait	Cheese yield			Coagulation trait					Acidification
	CY _{FRESH}	CY _{DM}	CY _{FAT-PROT}	K10/RCT _{PCC}	a _{PCC}	K10/RCT _{SC}	a _{SC}	a2 _{SC}	pH ₀ PCC
Fatty acids, g/100 g of milk									
FC	0.87	0.91	−0.57	−0.53	0.55	−0.47	0.51	0.48	−0.06
SFA	0.81	0.86	−0.52	−0.47	0.49	−0.40	0.45	0.42	−0.08
MUFA	0.69	0.69	−0.50	−0.50	0.50	−0.49	0.49	0.47	−0.01
UFA	0.72	0.71	−0.52	−0.53	0.53	−0.52	0.52	0.50	0.00
PUFA	0.14	0.14	−0.09	−0.12	0.13	−0.12	0.12	0.12	−0.01
ΣC4-C10	0.56	0.59	−0.42	−0.45	0.44	−0.38	0.41	0.41	−0.08
ΣC4-C12	0.69	0.71	−0.44	−0.48	0.50	−0.42	0.46	0.46	−0.11
C14:0	0.63	0.65	−0.45	−0.47	0.47	−0.41	0.43	0.42	−0.13
C16:0	0.77	0.82	−0.49	−0.42	0.44	−0.36	0.42	0.38	0.02
C18:0	0.36	0.37	−0.30	−0.08	0.07	−0.04	0.03	0.02	0.02
C18:1	0.61	0.59	−0.44	−0.40	0.42	−0.41	0.41	0.39	0.02
Fatty acids, g/100 g of fat									
SFA	0.32	0.37	−0.16	−0.14	0.16	−0.06	0.11	0.11	−0.13
MUFA	−0.33	−0.39	0.17	0.14	−0.15	0.06	−0.11	−0.10	0.08
UFA	−0.34	−0.40	0.17	0.13	−0.14	0.05	−0.10	−0.09	0.08
PUFA	−0.42	−0.47	0.30	0.00	−0.02	−0.04	0.01	0.04	0.03
ΣC4-C10	−0.06	−0.03	0.00	−0.07	0.08	−0.07	0.07	0.10	−0.09
ΣC4-C12	0.11	0.15	−0.02	−0.19	0.19	−0.16	0.17	0.20	−0.16
C14:0	0.21	0.24	−0.12	−0.21	0.20	−0.18	0.18	0.18	−0.19
C16:0	0.40	0.45	−0.24	−0.15	0.17	−0.09	0.17	0.14	0.12
C18:0	−0.33	−0.36	0.13	0.39	−0.41	0.39	−0.43	−0.42	0.02
C18:1	−0.38	−0.45	0.22	0.20	−0.22	0.13	−0.18	−0.17	0.10

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat; K10 = time to obtain 10 firmness index units (FI) from rennet coagulation time (RCT); a = curd firmness at RCT; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria; FC = fat content; ΣC4-C10 = sum of fatty acids with 4 to 10 carbon atoms; ΣC4-C12 = sum of fatty acids with 4 to 12 carbon atoms. SE varied between 0.002 and 0.022; full convergence was not achieved for values in italics.

and fatty acid content when they were expressed as a percentage of milk rather than as a percentage of protein or fat. Regardless of the protein or fatty acid considered, high levels in milk were always genetically associated with better CMP (Tables 4 and 5).

This result was particularly marked for caseins—namely, α_{S1}- and β-casein. As observed for total PC, the total casein content in milk was strongly genetically correlated with coagulation traits (−0.80 and −0.81 for K10/RCT_{PCC} and K10/RCT_{SC}, respectively, and 0.90 to 0.94 for curd firmness traits), whereas the genetic correlations between whey proteins in milk and coagulation traits were much weaker (0.15 to 0.32 in absolute values). In contrast, genetic correlations with relative amounts of proteins were more moderate (Table 4). The content of β-LG in total protein was negatively correlated with CY_{FRESH}, CY_{DM}, and curd firmness traits and positively correlated with CY_{FAT-PROT} and K10/RCT.

