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C. Machefert, Christèle Robert-Granié, J.M. Astruc, H. Larroque. Genetic parameters of milk mid-infrared spectra and their genetic relationships with milk production and feed efficiency traits in French Lacaune dairy sheep. Journal of Dairy Science, 2024, 107 (12), pp.11239-11253. 10.3168/jds.2024-25127 . hal-04809223

HAL Id: hal-04809223
https://hal.inrae.fr/hal-04809223v1

Submitted on 16 Dec 2024

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J. Dairy Sci. 107:11239–11253
https://doi.org/10.3168/jds.2024-25127
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Genetic parameters of milk mid-infrared spectra and their genetic relationships with milk production and feed efficiency traits in French Lacaune dairy sheep

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ABSTRACT

In French dairy sheep, Fourier transform infrared (FTIR) milk spectral data routinely predict the major milk components used in national genetic evaluations. The direct influence of genetic and environmental factors on milk FTIR spectra has been widely studied in dairy cattle, with relatively little focus on dairy ewes. In this study, 36,873 milk test-day records were available for 4,712 French Lacaune ewes farmed on 8 commercial farms. Our main goals were to provide the first description of spectral data and estimate the genetic parameters of French Lacaune dairy sheep during lactation. Principal component analysis results demonstrated the impact of lactation period on specific wavenumbers, allowing the identification of FTIR spectra collected at early (mo 2–4) and late (mo 5–7) lactation stages. The average estimated heritability (± mean SE) of the FTIR milk spectra from 2,971 to 926 cm^{-1} (446 wavenumbers) was 0.29 ± 0.02, ranging from 0.13 ± 0.01 to 0.42 ± 0.02. Furthermore, the heritabilities of spectra collected at the beginning or end of lactation changed at each point of the spectrum. However, at each wavenumber, the genomic correlation of transmittance values between these 2 lactation periods was high (>0.77), indicating the absence of a genotype–environment interaction. The genomic correlations between spectral regions and milk production traits (i.e., daily milk yield, fat and protein content, SCS) varied from moderate to high. The results suggested that the most heritable areas of the spectrum were also genetically associated with dairy traits. Finally, the genomic correlations observed between the ewes' feed efficiency traits and the FTIR spectrum were moderate to high, whereas the genomic correlations between the change in body condition score and spectral data were rather low to moderate. This study confirmed that spectral data from Lacaune ewe milk were heritable, evolved phenotypically and genetically during lactation, and were genetically correlated with traits included in breeding goals or traits of interest to the dairy industry.

Key words: dairy sheep, mid-infrared spectra, heritability, genomic correlation, feed efficiency

INTRODUCTION

Fourier transform infrared (**FTIR**) spectroscopy is the preferred global method for routine dairy product quality control, as this method provides thorough information on the chemical composition and molecular structure of milk (Pereira et al., 2020). The spectral data come from the interaction of an infrared beam with milk molecules, resulting in absorbance values at different wavelengths, which are subsequently converted into an infrared spectrum using Fourier transformation (Ghosh and Jayas, 2009). This method enables rapid, high-throughput (100–600 sample analyses per hour), and nondestructive quantification of milk composition using prediction equations, avoiding the need for reference methods that are costly and time-consuming (Pereira et al., 2020; Soyeurt, 2023).

In French dairy sheep, FTIR spectra derived from individual milk samples are used to predict the fat and protein contents (**FC** and **PC**) of milk. These traits have been routinely used in national genetic evaluations since the 1980s for the Lacaune breed (Barillet et al., 2001a; Duchemin et al., 2012). Quality control of individual or flock (tank sample) milk using FTIR spectra is also carried out for milk payment to the farmer and for flock management purposes. The milk FTIR spectral data have only been routinely stored and standardized since 2019 for the French Lacaune breed. The correction of spectral variability observed between different spectrometers and over time, originally developed for cows, consisted of normalizing spectral data from sheep milk using standard cow milk.

Received May 6, 2024.
Accepted August 6, 2024.
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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-24. Nonstandard abbreviations are available in the Notes.

Milk FTIR spectral data have been used for a wider range of prediction applications for milk-derived traits. The most accurate prediction equations can be used routinely for field applications (Coppa et al., 2010). In dairy sheep, prediction equations have been developed to predict milk fatty acid (Ferrand-Calmels et al., 2014; Lužová et al., 2014; Caredda et al., 2016; Correddu et al., 2021) and protein profiles (Ferrand et al., 2012), as well as cheese-making properties (Ferragina et al., 2017; Cellesi et al., 2019; Manuelian et al., 2019). More recently, FTIR spectra from dairy sheep have been shown to be a potential tool for predicting non-milk-derived traits, such as dietary regimens (Molle et al., 2021), methane emission (Correddu et al., 2023), and individual feed intake (Ledda et al., 2023).

Despite the accessibility of data, spectral information has been underused, primarily employed indirectly through predictive models of FC and PC for breeding purposes (Soyeurt et al., 2010; Dagnachew et al., 2013a; Du et al., 2020). Calculating heritability estimates for milk wavenumbers serves several purposes. First, it enables us to determine if genetic variability exists across the entire spectrum or is concentrated in specific regions. This helps us identify which parts of the spectrum are more genetically variable and if these regions are correlated with traits that are challenging to measure directly. A highly heritable wavenumber that predicts a difficult-to-measure trait can serve as a proxy, facilitating evaluation and selection. Second, a better understanding of the genetic determinism of milk spectra could clarify their relationship with the milk composition traits included in breeding programs and how these selected traits are influenced by genetic factors (Dagnachew et al., 2013a; Congiu et al., 2024).

Understanding the heritability of wavenumbers may guide the use of spectral data to improve animal evaluation methods. The studies of Dagnachew et al. (2013b) and Bonfatti et al. (2017) showed that more accurate estimated breeding values can be calculated using genetic components of milk FTIR spectra (latent traits from principal component analysis [**PCA**]) compared with milk components single-trait animal models. Dagnachew et al. (2013b) applied this direct approach for determining milk component traits in dairy goats, and Bonfatti et al. (2017) adapted the approach for determining the fine composition and technological properties of milk in Simmental cows. To improve the accuracy of dairy cow evaluation methods, milk FTIR spectra have also been used to better capture environmental variance in genomic models for unpredicted traits such as milk yield and SCS (Tiezzi et al., 2022). Finally, the use of spectral data instead of genomic data to assess individual similarities, focusing on wavenumbers with significant genetic variability, has been studied mainly in plants (Rincent et al., 2018).

The genetic variability of the FTIR spectra of milk has been mainly explored in dairy cattle, which showed moderate to high heritabilities (Soyeurt et al., 2010; Bittante and Cecchinato., 2013; Rovere et al., 2019). In dairy goats, Dagnachew et al. (2013a) also presented a similar pattern of heritability of FTIR milk spectra. Recently, Congiu et al. (2024), presented low to high heritability estimates ranging from 0.03 to 0.62, depending on spectral regions, in Italian Sarda dairy sheep breed. Certain heritable wavenumbers of cow and goat milk spectra have been reported to be phenotypically associated with milk fatty acids, proteins, and lactose (Bittante and Cecchinato, 2013; Dagnachew et al., 2013a; Zaalberg et al., 2019; Du et al., 2020). Thus, genetic correlations between FTIR spectra and milk composition traits, along with the heritabilities of the milk spectra, can help determine if the same highly heritable wavenumbers are also genetically associated with important economic traits. Congiu et al. (2024) revealed that the more absorbance related to chemical groups of a component, the more heritable the wavenumber, as it could be related to the heritability of the component in sheep milk. Our study was part of the European project Horizon 2020 Small Ruminants breeding for Efficiency and Resilience (**H2020 SMARTER**), providing multiple rich datasets to characterize animal feed efficiency. This project provides the opportunity to study the genetic parameters of milk spectra during lactation and estimate genomic correlations between spectral data and new original traits that are difficult and costly to record on sheep farms, such as feed efficiency. Therefore, the objectives of this study were to (1) provide the first description of FTIR spectra of ovine milk in the French Lacaune breed, (2) estimate the heritabilities of FTIR spectra of ovine milk at each wavenumber, (3) estimate genomic correlations of transmittance at individual wavenumbers between lactation stages, and (4) estimate genomic correlations between milk FTIR spectra and dairy traits, feed efficiency, and changes in body reserve dynamics.

