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Abstract
This study aimed to estimate the effect of temperature-humidity index (THI) and the magnitude of genotype-by-THI (GxTHI) interactions on milk production traits and on somatic cell score in Montbéliarde cows. Test-day records from first and second lactations from 2016 to 2020 were associated with the average THI of the three days before the test-day record. A total of 301,078 test-day records from 39,469 cows in first lactation and 292,648 test-day records from 37,593 cows in second lactation were analyzed. The average THI effect, estimated with an animal mixed model, indicated that the optimal THI was below 55 (*ie* ~ 12-13°C). Individual responses to THI were estimated simultaneously with the time-dependent response by random regression models. Regardless of the stage of lactation, genetic correlations along the THI gradient were > 0.80 and most of them were > 0.90, suggesting that GxTHI interactions were weak for production and for udder health traits.

Introduction
Heat stress negatively influences cattle welfare, health and productivity (Lees *et al*., 2019). To cope with global warming and forecasted increases in temperature and heat waves frequency, identifying high-producing animals tolerant to heat is of capital importance to satisfy the need for animal-sourced foods. Several measures exist to assess heat stress, one of them consists in determining the meteorological conditions that lead to a decrease in performance. The most widespread indicator for heat stress in cattle is a temperature-humidy index (THI) combining the effects of temperature and humidity. The first objective of the present study is to estimate the critical temperature marking the onset of heat stress through the decline in performance and to quantify the amplitude of this decline in the range of THI currently encountered in the French Montbeliarde breeding regions. The second objective is to perform genotype-by-environment studies to find out if there is individual variability in heat tolerance, and therefore if some animals may be better adapted to produce despite warm temperatures.

Materials & Methods
Performance and meteorological data
Performances, along with pedigree information, were available for this study from the French national database. Data were selected from first (L1) and second (L2) lactation test-day records of Montbéliarde cows from five French regions (Franche-Comté, Rhône-Alpes, Auvergne, Bretagne and Pays-de-Loire), gathered between August 2016 and December 2020. The phenotypes analyzed were milk yield (MY), fat content (FC), protein content (PC) and somatic cell score (SCS) obtained as a log-transformation of somatic cell concentration ($SCS=\log_2(SCC/100,000)+3$). Only animals with known parents and age at calving between 23-42 months and 35-60 months for first and second parity, respectively, were considered. Lactation length was limited to 305 days. Finally, a total of 301,078 test-day performances from

39,469 cows (94,476 animals in pedigree files) in L1 and 292,648 performances from 37,593 cows (98,015 animals in pedigree files) in L2 from herds were randomly selected in the whole population.
Meteorological data were provided by the Safran database from Météo-France. This database contains daily estimated temperature and humidity values on a grid of 9892 squares of 8x8km. Performance and meteorological databases were merged according to the zip code of each farm, and test-day records were associated with the average THI of the three days before the test-day. The daily THI was calculated (1.8*T+32)-(0.55-0.0055*RH)*(1.8*T-26), with T being the 24h-average temperature (Celsius), and RH the 24h-average relative humidity (%).

Estimation of THI effect on phenotypic performances
The model used to estimate the average effect of THI on MY, FC, PC, and SCS was:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Z_1\,a} + \mathbf{Z_2\,p} + \mathbf{e}, \qquad \textbf{(1)}$$

where **y**, **β**, **a**, **p**, and **e** are the vectors of recorded phenotypes, fixed effects, additive genetic effects, permanent environmental (pe) effects and the residuals of the model, respectively. **X**, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are the incidence matrices for **β**, **a** and **p** respectively. For each trait, the fixed effects considered were contemporary group (herd-year combination), days in milk (DIM), age at calving (in months), days carried calf (days from successful insemination until test-day, converted to months), month of calving (12 classes), and THI by classes.

To study the GxTHI interactions, the random regression model used was:

$$\mathbf{y} = \mathbf{X\beta} + \sum_{r=0}^{2}\mathbf{Z_r}(d)\,\mathbf{a_r} + \sum_{s=1}^{3}\mathbf{Z_s}(t)\,\mathbf{a_s} + \sum_{m=0}^{2}\mathbf{Z_m}(d)\,\mathbf{p_m} + \sum_{n=1}^{3}\mathbf{Z_n}(t)\,\mathbf{p_n} + \mathbf{e} \qquad (2)$$