Genetic correlations were moderate to high between CY_{FRESH} and CY_{DM} and fatty acids expressed as a percentage of milk, in particular with SFA and palmitic acid (C16:0). Coagulation traits were more genetically correlated with SFA, MUFA, and UFA than with PUFA (Table 5). For relative fatty acid contents, expressed as

a percentage of total fat, high amounts of SFA and low levels of MUFA, UFA, or PUFA were associated with better CMP (higher CY_{FRESH} and CY_{DM}, lower curd-firming times, and firmer curds). However, unlike saturated short-chain (C4-C12), myristic (C14:0), and palmitic (C16:0) fatty acids, lower levels of stearic acid content (C18:0), which represents about 10% of the total fatty acids in milk, were associated with better CMP.

Mineral composition and, in particular, Ca, P, and Mg contents were moderately genetically correlated with CY_{FRESH} and CY_{DM} (0.40 to 0.58) and coagulation traits (0.37 to 0.59 in absolute values). In contrast, genetic correlations between CMP and other minerals (K and Na), citrate, or lactose were weak (−0.16 to 0.17; Table 6).

DISCUSSION

Our study is the first to report genetic parameters of CMP and milk composition in Montbéliarde cows (the second largest dairy cattle breed in France) at a very large scale (more than 1 million test-day records) and for a large number of traits. The accuracies of MIR predictions for cheese-making traits were equivalent

Table 6. Genetic correlations between cheese-making properties for soft cheese (SC) or pressed cooked cheese (PCC) and the mineral, citrate, and lactose composition of milk

Trait ¹	Cheese yield			Coagulation trait				Acidification	
	CY _{FRESH}	CY _{DM}	CY _{FAT-PROT}	K10/RCT _{PCC}	a _{PCC}	K10/RCT _{SC}	a _{SC}	a2 _{SC}	pH _{0 PCC}
Mineral, mg/kg of milk									
Ca	0.40	0.41	-0.25	-0.46	0.45	-0.37	0.39	0.42	0.10
P	0.58	0.54	-0.44	-0.58	0.59	-0.58	0.54	0.54	-0.18
K	-0.09	-0.13	-0.02	0.13	-0.15	0.05	-0.13	-0.15	0.12
Mg	0.41	0.40	-0.31	-0.54	0.50	-0.53	0.42	0.40	-0.29
Na	-0.08	-0.04	0.13	-0.09	0.06	-0.10	0.12	0.06	0.17
Other compounds, g/kg of milk									
Citrate	-0.08	-0.09	0.00	0.05	-0.12	0.07	-0.16	-0.16	0.00
Lactose	0.03	-0.05	-0.04	0.03	0.01	0.05	0.00	0.07	0.04

¹CY_{FRESH} = fresh curd yield; CY_{DM} = curd yield in DM; CY_{FAT-PROT} = curd yield in protein and fat; K10 = time to obtain 10 firmness index units (FI) from rennet coagulation time (RCT); a = curd firmness at RCT; a2 = curd firmness at 2 times RCT; pH₀ = pH after adding lactic acid bacteria. SE varied between 0.009 and 0.023; full convergence was not achieved for values in italics.

to or higher than accuracies reported in other studies. For example, R^2 values were previously estimated to be between 0.67 and 0.85 for CY_{FRESH} or CY_{DM} (Ferragina et al., 2013; Bonfatti et al., 2016; Grelet et al., 2017), 0.20 and 0.52 for curd firmness (Cecchinato et al., 2009; Visentin et al., 2015; Bonfatti et al., 2016), and 0.71 and 0.79 for pH (Visentin et al., 2015; Bonfatti et al., 2016). However, the current study failed to accurately predict RCT, which had previously been predicted with R^2 values ranging from 0.55 to 0.69 (Cecchinato et al., 2009; Visentin et al., 2015; Bonfatti et al., 2016). These discrepancies might be due to differences in the equipment used to measure CMP or to the standardization of initial milk pH, which is the main factor influencing RCT. In our study, a Formoptic instrument was used and a pH standardization for measuring coagulation traits was applied. As a result, the coefficient of variation of RCT was more than 2 times smaller (11% for SC and 15% for PCC) than values reported in other studies that applied a computerized renneting meter (Cecchinato et al., 2009; Bonfatti et al., 2016) or Formagraph apparatus (Visentin et al., 2015) without pH standardization. Although we were not able to directly analyze RCT, we could assess curd-firming time using the ratio of K10 (time to obtain 10 FI) to RCT, which was predicted with R^2 of 0.62 for both PCC and SC.