MATERIALS AND METHODS

Milk and Spectral Data

The original data were provided by the European H2020 SMARTER project (2018–2023). The study population consisted of 4,712 French Lacaune dairy ewes, including 32% primiparous ewes, from 8 commercial farms located in southern France. The data were collected during 2 milk production years from September 2019 to September 2021, over several months of lactation. Lactation month defined the time gap between lambing and test day (in months). The criteria used to select the data were as follows: (1) the observation period was from 31

to 210 DIM, i.e., from the second to the seventh month of lactation (milking started one month after lambing, when the suckling period ended); (2) outliers revealed by the PCA were removed; and (3) sires had at least 3 offspring. After data editing, 36,873 milk records from 4,712 dairy ewes were available.

Milk samples were taken during the morning milking with a target of a 6-mo test day (lactation mo 2 to 7 after lambing, one test day per month and flock). The predicted FC and PC (g/L) and spectral information were determined by 2 MilkoScan FT+ analyzers (Foss, Hillerød, Denmark) using mid-infrared (**MIR**) spectrometry with defined routine Fourier transform MIR analyses at Agrolab's laboratory (Aurillac, France). The FTIR spectra of the milk samples contained 1,060 individual spectral points (wavenumbers), which were based on transmittance. Wavenumbers were included in the near- and mid-infrared regions between 5,012 and 926 cm^{-1} with a spectral resolution of 3.85 cm^{-1}. The acquisition of each spectrum was carried out in duplicate and then averaged by the constructor. For each analysis of milk test days, spectra were standardized by the piecewise direct standardization method proposed by Wang et al. (1991) and then developed by Grelet et al. (2015) to reduce the spectral variability between instruments and over time. No pretreatments were applied to the standardized spectra. In our study, analyses were performed by omitting 3 regions of the FTIR spectra (5,012–2,975 cm^{-1}, 2,431–2,276 cm^{-1}, and 1,713–1,547 cm^{-1}), following the manufacturer's recommendations (Foss, 1998). These spectral areas corresponded to water absorption characterized by strong instrumental noise or the absence of chemical bonds associated with a pure baseline (Bittante and Cecchinato, 2013; Grelet et al., 2015). These same spectral regions were not used to develop the prediction equations (Ferrand et al., 2011; Sanchez et al., 2019). Finally, the remaining 446 wavenumbers were selected.

The daily milk yield (**DMY**, L/d) was estimated by correcting the morning milk yield for the evening and morning differences using the ratio between the total volume of milk produced by the whole flock at 2 milkings (ICAR, 2018). Milk SCC (cells/L) was measured by flow cytometry at Agrolab's laboratory (Aurillac, France), and SCS was defined as SCS = log2 (SCC/100) + 3, with bounded values from 0 to 9 (Rupp et al., 2011).

Diet and Feed Efficiency Data

Feeding systems varied from flock to flock, with a diet based on grass, alfalfa or maize silage, hay, and concentrates in the sheepfold for the first months of lactation, after which the ewes were put out on pastures and supplemented with concentrates during the last part of their lactations, from the fourth to the sixth lactation months (Hassoun et al., 2018). On each test day, the approximated lactation feed conversion ratio (**LFCR**) and residual energy intake (**REI**) were calculated and considered lactation net energy feed efficiency traits. The LFCR reflects the portion of the energy input provided by feed and body reserves variation used to produce milk. The REI represents the difference between the energy provided by feed and the theoretical energy requirements estimated from the milk production level, body reserve dynamics and BW of the animals. Based on the LFCR and REI definitions, efficient animals had an upper LFCR but negative REI values. Residual energy intake is expressed in UFL/d, where one *unité fourragère lait* (**UFL**) is the net energy requirement for lactation equivalent to 1 kg of standard air-dried barley (Jarrige et al., 1986). Farm systems cannot provide individualized feed distribution, particularly for forage, so it was assumed that a large part of the ewes' diet was common on a given farm (Machefert et al., 2023). The on-farm approximated individual dry matter intake was calculated from the average of the fodder and part of the concentrates distributed collectively to the flock, which were added to another part of the concentrates distributed individually in the milking parlor. The average of collective feed intake (forages and concentrates) was calculated as the total amount of dry matter divided by the number of ewes per farm, assuming a 10% refusal for forages offered ad libitum (De Boissieu et al., 2019). Concentrate distribution in the milking parlor was adjusted based on various animal subcategories per farm, including factors such as productivity, age, BW, and season. Each subcategory received a consistent feed allocation without accounting for any refusals. For the grazing part, De Boissieu et al. (2019) suggested estimating pasture intake based on the duration of presence per ewe: 2 h = 0.4 kg DM, 4 h = 0.8 kg DM, 6 h = 1 kg DM. Without specific weights, ewes were assigned a parity-dependent reference BW (65 kg for primiparous and 75 kg for multiparous) based on technician expertise. The change in BCS (**BCSΔ**) is the difference between 2 successive BCS values and reflects body reserve dynamics. Body condition scores were evaluated from 0 (emaciated) to 5 (very fat) at targeted physiological stages throughout the lactation period (at the end of suckling, on the first test day, and before and after mating). Due to missing data, the copy mean longitudinal imputation method was applied to the BCS data using the kml package within R software 4.1.1 (http://christophe.genolini.free.fr/kml; Genolini and Falissard, 2011). A detailed description of the database and calculation is available at Machefert et al. (2023).

Genotypes

Among the 4,712 ewes with FTIR spectra, 1,794 ewes were genotyped with the Illumina Sheep LD consortium array (Illumina Inc., San Diego, CA), followed by imputation to obtain 38,523 SNPs that were retained for genomic evaluation of the French Lacaune dairy sheep breed. Quality control for a data set of 1,794 genotyped animals was performed. We removed SNPs with a minor allele frequency lower than 1% and a call rate lower than 97%, as well as monomorphic SNPs. The Hardy–Weinberg equilibrium for each SNP was also tested by calculating the associated chi-squared statistic. The SNPs with a *P*-value lower than 1.10^{-6} were removed (threshold of 5% corrected for multiple testing, as in Teissier et al., 2019). After quality control, 37,236 SNPs remained for further analysis.

Principal Component Analysis

We performed PCA on the 446 wavenumbers of the 36,873 FTIR spectra included in the database. The data were centered and scaled. The obtained score plot was used to identify possible outliers. We removed 6 spectra determined as outliers in relation to their score value (Supplemental Figure S1, see Notes) before running the PCA presented in this study. The PCA was carried out using the function prcomp in the stats package and the procedure fviz pca in the factoextra package (Kassambara and Mundt, 2020) implemented in R software.

Models for Genetic Analyses

Estimates of genetic parameters were obtained by fitting an animal model using an average information REML algorithm implemented in airemlf90 software (https://nce.ads.uga.edu/wiki/doku.php?id=readme.aireml&s[]=airemlf90). For each of the 446 FTIR wavenumbers, heritability and repeatability were estimated with a single-trait repeatability animal mixed model including pedigree and genomic relationship matrices. This animal model is commonly referred to as single-step GBLUP (Legarra et al., 2014). The pedigree consisted of 17,665 animals extracted from 6 generations. The model was defined as follows:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Zu} + \mathbf{Wp} + \mathbf{e}, \quad [1]$$

where $\mathbf{y}$ is the vector of transmittances for one wavenumber and $\mathbf{X}$ is the incidence matrix relating environmental fixed effects ($\boldsymbol{\beta}$) to the individuals. The fixed effects considered were flock × year × lactation month and parity (1, 2, 3, 4+). $\mathbf{Z}$ is the design matrix allocating observations to the vector of random additive genetic effects ($\mathbf{u}$) normally distributed $\left[N\left(\mathbf{0},\mathbf{H}\sigma_u^2\right)\right]$, $\mathbf{H}$ is the genetic relationship matrix based on pedigree data and SNP information, σ_u^2 is the additive genetic variance, $\mathbf{W}$ is the design matrix allocating observations to the vector of random permanent environmental effects ($\mathbf{p}$) $\left[N\left(\mathbf{0},\mathbf{I}\sigma_p^2\right)\right]$, and σ_p^2 is the permanent environmental variance; $\mathbf{e}$ is the vector of random normal errors $\left[N\left(\mathbf{0},\mathbf{I}\sigma_e^2\right)\right]$, and σ_e^2 is the residual variance, with $\mathbf{I}$ being the identity relationship matrix. Matrix $\mathbf{H}$ is the genetic relationship matrix combining SNP information and pedigree data, implemented as in Legarra et al. (2009):

$$\mathbf{H} = \begin{pmatrix} \mathbf{A}_{11} + \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\left(\mathbf{G} - \mathbf{A}_{22}\right)\mathbf{A}_{22}^{-1}\mathbf{A}_{21} & \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{G} \\ \mathbf{G}\mathbf{A}_{22}^{-1}\mathbf{A}_{21} & \mathbf{G} \end{pmatrix},$$

where $\mathbf{A}$ is a pedigree-based relationship matrix with indices of 1 for ungenotyped animals and 2 for genotyped animals, and $\mathbf{G}$ is the genomic relationship matrix (VanRaden, 2008).