where **y**, **β**, and **e** are the same as described for model (1). **X** is the incidence matrices for **β**. The contemporary group was defined by herd-test-day with at least three cows. The other fixed effects considered were as for model (1) excluding THI. The effect of THI was considered using polynomials along with DIM for the genetic and pe effects. Thus, for the genetic effect, $\mathbf{Z_r}$ and $\mathbf{Z_s}$ are vectors of covariates of the r^{th} and s^{th} polynomials, respectively, evaluated at DIM d or THI t; $\mathbf{a_s}$ and $\mathbf{a_r}$ are the genetic random regression coefficients. For the pe effect, the model is the same with $\mathbf{Z_m}$ and $\mathbf{Z_n}$, the vectors of the polynomials depending respectively on DIM or THI and $\mathbf{p_m}$ and $\mathbf{p_n}$, the pe random regression coefficients. For all traits we used Legendre polynomials of order 3 for THI and order 2 for DIM with an overall mean. The residual variances were considered heterogeneous for the 55 possible combinations of five THI classes and 11 DIM classes. These random regression models allowed to estimate the variances components and individual breeding values (EBV) for all combinations of THI and DIM.

For the analyzes MY, FC, PC, and SCS were considered separately. The pedigree was traced back three generations and trimmed. Variance components and all effects were estimated using the software WOMBAT (Meyer, 2007).

Results & Discussion
Effect of THI on performances
The least-squares solutions of each classes of THI are presented in Figure 1. For MY, THI was optimal in the range of 50-55 (*ie* 7 to 13°C) with both cold and heat stress effects, whereas FC, PC and SCS tended to present only heat stress effect, declining for THI above 35 (*ie*. -3 to 2°C). These results indicate a lower comfort THI than commonly found in high-producing dairy cows (Carabaño *et al*., 2017). However, the fact that a large part of the studies on high-producing dairy cows concerns cows intensively raised in countries warmer than France may mitigate the effect of high outdoor temperatures due to controlling inside barns, sometimes with cooling systems, and a probable acclimatization to warmer temperatures from a young age. Most of the French Montbeliarde cows are kept outdoor in spring and summer and thus probably more faced

to hot weather events. In terms of phenotypic standard deviations (sd), the decrease in performances due to heat stress was more prominent for FC and PC (respectively 0.8 for FC in all parities, 1.2 and 0.6 phenotypic sd for PC in L1 and L2) than for MY (0.2 and 0.3 phenotypic sd for L1 and L2 respectively) and SCS (<0.2 phenotypic sd for all parities).

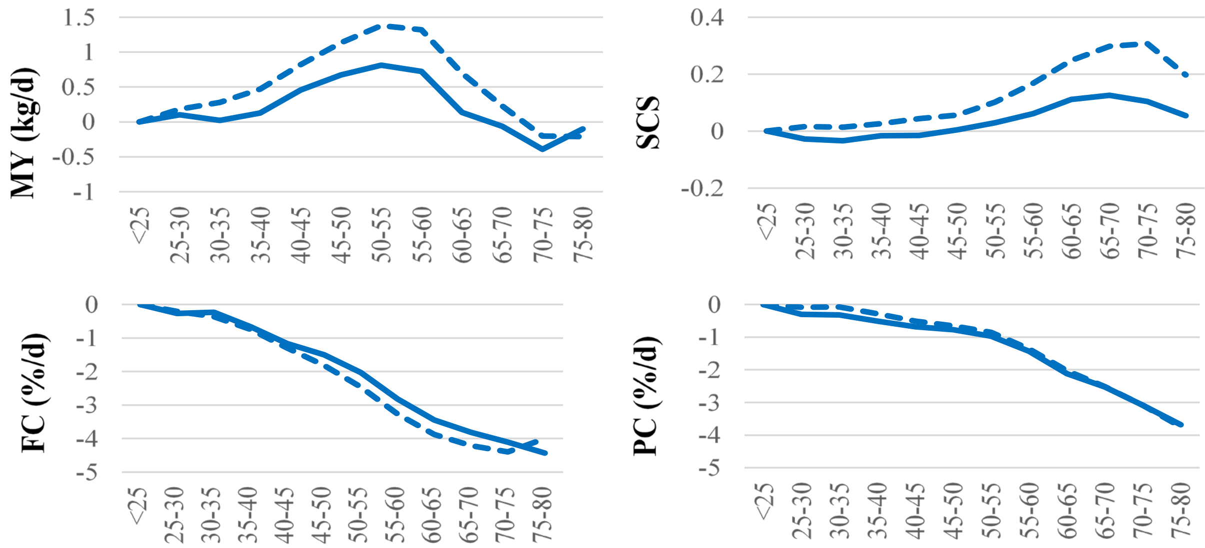

Figure 1. Least-squares solutions for MY, SCS, FC and PC in first (solid line) and second (dotted line) lactation.