Heritabilities

Despite some discrepancies that were probably due to different equipment or protocols used, we found that our estimates of heritability were globally in agreement with previously reported results. For CY, heritabilities were estimated to be between 0.13 and 0.21 using reference measurements in Brown Swiss milk (Bittante et al., 2013; Cecchinato and Bittante, 2016) and between 0.09 and 0.33 using MIR predictions in Italian Holstein,

Brown Swiss, and Simmental milk (Cecchinato et al., 2015; Bonfatti et al., 2017). Depending on the study, heritability estimates of coagulation, expressed as curd-firming time, varied between 0.21 and 0.43, whereas those for curd firmness (measured at different times after addition of rennet) varied between 0.12 and 0.41 (Vallas et al., 2010; Cecchinato et al., 2011; Tiezzi et al., 2013; Poulsen et al., 2015; Cecchinato and Bittante, 2016; Bonfatti et al., 2017; Visentin et al., 2017). In these studies, acidification assessed by a single measurement of milk pH showed low heritability (0.06 to 0.27; Vallas et al., 2010; Cecchinato et al., 2011; Tiezzi et al., 2013; Bonfatti et al., 2017; Visentin et al., 2017). We found estimates of heritability very similar to or higher than those obtained using reference measurements, indicating that MIR predictions are sufficiently accurate to be used for genetic investigations. Nevertheless, it is possible that, by decreasing environmental variance, pH standardization led to an increase of CMP heritabilities.

We also found relatively high coefficients of genetic variation for CY and coagulation traits (3.3 to 13.8%) and low coefficients of genetic variation for pH_{0 PCC} (0.5%). These were all strongly consistent with values reported from reference measurements by Visentin et al. (2017) in Holstein-Friesian cows for both coagulation traits (3.1 to 11.5%) and pH (0.3%). In addition, for all CMP traits analyzed, the additive genetic variance was larger than the PE variance. Our CY traits were less influenced by PE variance than those of Cecchinato et al. (2015), whereas the PE effect on coagulation traits here was slightly higher than or similar to previous reports (Vallas et al., 2010; Tiezzi et al., 2013; Visentin et al., 2017). The effect of PE variance on pH_{0 PCC} was higher than the one published by Vallas et al. (2010) and Tiezzi et al. (2013) but similar to the effect reported by Visentin et al. (2017).

In addition to the moderate to high heritability estimates (0.37 to 0.48) obtained here for single test-day records, all these results suggest that CMP could be improved by selection. For instance, these values of heritability are higher than those found for milk yield, which has been included in breeding goals for many years and which has more than doubled in the last few decades (Ducrocq and Wiggans, 2015).

For all milk composition traits that were predicted from MIR spectra, we found heritability estimates that were very consistent with those from previous studies. For example, with regard to milk protein and fatty acid composition, our results were in complete agreement with previous studies in Montbéliarde cows (Boichard et al., 2014; Sanchez et al., 2017). For mineral composition, we found heritability values similar to those reported from reference analyses (van Hulzen et al., 2009) and MIR predictions (Govignon-Gion et al., 2015) but higher than the estimates from MIR predictions reported by Toffanin et al. (2015) and Bonfatti et al. (2017). Furthermore, in our samples the content of citrate and lactose was highly heritable, which was similar to previously reported values for citrate (Buitenhuis et al., 2013) but higher than those reported for lactose (Buitenhuis et al., 2013; Haile-Mariam and Pryce, 2017).