The heritability (h^2) of the transmittance at each wavenumber was calculated as follows:

$$h^2 = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_p^2 + \sigma_e^2}.$$

Repeatability (t) was calculated on the basis of variance estimates obtained from heritability analyses:

$$t = \frac{\sigma_u^2 + \sigma_p^2}{\sigma_u^2 + \sigma_p^2 + \sigma_e^2}.$$

The genetic variability of part of the FTIR spectrum was then studied by dissociating lactation stage periods. The heritabilities and genomic correlations at each of the 446 selected wavenumbers between transmittance values obtained for 2 lactation stage groups, from the second to the fourth and from the fifth to the seventh lactation months, were estimated using a bivariate repeatability animal mixed model including pedigree and genomic relationship matrices. The following model was applied:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix}\begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix}\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix}\begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}, \quad [2]$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are vectors of observations for traits 1 and 2, respectively (one spectral point from 2 lactation stage groups); $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of environmental

Table 1. Descriptive statistics of the infrared wavenumbers, milk production and quality traits (DMY, FC, PC, SCS), approximated feed efficiency (LFCR, REI), and BCSΔ in French Lacaune dairy sheep[1]

Trait (unit)	No.	Mean	SD	Minimum	Maximum
Transmittance (n = 446 wavenumbers)	36,873	0.9	0.2	0.1	1.7
DMY (L/d)	36,317	2.1	0.8	0.1	6.3
FC (g/L)	36,261	72.7	14.1	25.1	139.2
PC (g/L)	36,261	60.1	8.8	37.0	104.9
SCS	34,499	2.9	1.6	0.06	9.0
LFCR	27,691	0.9	0.3	0.07	1.9
REI (UFL/d)	27,691	−0.002	0.305	−0.891	1.577
BCSΔ	27,691	0.01	0.03	−1.25	1.25

[1]DMY = daily milk yield; FC = fat content; PC = protein content; LFCR = lactation feed conversion ratio; REI = residual energy intake; UFL = unité fourragère lait; BCSΔ = change in body condition score.

fixed effects, such as flock × year and parity (1, 2, 3, 4+); and $\mathbf{X}_1$ and $\mathbf{X}_2$ are associated incidence matrices; $\mathbf{u}_1$ and $\mathbf{u}_2$ are vectors of random additive genetic effects; $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are associated incidence matrices; $\mathbf{p}_1$ and $\mathbf{p}_2$ are vectors of random permanent environmental effects; $\mathbf{W}_1$ and $\mathbf{W}_2$ are the associated incidence matrices; and $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals. The following variance–covariance structure was assumed:

$$\text{var}\begin{pmatrix}\mathbf{u}\\ \mathbf{p}\\ \mathbf{e}\end{pmatrix}=\begin{pmatrix}\mathbf{G}\otimes\mathbf{H} & 0 & 0\\ 0 & \mathbf{P}\otimes\mathbf{I}_p & 0\\ 0 & 0 & \mathbf{R}\otimes\mathbf{I}_e\end{pmatrix},$$

where **G** is the genetic variance–covariance structure of traits 1 and 2; **H** is the genetic relationship matrix based on pedigree data and SNP information; **P** is the permanent environmental variance–covariance structure of traits 1 and 2; $\mathbf{I}_p$ and $\mathbf{I}_e$ are identity matrices; and **R** is the diagonal matrix of residual variances for traits 1 and 2.

In addition, genomic correlations between FTIR spectra and milk yield, milk components, feed efficiency traits, and body reserve changes were estimated. For the estimation, bivariate models were used with each wavenumber (n = 446) as trait 1 ($\mathbf{y}_1$) and trait 2 ($\mathbf{y}_2$) consisting of each of the following traits: DMY, FC, PC, SCS, LFCR, REI, and BCSΔ. For wavenumber ($\mathbf{y}_1$), the fixed effects considered ($\mathbf{b}_1$) were flock × year × lactation month and parity (1/2/3/4+). The fixed effects considered for the other traits ($\mathbf{b}_2$) included parity × lactation month, litter size (single/multiple) × lactation month, lambing period (start/end according to parity) × lactation month, mating mode (animal insemination/natural breeding) × lactation month, and flock × year × lactation month. The same random effects ($\mathbf{u}_1$, $\mathbf{u}_2$, $\mathbf{p}_1$, $\mathbf{p}_2$, $\mathbf{e}_1$, and $\mathbf{e}_2$) and variance–covariance structures as defined in model 2 were used, except for the residual matrix **R**, where covariance was assumed between traits 1 and 2.

RESULTS

Descriptive Statistics

The descriptive statistics (mean, SD, minimum, and maximum) for the studied traits measured over the lactation period (mo 2–7) in the edited data set are given in Table 1. The mean transmittance value (± SD) for the FTIR spectra of ovine milk samples, including the 446 selected wavenumbers, was 0.9 ± 0.2. The mean values (± SD) for the dairy traits were 2.1 ± 0.8 L/d for DMY, 72.7 ± 14.1 g/L for FC, 60.1 ± 8.8 g/L for PC, and 2.9 ± 1.6 for SCS. The average values (±SD) of feed efficiency-related traits were 0.9 ± 0.3 for LFCR, −0.002 ± 0.305 UFL/d for REI, and 0.01 ± 0.03 for BCSΔ.

Figure 1 shows the average transmittance over the lactation period for the full FTIR spectra (1,060 wavenumbers, Figure 1A) and for the 446 selected wavenumbers (Figure 1B) in Lacaune sheep milk. The overlap of the corresponding 36,873 full FTIR spectra is plotted in Supplemental Figure S2 (see Notes). As expected, 2 of the nonselected regions between 5,012 and 2,975 cm^{-1} and between 1,713 and 1,547 cm^{-1} showed greater variation than the other regions due to the absorption peak of water. The phenotypic variability of spectral zones in the 446 wavenumbers was rather low along the spectra; however, greater variability was observed for transmittance peaks.