Estimation of GxTHI interactions

Figure 2 illustrates genetic correlations between all combinations of THI for MY at DIM 150d. These correlations, as well as those for all other traits (Table 1) were very high, mostly higher than 0.9, suggesting that there is no GxTHI interactions and therefore few differences between animals in terms of individual response to heat stress.

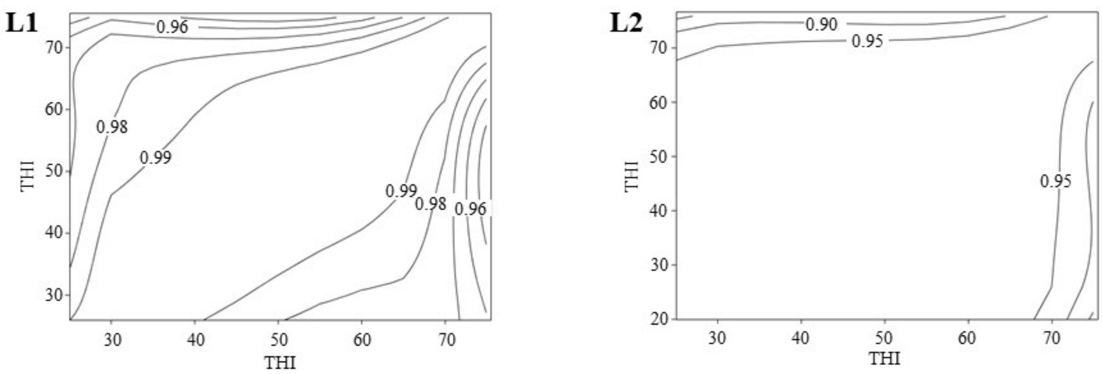

Figure 2. Genetic correlation estimates for MY at DIM 150d in L1 (left) and L2 (right) between all combinations of THI.

Table 1. Genetic correlations from random regression model analyses for MY, FC, PC and SCS between THI=40 and THI=70 at different stages of lactation (60d, 120d and 210d) and lactations rank (L1 or L2)

	MY		FC		PC		SCS	
DIM (d)	L1	L2	L1	L2	L1	L2	L1	L2
60	0.97	0.96	0.96	0.92	0.96	0.95	0.98	0.89
120	0.97	0.96	0.97	0.93	0.97	0.96	0.98	0.91
210	0.98	0.97	0.98	0.95	0.98	0.97	0.98	0.93

Even weak, GxTHI interactions allow slight variability in individual response to heat stress. An illustration of this variability in tolerance to heat is given in Table 2 presenting the EBV across THI and the corresponding rank for the MY in L2 for the seven sires with at least 500 daughters in the dataset. Although ranking of sires was rather stable and the best sires were always the same, some changes in ranking could be observed. For example, the sire S4 was intermediate at cold and comfort THI but appeared to be one of the least tolerant to high THI (THI=75).

Table 2. EBV and rankings for MY in L2 of the sires with at least 500 daughters with performances. Results obtained at DIM=150d.

	THI=30		THI=55		THI=75	
sire	EBV*	Rank	EBV*	Rank	EBV*	Rank
S1	0.95	1	0.88	1	1.74	1
S2	0.52	2	0.50	3	0.42	3
S3	0.33	3	0.58	2	0.42	2
S4	0.02	4	0.08	4	-0.67	6
S5	-0.27	5	-0.32	5	0.02	4
S6	-0.63	6	-0.65	6	-0.33	5
S7	-1.14	7	-0.94	7	-1.30	7

*EBV: expressed in genetic standard deviation unit, respectively 1.40 kg/d, 1.41 kg/d and 1.24 kg/d for MY in L2 at DIM=150d.

Conclusion

These first results confirm that the increase in temperature and in the frequency of heat peaks expected in next decades will lead to a decrease in milk production and to an increase of udder health problems in Montbéliarde cows raised in France. The selection of animals more heat-tolerant within high-producing cattle is one of the solutions presently studied to limit this decline in performance. Further studies on this topic are needed, especially concerning the reproduction of animals under heat stress. Nevertheless, although we observed only weak GxTHI interactions, it seems that it is still possible to identify the animals that are more tolerant to heat stress and therefore, more adapted to global warming.

Acknowledgments

This study received funding from the European Union's Horizon 2020 research and innovation program under grant number 101000226 (Rumigen). This project adheres to EuroFAANG (https://eurofaang.eu). The CAICalor project was funded by APIS-GENE. The authors thank Meteo-France for the Safran database.

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