Genetic Correlations Between CMP

Our study also revealed high genetic correlations between different cheese-making traits, especially between different measures of CY, which corroborates the results of Bittante et al. (2013) and Cecchinato et al. (2015) obtained from the production of micro-cheese. Likewise, our observation of high genetic correlations between coagulation traits is consistent with results obtained from a computerized renneting meter (Cecchinato et al., 2011) and a Formagraph device (Visentin et al., 2017). We also found a strong genetic link between CY and coagulation traits, and the values obtained were higher than those recently reported by Cecchinato and Bittante (2016). In contrast, the genetic correlations between pH_0 PCC and other cheese-making traits were low, which was inconsistent with the high positive genetic correlations (0.69 to 0.94) between RCT and pH that have been reported in some studies (Vallas et al., 2010; Cecchinato et al., 2011); however, this can be explained by the pH standardization procedure we applied.

We found strong, favorable genetic correlations between CY and coagulation traits as well as between coagulation traits measured for PCC and SC cheeses. The implication of this is that the inclusion in breeding goals of a single CMP trait (e.g., the best-predicted one

or the most heritable one) could generate progress for the overall cheese yield and coagulation abilities in a wide range of cheese-production systems.

Genetic Correlations Between CMP and Milk Composition

The genetic relationships between milk composition and CMP are strong. Two previous studies investigated the genetic correlations between CY and both PC and FC in Holstein, Brown Swiss, and Simmental cows (Bittante et al., 2013; Cecchinato et al., 2015) and found, as we report here, high genetic correlation estimates with both PC (0.75 to 0.93) and FC (0.84 to 0.97). In contrast, estimates of genetic correlations between milk coagulation traits and PC or FC varied widely among studies. Vallas et al. (2010) and Cecchinato et al. (2011) found very weak genetic correlations between curd-firming time and PC or FC (−0.11 to 0.19), whereas Visentin et al. (2017) reported higher values, closer to those reported in the present study for FC (−0.46) but lower for PC (−0.56). Genetic correlation estimates between curd firmness and PC or FC have been more consistent. As in our study, these values were always positive, varying between 0.35 and 0.90 for PC and between 0.25 and 0.62 for FC (Vallas et al., 2010; Cecchinato et al., 2015; Visentin et al., 2017). With pH, the slightly negative correlation estimates recovered in our study were lower than those reported in Visentin et al. (2017); these authors found low correlations between pH and PC (−0.33) or FC (−0.24).

The genetic correlations estimated between protein composition and CMP were consistent but higher than results reported in the few studies that have been conducted to date. So far, only 1 study has reported genetic correlations between milk coagulation traits and milk protein composition as a percentage of milk or of total protein (Bonfatti et al., 2011), whereas 3 other studies indicated genetic correlations between CMP and total caseins in milk (Cecchinato et al., 2011; Gustavsson et al., 2014) or with κ -casein and β -LG expressed as percentage of proteins (Gustavsson et al., 2014). Furthermore, to our knowledge, our study is the first to investigate the genetic relationships between milk fatty acid composition and CMP.

High levels of Ca, P, and Mg were associated with better CY and coagulation properties, in agreement with previous results (Amenu and Deeth, 2007). In contrast, although phenotypic associations were previously identified between coagulation properties and K, Na, citrate, or lactose (Glantz et al., 2010; Sundekilde et al., 2011; Bland et al., 2015), only low genetic correlations were observed in our study.