The PCA score plot of the 446 wavenumbers presented in Figure 2 indicated that the first 2 principal components (**PC1** and **PC2**) explained 86% of the spectral variability (59.5% for PC1 and 26.5% for PC2). Moreover, the first 4 principal components explained 98% of the total variance. The low number of principal components explaining almost all of the spectral variability indicated that the wavenumbers were highly correlated with each other (Supplemental Figure S3, see Notes). On the score plot, 2 groups of observations with distinct sizes can be distinguished (Figure 2): a small group of data on the

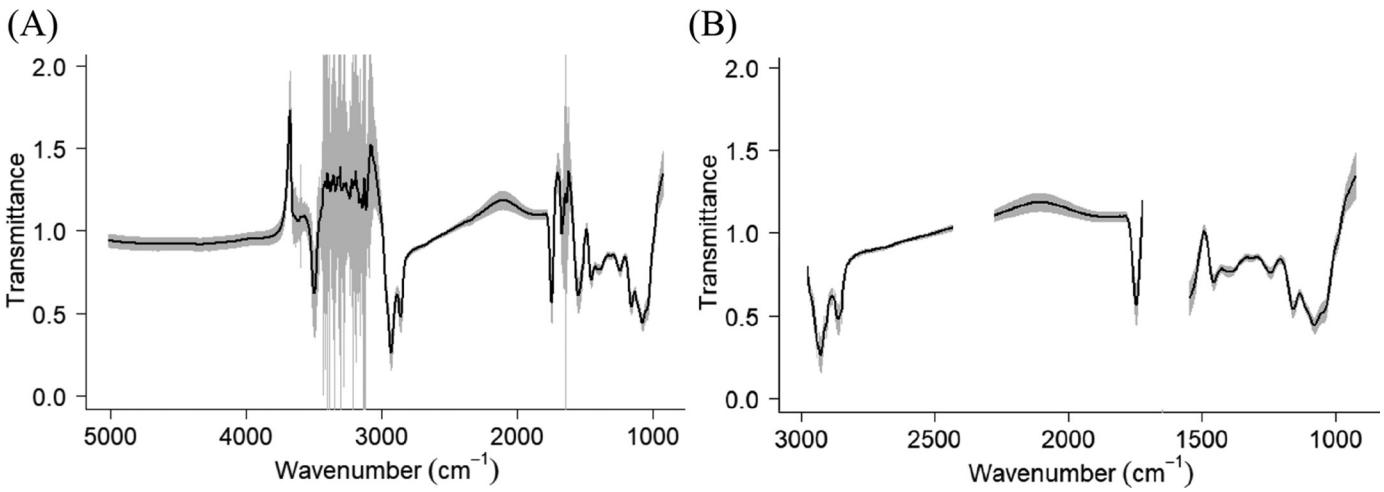

Figure 1. Average transmittance for (A) 1,060 infrared wavenumbers and (B) the corresponding 446 selected spectral points from FTIR milk spectra in French Lacaune dairy sheep. The black lines refer to the average transmittance, and the gray lines refer to the average transmittance ± 2 SD.

bottom left of the figure (below PC1: −18 and PC2: −31) and a larger group of data centered on the point (0, 0). Then, an overlapping stratification, indicating how the groups were distributed across different lactation stage classes, could be described by principal component 1. The larger group included spectra collected at the beginning and end of lactation at a ratio of 53% to 47%, whereas the small group was 90% composed of spectra collected at the end of lactation (mo 5–7). The first principal component was also strongly related to additional dairy traits, with DMY as opposed to the milk components, i.e., FC and PC. The additional SCS variable possibly highlighted the division of scores into a small group separate from the rest of the individuals. The SCS seemed to be moderately related to the first 2 principal components. The mean values (± SD) of DMY, FC, PC, and SCS for the larger group were 2.1 ± 0.8, 72.7 ± 14.1, 59.9 ± 8.7, and 2.9 ± 1.6, respectively. In contrast, the small group exhibited mean values (± SD) of 1.6 ± 0.7, 76.7 ± 13.6, 67.5 ± 7.3, and 3.1 ± 1.7 for the same parameters. The additional traits of feed efficiency and change in body reserves were not related to these 2 main principal components. The second principal component showed a wider dispersion of the scores presented by FTIR spectra collected at the end of lactation than at the beginning of lactation.

The eigenvector (loading) plot of the 446 wavenumbers is presented in Figure 3. Some areas of the FTIR spectrum were strongly linked to the structuring of scores on the 1–2 plane of the PCA. Loadings for the first principal component showed peaks in the region between 2,971 cm^{-1} and 2,840 cm^{-1} and between 1,770 cm^{-1} and 1,150 cm^{-1}, as well as a large contribution between 2,500 cm^{-1} and 1,790 cm^{-1}. Loadings for the second principal component showed a greater contribution in the 2 infrared areas between 2,840 cm^{-1} and 2,600 cm^{-1} and between 1,500 cm^{-1} and 1,100 cm^{-1}.

Heritabilities of FTIR Spectra

The heritabilities and repeatabilities of the transmittance for 446 individual wavenumbers in the FTIR region from 2,971 to 926 cm^{-1} are presented in Figure 4. The average heritability (± mean SE) of the 446 wavenumbers was 0.29 ± 0.02, ranging from 0.13 ± 0.01 to 0.42 ± 0.02. The repeatability estimates showed a pattern similar to heritability, with values between 0.15 and 0.53 (average of 0.39) for 446 wavenumbers, and between 0 and 0.53 (average of 0.29) for 1,060 wavenumbers. Describing more precisely the values of the estimates for the 446 wavenumbers starting from 2,971 cm^{-1}, both parameters have very high values (heritability greater than 0.40 and repeatability greater than 0.50) and then decrease sharply to lower values (0.13 and 0.15 for both estimates) around the wavenumber 2,600 cm^{-1}. The estimates on either side of the 2,000 cm^{-1} (2,300–1,800 cm^{-1}) wavenumber became stable again (heritability from 0.31 ± 0.02 to 0.34 ± 0.01 and repeatability from 0.39 to 0.44), with a major difference. Below 1,800 cm^{-1}, heritability and repeatability appeared to be irregular, with average (± mean SE) values of 0.30 ± 0.09 and 0.41, respectively. The same estimates for the full spectra (1,060 individual wavenumbers) in the FTIR region from 5,012 to 926 cm^{-1} have been reported in Supplemental Figure S4 (see Notes). The average heritability (± mean SE) of the 1,060 wavenumbers was 0.20 ± 0.01, ranging from 0.00 ± 0.00 to 0.42 ± 0.02. In total, 421 spectral points had estimated heritabilities between 0.10 and 0.20, 179 spectral points

Figure 2. Score plot for the first 2 principal components (PC1 and PC2) of the PCA performed on 446 wavenumbers from the FTIR spectra of French Lacaune sheep milk belonging to 2 different classes of lactation months. The additional variables related to milk and feed efficiency were associated with the individuals. DMY = daily milk yield; FC = fat content; PC = protein content; LFCR = lactation feed conversion ratio; REI = residual energy intake; BCSΔ = change in body condition score.

had estimated heritabilities between 0.20 and 0.30, and 296 spectral points had estimated heritabilities greater than 0.30. The 164 wavenumbers with very low or null heritability were located in the water absorption areas between 1,671 and 1,624 cm^{-1} and between 3,662 and 3,083 cm^{-1}.

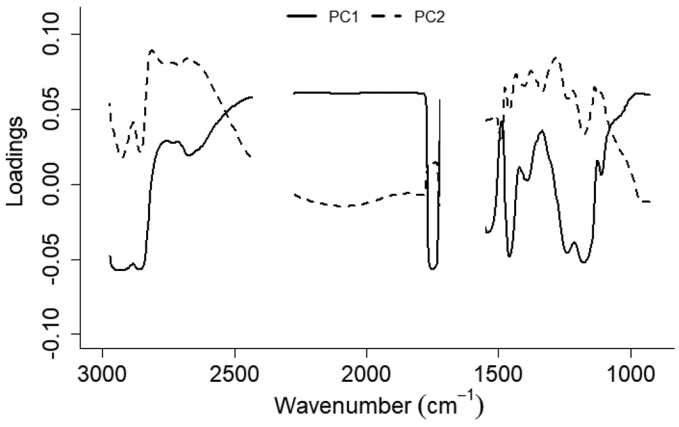

Figure 3. Eigenvector plot from the first 2 principal components (PC1 and PC2) of a PCA linked to spectral regions, performed on 446 wavenumbers from the FTIR spectra of French Lacaune sheep.

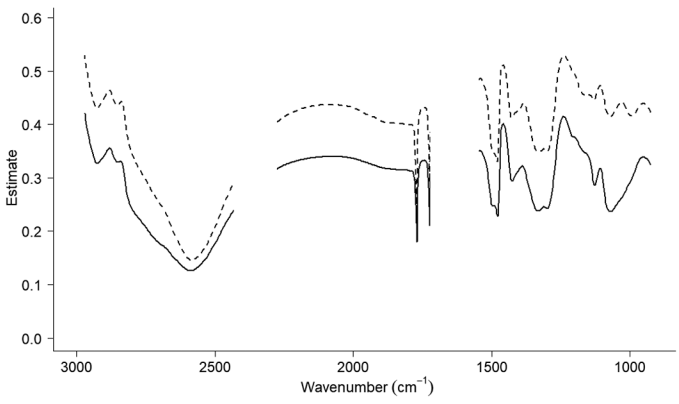

Figure 4. Heritabilities (solid line) and repeatabilities (dotted line) for the transmittance of 446 individual spectral points in the infrared region from 2,971 to 926 cm^{-1} from French Lacaune dairy sheep milk. The SE for heritabilities ranged from 0.00 to 0.02.

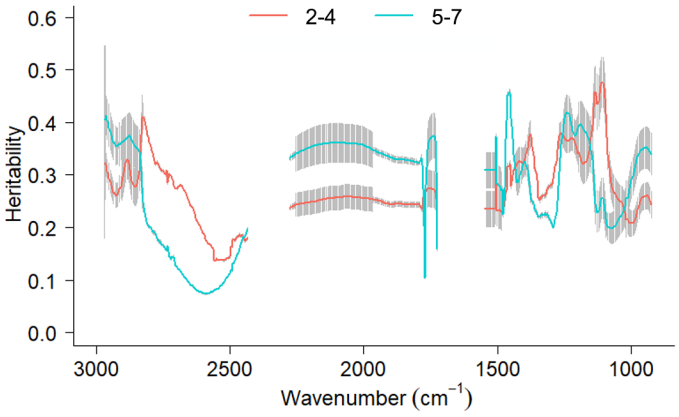

Figure 5. Heritabilities of transmittance for 446 individual spectral points in the MIR region for milk samples collected at early (mo 2–4, red line) or late (mo 5–7, blue line) lactation stages from French Lacaune dairy sheep. The gray lines indicate SE ranging from 0.00 to 0.07.

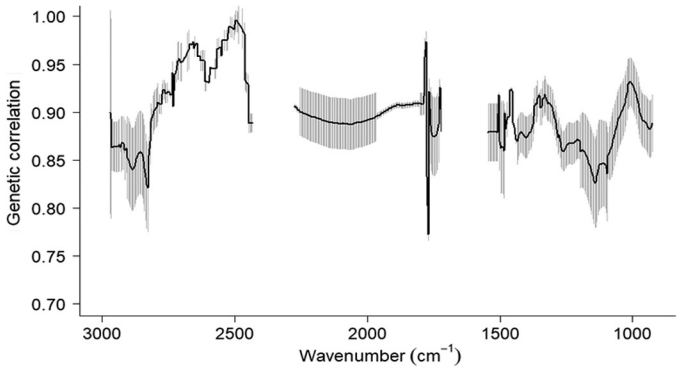

Figure 6. Genomic correlations estimated for each of the 446 individual spectral points in the MIR region between milk samples collected at early (mo 2–4) or late (mo 5–7) lactation stages from French Lacaune dairy sheep. The gray lines indicate SE ranging from 0.00 to 0.05.

The heritabilities of transmittance for 446 wavenumbers estimated separately for each group of lactation stages (mo 2–4 and mo 5–7) are presented in Figure 5. Analysis by lactation stage group revealed a wider range of heritabilities, ranging from 0.07 ± 0.001 to 0.48 ± 0.02, than pooling all the data together (ranging from 0.13 ± 0.01 to 0.42 ± 0.02 for the commonly selected wavenumbers; see Figure 4). The heritability profiles of the FTIR spectra from the early and late lactation stage groups were similar for some of the spectral regions, with a notable difference in the level of estimated values. From 2,971 to 2,800 cm^{-1}, heritability estimates started with moderate to high values for all stages of lactation (from 0.20 ± 0.001 to 0.41 ± 0.02). Up to 2,800 cm^{-1}, the estimated values decreased with a stronger slope specifically for the late lactation stages (minimum heritability was 0.14 ± 0.00 for mo 2–4 and 0.07 ± 0.00 for mo 5–7). From 2,276 to 1,800 cm^{-1}, the estimated heritabilities of wavenumbers were considered stable, with a difference between the 2 groups (average (± mean SE) of 0.25 ± 0.01 for mo 2–4 and 0.35 ± 0.01 for mo 5–7). The last part of the studied spectrum, from 1,543 to 926 cm^{-1}, showed large variability in heritability estimates for the first months of lactation (from 0.21 ± 0.01 to 0.48 ± 0.02) and for the last months of lactation (from 0.20 ± 0.01 to 0.46 ± 0.003). The genetic variance estimated across the 446 wavenumbers of the FTIR spectrum became increasingly high during lactation, with mean variances ranging from 0.006 for mo 2 to 0.02 for mo 7 (Supplemental Figure S5, see Notes). The 2 groups of lactation stages differed in the residual variance and, to a lesser extent, in the permanent environmental variance, which were greater for the late lactation stages (the mean values for residual and permanent environmental variances were 0.012 and 0.002 for mo 2–4 and 0.019 and 0.004 for mo 5–7, respectively).

Genomic Correlations of FTIR Spectra Between Lactation Stages

The estimated genomic correlations between transmittances for 446 individual spectral points from FTIR spectra of milk measured in 2 different lactation stage groups (mo 2–4 and mo 5–7) are presented in Figure 6. The genomic correlations at all wavenumbers along the spectra were positive and high, ranging from 0.77 ± 0.003 to 0.99 ± 0.01. From 2,971 to 2,830 cm^{-1}, the estimated values decreased from 0.90 ± 0.05 to 0.82 ± 0.02. In the 2,830 to 2,470 cm^{-1} wavenumber region, high and increasing genomic correlations were observed from 0.82 ± 0.02 to 0.99 ± 0.01. The highest genomic correlations were found in the area between 2,550 and 2,470 cm^{-1} (from 0.96 ± 0.00 to 0.99 ± 0.01). Over a specific length of the spectrum, from 2,276 to 1,800 cm^{-1}, strong and stable genomic correlations ranging from 0.89 ± 0.01 to 0.91 ± 0.001 were observed. The lowest genomic correlation was observed at wavenumber 1,771 cm^{-1}, with an estimated value of 0.77 ± 0.003. Between 1,543 and 926 cm^{-1}, the genomic correlations ranged from 0.83 ± 0.02 to 0.93 ± 0.01.

Genomic Correlations Between FTIR Spectra and Milk- and Feed Efficiency-Related Traits

The average heritability estimates (± mean SE) for milk-related traits were 0.15 ± 0.02 for DMY, 0.32 ± 0.02 for FC, 0.39 ± 0.02 for PC, 0.09 ± 0.01 for SCS, and 0.29 ± 0.02 for all 446 wavenumbers of the FTIR spectra. The mean heritabilities (± mean SE) of approximated feed

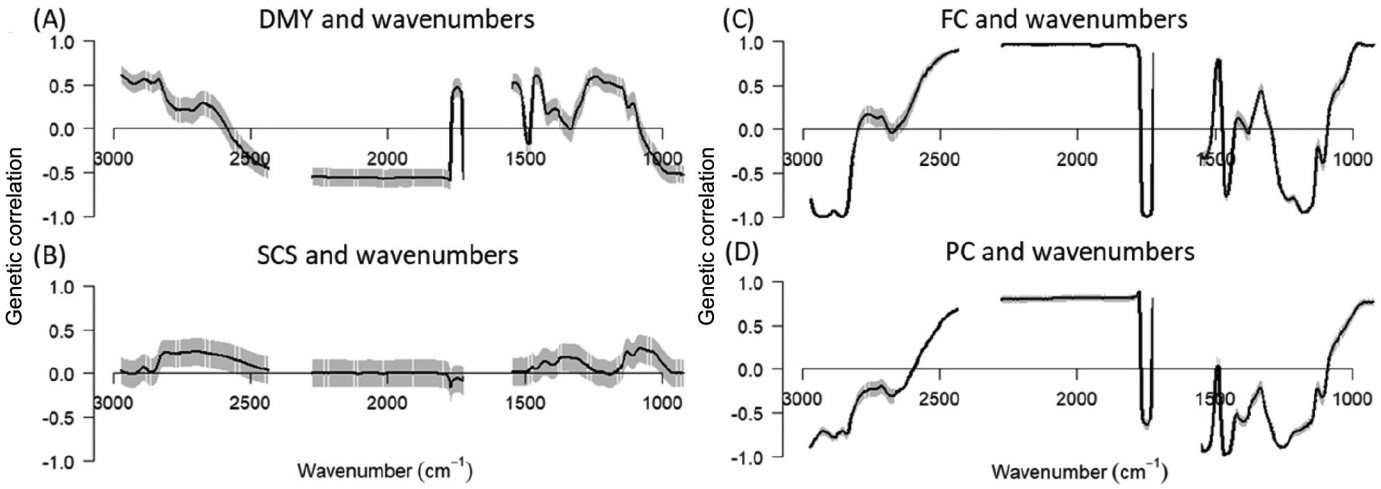

Figure 7. Genomic correlations between 446 individual spectral points in the MIR region and 4 milk-related traits with (A) DMY, (B) FC, (C) SCS, and (D) PC from French Lacaune dairy sheep milk. The gray lines refer to the SE. DMY = daily milk yield; FC = fat content; PC = protein content.