Cheese yields and coagulation traits were strongly genetically correlated with individual proteins (mainly κ -casein) and, to a lesser extent, with fatty acids (mainly SFA and C16:0) and with mineral (Ca, P, and Mg) composition. These relationships can be interpreted considering the mechanisms behind the cheese-making process. Caseins are aggregated in micelles that mainly comprise caseins (92%), calcium phosphate (7%), citrate (0.5%), and magnesium (0.2%). In these micelles, α_{S1} -, α_{S2} -, β -, and κ -caseins are present in relative amounts of 3:1:3:1. Most κ -casein is found on the surface of the micelles, whereas the other caseins (α_{S1} , α_{S2} , and β) are located inside. Moreover, two-thirds of total Ca, one-third of Mg, and one-half of P contents are associated with casein molecules, whereas Na and K are diffusible ions. During the cheese-making process, enzymes of rennet (chymosin) degrade the κ -casein, which causes a decrease in the colloidal stability and promotes the coagulation of micelles. Casein micelle size was found to affect the kinetics of the coagulation process. Milk with smaller casein micelles, containing higher levels of κ -casein and minerals, form firmer curds earlier (Glantz et al., 2010; Logan et al., 2014, 2015).

To a lesser extent, the size of fat globules, which is influenced by fatty acid composition (Timmen and Patton, 1988; Couvreur and Hurtaud, 2017), is also associated with milk coagulation via their interaction with the aggregation of casein micelles. However, results have not always been consistent. Logan et al. (2015) found that large fat globules, combined with small casein micelles, gave the firmest curds. Luo et al. (2017) showed that a reduction in fat globule size accelerated casein micelle aggregation during renneting and led to firmer gels. In the present study, the relative content of different fatty acids was not strongly genetically associated with coagulation properties with 1 exception: high levels of C18:0, which has been found to be associated with larger fat globules (Timmen and Patton, 1988), were genetically associated with undesirable coagulation properties (longer curd-firming time and less-firm curds). Our results are therefore in agreement with those of Luo et al. (2017) and support their observation that a reduction of fat globule size accelerated the aggregation of casein micelles during renneting and increased curd firmness.

CONCLUSIONS

This large-scale study carried out in Montbéliarde cows from the Franche-Comté cheese production area (protected designation of origin and protected geographical indication) shows that MIR predictions of cheese yields and milk coagulation properties are sufficiently accurate for genetic analyses. Cheese-making

traits, as predicted from MIR spectra, are moderately heritable and could be integrated without additional cost into breeding objectives, thus promoting their efficient improvement via selection. Using genotyping data produced for routine genomic selection, additional analyses will be performed to estimate the effects of milk protein variants on CMP and to identify novel genetic variants with an effect on CMP that could be included in genomic evaluation models.

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APPENDIX

Table A1. Descriptive statistics, heritability (h^2), proportion of phenotypic variance explained by permanent environmental (PE) effect, and repeatability (t) of milk protein composition

Trait ¹	No.	Mean	SD	h^2	SE h^2	PE	SE PE	t
Proteins, g/100 g of milk								
PC	1,100,238	3.35	0.29	0.48	0.008	0.15	0.006	0.63
α-LA	1,097,749	0.13	0.02	0.41	0.053	0.18	0.044	0.59
β-LG	1,098,516	0.41	0.06	0.42	0.012	0.29	0.010	0.71
α _{S1} -CN	1,100,094	1.08	0.09	0.46	0.009	0.21	0.007	0.67
α _{S2} -CN	1,099,402	0.32	0.03	0.44	0.025	0.18	0.017	0.62
β-CN	1,099,217	0.99	0.08	0.44	0.009	0.23	0.008	0.67
κ-CN	1,098,790	0.29	0.03	0.43	0.025	0.18	0.018	0.61
ΣWP	1,099,055	0.56	0.08	0.46	0.011	0.27	0.010	0.73
ΣCN	1,099,594	2.70	0.24	0.48	0.007	0.15	0.006	0.63
Proteins, g/100 g of protein								
α-LA	1,099,358	3.97	0.34	0.35	0.006	0.094	0.005	0.44
β-LG	1,100,013	12.32	1.58	0.58	0.007	0.054	0.005	0.63
α _{S1} -CN	1,100,073	32.26	0.26	0.46	0.007	0.097	0.005	0.56
α _{S2} -CN	1,097,360	9.69	0.32	0.38	0.007	0.11	0.005	0.49
β-CN	1,099,976	29.75	1.05	0.38	0.006	0.097	0.005	0.48
κ-CN	1,099,282	8.74	0.43	0.38	0.007	0.11	0.005	0.49
ΣWP	1,100,030	16.73	1.69	0.60	0.007	0.052	0.006	0.65
ΣCN	1,099,731	80.81	1.23	0.46	0.007	0.091	0.005	0.55

¹PC = protein content; ΣWP = sum of whey proteins; ΣCN = sum of caseins.