efficiency-related traits were lower, at 0.09 ± 0.01 for LFCR, 0.11 ± 0.01 for REI and 0.04 ± 0.01 for BCSΔ.

The estimated genomic correlations of transmittance for 446 individual spectral points of the FTIR milk spectra and the DMY, FC, PC, or SCS traits are presented in Figure 7. Fat content and PC showed strong and similar genomic correlation patterns with the transmittance values of the milk FTIR spectra, as opposed to the pattern observed for DMY, which had a lower amplitude. Genomic correlations between the SCS and transmittances were lower, with predominantly positive values. The estimated extreme genomic correlation values ranged from −0.57 ± 0.04 to 0.61 ± 0.05 for DMY, from −0.99 ± 0.001 to 0.98 ± 0.002 for FC, from −0.98 ± 0.003 to 0.90 ± 0.01 for PC, from −0.16 ± 0.08 to 0.28 ± 0.08 for SCS, and from 2,971 to 926 cm^{-1} for the FTIR milk spectra. Over the same spectral range, the average absolute genomic correlations (± mean SE) and transmittances obtained were 0.41 ± 0.06 for DMY, 0.66 ± 0.02 for FC, 0.60 ± 0.02 for PC, and 0.09 ± 0.08 for SCS. From 2,971 to 2,850 cm^{-1}, the genomic correlations between FC or PC and wavenumbers were high and negative (−0.96 for FC and −0.76 for PC, on average), whereas the values were close to a positive correlation of 0.5 for DMY and close to 0 for SCS. At 2 specific wavenumbers, at 2,850 and 2,650 cm^{-1}, the genomic correlation profiles tended to change for the dairy traits studied. For example, genomic correlations between milk spectra and FC were close to −1 before suddenly increasing to zero from wavenumber 2,850 cm^{-1} and then reaching positive correlations at approximately 1 from wavenumber 2,650 cm^{-1}. Within the spectral area from 2,276 to 1,800 cm^{-1}, the genomic correlations estimated were very stable, with highly differentiated values between the 4 dairy traits and transmittances, with values close to 1 for FC, 0.8 for PC, 0 for SCS, and −0.5 for DMY. Between 1,543 and 926 cm^{-1}, the genomic correlations showed erratic trends, with estimated values ranging from −0.43 ± 0.05 to 0.59 ± 0.05 for DMY, from −0.95 ± 0.01 to 0.98 ± 0.002 for FC, from −0.98 ± 0.003 to 0.77 ± 0.02 for PC, and from −0.01 ± 0.07 to 0.28 ± 0.08 for SCS, from the 446 wavenumbers.

Genomic correlations between transmittance for 446 wavenumbers of the FTIR milk spectra and approximated feed efficiency-related traits are presented in Figure 8. The regions of the spectra had strong genomic correlations with the REI (from −0.75 ± 0.04 to 0.67 ± 0.04), modest correlations with the LFCR (from −0.35 ± 0.08 to 0.44 ± 0.07), and weak correlations with the BCSΔ (from −0.31 ± 0.1 to 0.22 ± 0.1). Over the spectral range studied, the average absolute genomic correlations (± mean SE) were 0.46 ± 0.06 for REI and 0.15 ± 0.09 for LFCR and BCSΔ for the transmittances. Similarities can be observed between the genomic correlation profiles for approximated efficiency traits and those studied for dairy traits. The pattern of genomic correlations between REI and transmittance along wavenumbers was very close to that between PC and transmittance, with a difference in value levels.

DISCUSSION

Change of the FTIR Spectrum During Lactation

In this study, we carried out an initial description of French Lacaune dairy sheep spectra before genetic analysis. The original spectral data used presented a wider

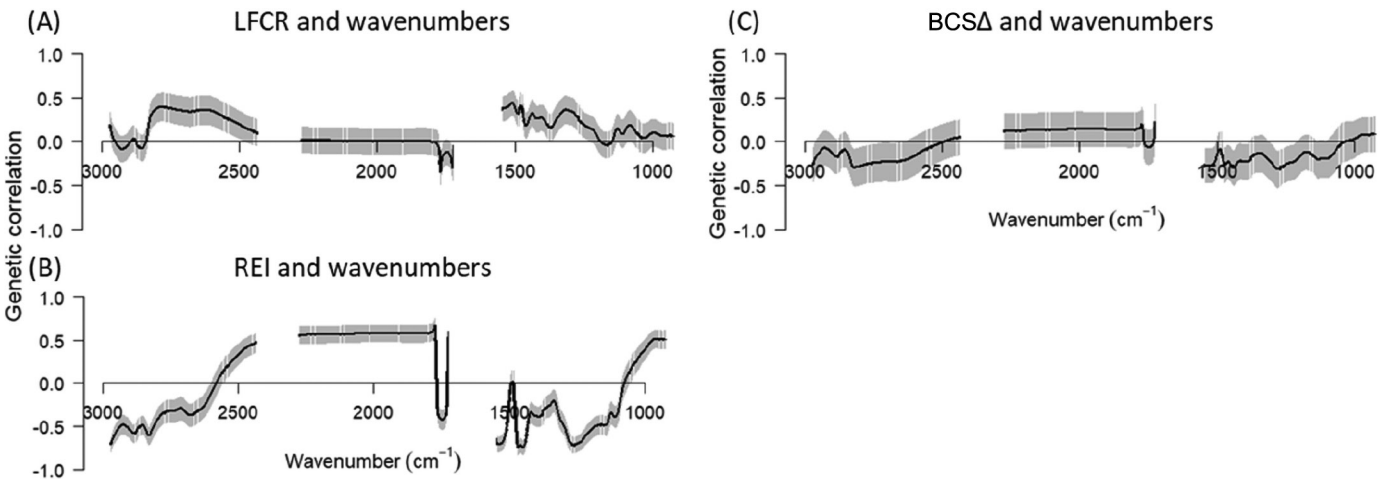

Figure 8. Genomic correlations between 446 individual spectral points in the MIR region and between approximated feed efficiency traits and (A) LFCR, (B) REI, and (C) BCSΔ from French Lacaune dairy sheep milk. The gray lines refer to the SE. LFCR = lactation feed conversion ratio; REI = residual energy intake; BCSΔ = change in body condition score.

range of lactation stage variability compared with that routinely recorded on farms in the national recording system (ICAR, 2018); this allowed us to study spectral variability over the entire exclusive lactation period. The spectral data were described using PCA to represent the set of individuals initially in a 446-dimensional space (wavenumbers selected as the most informative by the manufacturer) in a lower-dimensional space (Figures 2 and 3). The 86% of the total spectral variance of the 446 wavenumbers was explained by the first 2 principal components. When very few principal components explained much of the total variability, we found a high correlation among the wavenumbers. High correlations between adjacent spectral points were observed on the heatmap with more or less large windows of strongly correlated neighboring wavenumbers, illustrating the redundancy between the variables (Supplemental Figure S3). A similar heatmap with strong correlations between wavenumber absorbances was observed by Nan et al. (2023) in their study of milk from Chinese Holstein cows. The authors linked this heatmap structure with a division of the spectrum into 5 parts, each of which is characteristic of particular chemical events. The subdivision of the FTIR spectrum reflected regions devoid of chemical bond absorbance peaks linked to water absorption, milk fatty acids, and proteins (Bittante and Cecchinato, 2013; Rovere et al., 2019; Nan et al., 2023). In our results, the first principal component enabled us to clearly distinguish milk samples from the first part of lactation and those from the second part of lactation (Figure 2). In Holstein dairy cows, Du et al. (2020) showed that the lactation stage had significant effects on most of the wavenumbers linked to lactose (from 1,200 to 926 cm^{-1}), proteins (1,600 to 1,240 cm^{-1}), and fat molecules (3,015 to 2,800 cm^{-1} and 1,770 to 1,680 cm^{-1}), and a few wavenumbers related to water absorption regions. The stratification of spectral data by lactation period highlighted by the first principal component in our study was also directly related to the FC and PC. Primary changes in dairy sheep milk over time were observed, notably with FC being influenced by a concentration-dilution effect due to decreasing milk yield during lactation. Moreover, PC exhibited less variation, and lactose remained a relatively stable component (Hassoun et al., 2018; Oravcová et al., 2018; Inostroza et al., 2020; Tatar et al., 2022). The loadings on PC1 showed large contributions across 3 spectral ranges: between 2,971 and 2,840 cm^{-1}, between 2,500 and 1,790 cm^{-1}, and between 1,770 and 1,150 cm^{-1} (Figure 3). These regions provide specific chemical information about the fat, protein, and lactose composition of milk (Bittante and Cecchinato, 2013; Dagnachew et al., 2013a; Du et al., 2020). A study of the loadings of FTIR spectra in dairy goats by Dagnachew et al. (2013a) showed very similar results to those presented in our study. In particular, the specific regions from 3,000 to 2,800 cm^{-1} and from 1,760 to 1,720 cm^{-1} revealed significant contributions to PC1. These regions, which were also observed in the goat study for the first latent trait, were crucial for determining FC.

In Lacaune French dairy sheep, the transition from an indoor to an outdoor feeding system during mid-lactation can lead to confusion in the interpretation of our results studied throughout lactation. The effects of the stage of lactation and the feed have been studied more closely on the milk composition than directly on spectral data. Tatar et al. (2022) maintained a constant type of diet in

the Lacaune breed and revealed significant increases in fat, casein, total protein, and most mineral content of milk throughout the lactation period. Due to the dairy sheep management system, confusion between lactation stage and environment can often be observed. For example, Correddu et al. (2021) observed that in Sarda ewes, the influence of the mid-to-late lactation stage on the milk fatty acid composition did not distinctly separate physiological stage from pasture quality. The effects of pasture on milk fatty acid contents were reviewed in dairy sheep by Nudda et al. (2014) and in dairy cows by Coppa et al. (2019). Increased pasture availability combined with lower hay intake has increased the content of certain fatty acids in sheep milk, e.g., α-linolenic acid and CLA in Latxa sheep (de Renobales et al., 2012; Nudda et al., 2014). The results reported by Coppa et al. (2019) showed a seasonal influence on milk constituents, with dairy cow milk being richer in PUFA and CLA *cis*-9 during the outdoor period. The spectral stratification observed during lactation in our study could be linked to changes in milk composition on pasture, particularly for unsaturated fatty acids.

Finally, observing the spectral data based on their scores and eigenvectors, the smallest group was separated from the largest by the second principal component with high contribution in lactose infrared region (from 1,500 to 1,100 cm^{-1}) and from 2,840 to 2,600 cm^{-1} (Figure 3). In addition, the supplementary variable SCS, which is a good indicator of udder mastitis in ruminants, allowed the 2 groups to be dissociated. Gruber et al. (2023) predicted bovine clinical mastitis based directly on FTIR spectra (5,000 to 925 cm^{-1}) and obtained moderate validation specificities (0.597–0.653) and sensitivities (0.525–0.567) using various statistical methods. The authors identified a few important wavenumbers across the entire spectral range for predicting mastitis, attributed to specific chemical bonds corresponding to lactose, carbohydrates, casein, specific lipids, and water in the literature. A possible hypothesis for the dissociation of the small group from the rest of our data set was that the spectra collected came from sick ewes suffering from mastitis. However, the mean (± SD) SCS values of each group were similar (2.9 ± 1.6 for the larger group and 3.1 ± 1.7 for the small group). The majority of the spectra included in the small cluster were collected at the end of lactation (90%). Nevertheless, Kaskous et al. (2022) reported conflicting results in small ruminant studies, with however a strong tendency to observe an increase in SCC toward the end of lactation due to a decrease in milk production in the ovine studies cited. In the French Lacaune breed, according to Barillet et al. (2001b), the SCS increased during lactation (from 3.08 to 3.43).

Genetic Parameters of FTIR Ovine Milk Spectra

To our knowledge, little investigation has focused on the genetic variability of wavenumbers in the FTIR spectra of dairy sheep. In the present study, moderate to high heritabilities (from 0.13 ± 0.01 to 0.42 ± 0.02) were estimated for 446 of the wavenumbers selected from the FTIR spectra of Lacaune dairy ewes, excluding areas of water absorption, whose heritability was close to zero (Figure 4, Supplemental Figure S4). A lower average (0.13 ± 0.06) and a different pattern of heritabilities, with water spectral zones having nonzero heritabilities, were reported for the 1,060 wavenumbers milk absorbance spectra in the Sarda dairy sheep breed (Congiu et al., 2024) compared with our result (average of 0.20 ± 0.01). A difference in milk composition, particularly in fatty acids, can be observed between dairy ewe breeds, with the French Lacaune breed showing a higher saturated fatty acid content of 74.22 g/100 g of fat compared with 67.72 g/100 g in the Italian Sarda breed (Ferrand-Calmels et al., 2014; Cesarani et al., 2019). Overall, a greater difference in milk composition was observed between sheep, goat, and cattle species than between the 2 sheep breeds. However, our heritability results were closer to those already known for dairy cows and dairy goats in terms of patterns and levels. In dairy cattle, heritabilities for wavenumbers of FTIR milk spectra ranged from 0.00 to 0.42 in first-parity Belgian Holstein cattle (Soyeurt et al., 2010), from 0.00 to 0.27 in Brown Swiss cattle (Bittante and Cecchinato, 2013), from 0.00 to 0.63 in first-parity Holstein Friesians in the Netherlands (Wang et al., 2016), and from 0.00 to 0.31 in Danish Holstein cattle and 0.00 to 0.30 in Danish Jersey cattle (Zaalberg et al., 2019). Lower estimates were reported in Chinese Holstein cattle, with values ranging from 0.00 to 0.11 (Du et al., 2020). In Norwegian dairy goats, the estimated heritabilities of spectral variables ranged between 0.02 and 0.41 (Dagnachew et al., 2013a). In summary, our results indicated that 45% of the wavenumbers across the entire spectrum (1,060 wavenumbers) have a heritability above 0.20, compared with the range of 0.20 to 0.60 that Wang et al. (2016) reported for most variables, and the low averages of 0.04 and 0.09 reported by Du et al. (2020) and Bittante and Cecchinato, (2013), respectively.

Our study examined the genetic variability of FTIR spectra over the entire lactation period and then focused on determining whether the genetic variability of wavenumbers changed over time. The PCA results, as discussed earlier, revealed a distinct stratification of scores corresponding to the lactation period between the beginning and end of lactation. Moreover, heritability for a given wavenumber varied between early lactation (mo 2–4) and late lactation (mo 5–7), as illustrated in Figure 5.