Table A2. Descriptive statistics, heritability (h^2), proportion of phenotypic variance explained by permanent environmental (PE) effect, and repeatability (t) of milk fatty acid composition

Trait ¹	No.	Mean	SD	h^2	SE h^2	PE	SE PE	t
Fatty acid, g/100 g of milk								
FC	1,100,238	3.73	0.46	0.36	0.006	0.081	0.005	0.44
SFA	1,099,073	2.61	0.39	0.41	0.007	0.11	0.005	0.52
MUFA	1,091,310	0.99	0.20	0.16	0.004	0.066	0.003	0.23
UFA	1,091,353	1.12	0.22	0.16	0.004	0.067	0.003	0.23
PUFA	1,098,459	0.12	0.03	0.20	0.035	0.20	0.039	0.40
Σ C4–C10	1,098,322	0.42	0.06	0.34	0.010	0.31	0.009	0.65
Σ C4–C12	1,098,394	0.52	0.08	0.37	0.008	0.21	0.007	0.58
C14:0	1,097,898	0.40	0.08	0.34	0.009	0.27	0.008	0.61
C16:0	1,098,428	1.06	0.24	0.40	0.006	0.090	0.005	0.49
C18:0	1,096,470	0.40	0.11	0.18	0.007	0.18	0.005	0.36
C18:1	1,090,057	0.87	0.18	0.14	0.004	0.070	0.003	0.21
Fatty acid, g/100 g of fat								
SFA	1,100,225	69.99	5.53	0.21	0.005	0.10	0.004	0.31
MUFA	1,100,201	26.91	4.77	0.23	0.005	0.10	0.004	0.33
UFA	1,100,200	30.44	5.20	0.24	0.005	0.11	0.004	0.35
PUFA	1,100,235	3.33	0.67	0.18	0.004	0.073	0.003	0.25
Σ C4–C10	1,099,969	11.39	1.17	0.27	0.010	0.093	0.004	0.36
Σ C4–C12	1,100,237	14.04	1.56	0.26	0.008	0.085	0.004	0.35
C14:0	1,100,238	10.84	1.93	0.19	0.009	0.062	0.003	0.25
C16:0	1,100,233	28.45	4.89	0.25	0.006	0.080	0.004	0.33
C18:0	1,100,153	10.70	2.76	0.20	0.007	0.053	0.003	0.25
C18:1	1,100,229	23.64	4.61	0.23	0.004	0.10	0.004	0.33

¹FC = fat content; Σ C4–C10 = sum of C4 to C10 fatty acids; Σ C4–C12 = sum of C4 to C12 fatty acids.

Table A3. Descriptive statistics, heritability (h^2), proportion of phenotypic variance explained by permanent environmental (PE) effect, and repeatability (t) of milk mineral composition and citrate and lactose content

Trait	No.	Mean	SD	h^2	SE h^2	PE	SE PE	t
Mineral, mg/kg of milk								
Ca	982,586	1,161.4	92.6	0.50	0.008	0.12	0.006	0.62
P	979,649	1,007.0	77.5	0.56	0.008	0.15	0.007	0.71
K	983,218	1,473.8	104.5	0.53	0.008	0.12	0.007	0.65
Mg	982,517	100.5	7.2	0.52	0.008	0.15	0.007	0.67
Na	982,511	341.7	44.5	0.32	0.008	0.19	0.006	0.51
Other compounds, g/kg of milk								
Citrate	624,731	8.27	1.49	0.48	0.014	0.19	0.012	0.67
Lactose	1,018,276	49.6	1.95	0.47	0.007	0.14	0.006	0.61