Rovere et al. (2019) investigated the heritability profiles of FTIR spectra in Holstein cows, categorizing them by parity and lactation month. We found significant differences between the first month of lactation and the other months at most of the wavenumbers studied. From the third to the sixth month, the heritability profiles showed minimal contrast. Comparison of the results of Rovere et al. (2019) with our own shows that common spectral regions were used to distinguish the lactation period from heritability estimates, which were located between 2,971 and 2,800 cm^{-1} (alkyl chain of fatty acids) and between 2,546 and 2,526 cm^{-1} (amino acids cystine and cysteine present in whey protein). The region from 2,276 to 1,800 cm^{-1} clearly distinguished the heritability patterns from early- and late-lactation milk samples in our study, which were highlighted only for primiparous cows. However, our findings demonstrated robust and strong genomic correlations of FTIR milk spectra between the 2 lactation periods (Figure 6), indicating negligible genetic-environmental interactions (Mulder and Bijma, 2006). The lowest genomic correlation observed at wavenumber 1,771 cm^{-1}, with an estimated value of 0.77 ± 0.003, was included in the spectral region linked to fatty acids (Bittante and Cecchinato, 2013).

In our study, genetic analyses linking the FTIR spectrum to another trait focused first on the dairy traits integrated into the breeding goals of dairy ewes (Figure 7), i.e., DMY, FC, PC, and SCS (Barillet et al., 2001a). The milk spectra were moderately to highly genetically correlated with DMY. Daily milk yield, which had negative genetic correlations of −0.50 ± 0.05 with FC and −0.62 ± 0.05 with PC (Machefert et al., 2023), showed an opposite and lower amplitude pattern of genomic correlations with wavenumbers than milk quality traits. As FC and PC were predicted by FTIR spectroscopy, high genomic correlation values were expected between these milk components and milk spectra. Du et al. (2020) reported a very similar pattern with a slightly lower amplitude of genetic correlations between common wavenumbers and milk fat and protein percentages in Holstein dairy cows. The authors reversed the patterns by using absorbance (A) data, whereas we used transmittance (T) values, which are connected by the equation $A = -log_{10}T$ (Bittante and Cecchinato, 2013). The spectral region reflecting proteins of milk, called the protein region by Du et al. (2020), from 1,600 to 1,240 cm^{-1} was strongly genetically correlated with the protein percentage trait (from −0.42 to 0.94) in Holstein cows. The same observation could be made for fat regions from 3,015 to 2,800 cm^{-1} and 1,770 to 1,680 cm^{-1} and fat percentage traits (genetic correlations from −0.88 to 0.80) in dairy cattle (Du et al., 2020). In our study, wavenumbers located in the fat and protein spectral regions, defined by Du et al. (2020), were strongly genetically correlated with FC and PC, and few spectral points had a low estimate. The genomic correlations between the FC and transmittance values within fat regions ranged from −0.99 ± 0.001 to 0.92 ± 0.01, and those between the PC and transmittance values within protein regions ranged from −0.79 ± 0.01 to 0.80 ± 0.02. Combining these results with spectral heritability in our study showed that some areas of spectra that exhibited large heritability were also strongly genetically correlated with DMY, FC, and PC. More specifically, 3 highly heritable spectral peaks (>0.40) observed on Figure 3 around wavenumbers 2,971 (fat region), 1,458 (protein region), and 1,242 cm^{-1} (close to lactose-region) were associated with milk yield and milk composition with high genomic correlations (>|0.5| for DMY and >|0.7| for FC and PC). Compared with the other studied dairy traits, SCS was weakly genetically correlated with the FTIR spectra. The study of the most informative wavenumbers for predicting mastitis by Gruber et al. (2023) in dairy cows revealed spectral regions similar to those strongly genetically correlated with SCS. Three genomic correlation peaks were observed in Figure 7 for SCS and pointed out in the study in dairy cows as being the 1% most important variables of interest for mastitis prediction in the infrared region from 1,700 to 926 cm^{-1} for 2 of them and from 3,000 to 2,500 cm^{-1}.

The determination of feed efficiency traits requires precise individual measures that are unavailable on commercial dairy sheep farms with collective feeding strategies and pastures. Moreover, the proposed approximated feed efficiency traits in our study were weakly heritable, with values of 0.10 ± 0.01 for LFCR and 0.11 ± 0.01 for REI (Machefert et al., 2023). If strong genomic correlations were observed between traits that were difficult to measure and traits that were easier to assess, then the prediction of feed efficiency trait using spectra will be facilitated. To compare, there have been very few reports on genetic correlations between milk spectra and feed efficiency. Toledo-Alvarado et al. (2022) estimated the genetic correlations between FTIR spectra from bovine milk and residual feed intake (**RFI**) from individual daily feed intake measurements. In this study, RFI showed low to moderate genetic correlations along spectra ranging from −0.24 to 0.22, with the highest values between 3,048 and 1,701 cm^{-1}. Some of these wavenumbers were located in 2 specific spectral regions related to the chemical structure of the fat molecules (Lei et al., 2010; Dagnachew et al., 2013a; Du et al., 2020). Our results revealed a greater range of genomic correlations between FTIR spectra and the 2 approximated feed efficiency traits studied, ranging from −0.35 to 0.44 for the LFCR and from −0.75 to 0.67 for the REI. Previous results showed that LFCR and REI traits, measured in the commercial farm context imposing collective feed intake collection, were phenotypically and genetically

dependent on milk production traits (the genetic correlations between LFCR and DMY, FC and PC were 0.74 ± 0.04, 0.11 ± 0.07, and −0.18 ± 0.07, respectively, and between REI and DMY, FC, and PC were −0.79 ± 0.04, 0.46 ± 0.06, and 0.75 ± 0.04, respectively) and strongly influenced by environmental factors (Machefert et al., 2023). Despite the lower accuracy of the estimation of efficiency traits in our study, the genomic correlation profile between REI and transmittances was similar, with a larger amplitude than that obtained between RFI and absorbances in the study of Toledo-Alvarado et al. (2022). For a trait unrelated to milk measurement, such as BCSΔ, with very low heritability (0.04 ± 0.01), our results revealed modest genomic correlations depending on the targeted spectral region (from −0.31 ± 0.1 to 0.22 ± 0.1). However, McParland et al. (2015) in Irish Holstein-Friesian cows, showed high phenotypic correlations between BCSΔ and the same predicted trait using FTIR spectra (from 0.63 to 0.76). Although this trait had a low heritability (0.07 ± 0.02), these authors suggested the development of reliable calibration predictions BCSΔ from milk spectra to generate estimates of genetic breeding values at the routine level.

CONCLUSIONS

The study demonstrated that the transmittance of individual FTIR bands in Lacaune ewe milk was heritable, with a different evolution of the genetic variability of the spectrum during lactation. This study revealed moderate to strong genomic correlations between dairy traits included in breeding goals and wavenumbers. More importantly, specific wavenumbers that were highly heritable were also strongly genetically associated with economically important dairy traits. FTIR spectral data also represent a useful source of information for the study of complex traits, such as the proposed feed efficiency traits. However, it would be interesting to confirm our results with more precisely phenotyped feed efficiency traits at the individual level. Further analyses, such as genomic association studies, are needed to identify the specific regions of the genome that contribute to the genetic variability of the transmittance along milk FTIR spectra and feed efficiency traits to better understand their genetic relationships. The present study highlighted the importance of routinely phenotyping the FTIR spectrum.

NOTES

This project received funding from the European Union's Horizon 2020 Research and Innovation Program under grant agreement no. 772787 (SMARTER). The first author also received financial support from the Occitanie region and the Animal Genetic Division of the National Research Institute for Agriculture, Food and Environment (INRAE, Paris, France). The authors thank the breeders and technicians of the breeding organizations UNOTEC/OVITEST (Onet-Le-Château, France) and Service Elevage Confédération Générale de Roquefort (Millau, France) for providing the data. Supplemental material for this article is available at https://doi.org/10.6084/m9.figshare.27088651.v2. No human or animal subjects were used, so this analysis did not require approval by an Institutional Animal Care and Use Committee or Institutional Review Board. The authors have not stated any conflicts of interest.

Nonstandard abbreviations used: BCSΔ = change in BCS; DMY = daily milk yield; FC = fat content; FTIR = Fourier transform infrared; H2020 SMARTER = Horizon 2020 Small Ruminants breeding for Efficiency and Resilience; LFCR = lactation feed conversion ratio; MIR = mid-infrared; PC = protein content; PC1 and PC2 = first and second principal component; PCA = principal component analysis; REI = residual energy intake; RFI = residual feed intake; UFL = unité fourragère lait.

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