Genotype x Climate interactions for protein yield using four European Holstein Populations

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ABSTRACT: Reaction norm models were applied to investigate genetic variation in heat tolerance of Holsteins across environments using long term protein milk yield test-day records and weather variables as proxy of climate change. Data represented four European regions characterized by different management systems and environments. Daily protein yield changed across the trajectory of temperature humidity index (THI) for all studied populations, pointing out negative associations between warm conditions and cow performance. For most regions, additive genetic variances for daily protein yield decrease when THI increases. Antagonistic relationships between level and intercept were relatively limited for Slovenia compared to the three other regions. Rank correlations of estimated breeding values for three proposed heat tolerance measures ranged from 0.56 (Spain and Slovenia) to 0.81 (Walloon Region of Belgium and Luxembourg), indicating a possibility of genotype by environment (G x E) for some pairs of regions.
Keywords: dairy cattle; heat tolerance; temperature humidity index; protein

Introduction

Holsteins have benefited for a long period from high-nutrient-input systems and selection. However, the increasing direct and indirect risk due to climate change prompts breeding organizations to get more knowledge about the associations between climate and genetics in order to improve cow resilience, and avoid consequences of high G x E levels.

Most studies dealing with estimation of genetic components of heat tolerance for sheep (Finocchiaro et al., 2005), pigs (Zumbach et al., 2008), and dairy cattle (Sánchez et al., 2009) followed a similar approach proposed by Ravagnolo and Misztal (2000) for dairy cattle. These studies included a dummy regression variable on THI and provided two parameters, a threshold point for thermo tolerance and, a slope, defined as the decline on milk yield due to heat stress above that point. This approach has been expanded due to its direct biological interpretation of parameter estimates. However, the assumptions of the same fixed threshold for all individuals and an abrupt linear slope are still questionable. Sánchez et al. (2009) assumed a differentiated threshold and rate of decline on an individual basis but concluded that those assumptions require complicated, highly parameterized models and fail to yield accurate estimates.

Random regression models have been widely explored for G x E evaluations and recently in heat stress studies (Brügemann et al., 2011). These models are more attractive because of their ability to 1) fit smoother patterns among THI trajectory without needs to fix a threshold point *a priori* and 2) providing better opportunities to select high merit animals with low environmental sensitivity. However, the biological interpretation of parameter estimates rely on the decomposition of the genetic covariance matrix.

With regard to Europe, knowledge about phenotypic and genetic effects of heat stress is not yet sufficient. The few genetic studies on heat stress reported only minor effects of G x E under the production systems considered (Brügemann et al., 2011). However, preventing deterioration of heat tolerance under expected climate change would be more beneficial if relying on a combined genetic evaluation of heat tolerance across several regions with specific weather conditions and high genetic ties between their dairy populations.

The main objective of this study was to estimate variance components and genetic parameters for protein yield considering heat stress effects in four selected regions: Walloon Region of Belgium (BEL), Luxembourg (LUX), Slovenia (SLO), and Andalusia and Castile la Mancha regions of Spain (SPA). Rank correlations between EBV of sires for protein yield will be used to appraise their ranking for heat tolerance in the four studied regions.

Materials and Methods

Data. Test-day records (TD) of first-lactation protein yield (kg) and pedigree information covering the period from 2000 to 2010 were provided by national milk recording organizations of BEL, LUX, SLO and SPA. Data from SPA represented two regions known for their high summer temperatures and where 20% of national dairy farms are located.

The number of sires of cows with data ranged from 1,950 (with 89,631 daughters) in SPA to 350 (with 54,615 daughters) in SLO. Among them, there were only 26 sires with 14,747 common daughters in total in the four regions. Sires with common daughters in different pairs of regions ranged from 51 (LUX-SLO) to 375 (BEL-SPA).

Daily minimum, maximum, and average ambient temperature (T_{db}, °C) and relative humidity (RH, %) from national meteorological stations of each region were available for the same period. In addition to differences in production systems and levels, these regions differed also with respect to T_{db} and RH. To identify the appropriate thermal index to be chosen for genetic analysis later, THI were defined as 1) THI_{avg} using average daily T_{db} and average RH and 2) THI_{max} using maximum T_{db} and

minimum RH. Both THI values were calculated as in Hammami et al. (2013). SPA regions are known for high T_{db} and low RH in summer compared to more moderate T_{db} and slightly high RH under similar seasonal conditions in LUX and BEL. SLO is characterized by the coldest situations in winter among countries but still had high T_{db} and low RH during summer like SPA. THI_{max} ranged from 32 to 78 (BEL and LUX), 28 to 84 (SLO), and 46 to 83 (SPA).

Model. The within-region model for protein yield used the same fixed effects for the different regions but with appropriate levels for each of them. They included herd-TD-date, gestation stage, lactation stage×age at calving×season of calving, and fixed Legendre polynomial on THI value standardized in the interval [-1, 1]. Random effects included animal (AG) and permanent environment (PE) modeled using Legendre polynomials on standardized THI value, and a random residual error effect. Models were progressively extended from first to third order Legendre polynomials for protein yield on THI_{avg} as well as on THI_{max}. Thus, six models were applied for each region. Within-country models were compared according to their goodness of fit using the Deviance Information Criterion (DIC) and the Percentage of Squared Bias Criterion. Models using THI_{max} as thermal index and when modeled with third order of Legendre polynomials was ranked first mainly in LUX and BEL. Therefore, it was retained for the subsequent genetic analysis in this study.

A Bayesian approach via Gibbs sampling was used to estimate posterior means of covariance components from a single chain of 120,000 samples (with 20,000 discarded). Breeding values were estimated by BLUPF90 package (Misztal et al., 2002). Estimated breeding values (EBV_i) were obtained for each THI point i. Three different measures of heat tolerance were computed as follows:

- $HT_1 = \sum_{j=thr}^{80} EBV_j - \sum_{k=35}^{thr-1} EBV_k$
- $HT_2 = EBV_i$ where i= 72
- $HT_3 = EBV_i$ where i is the threshold point (thr)

Spearman rank correlations were estimated for sires having more than 30 daughters in common in both pairs of regions.

Results and Discussion

Variation of phenotypic and environmental descriptors. Average daily protein TD yields were of 0.76, 0.79, 0.74, and 0.94 kg for BEL, LUX, SLO, and SPA respectively, indicating a high level of selected populations as for German Holsteins (Brügemann et al., 2011).

Association between TD protein and THI_{max} was examined using graphical inspection of least square means from analysis of variances. The decline of daily protein observed at high THI values for all populations agreed with studies in Europe and USA (Aguilar et al., 2009, Brügemann et al., 2011, Hammami et al., 2013). Tipping points were 62 (BEL and LUX), 65 and 68 respectively for SLO and SPA. Highest thresholds in SPA are accordant with results obtained under tropical and Mediterranean conditions (Ravagnolo and Misztal., 2000; Bouraoui et al.,

2002). Cows under those conditions are mostly in conventional housing and receive more effective shade management. However, lowest values for BEL and LUX correspond to those reported by other studies in Central Europe (Brügemann et al., 2011, Hammami et al., 2013, Lambetz et al., 2014) indicating a greater sensitivity of Holsteins under temperate climate and production systems characterized by more outdoor presence of cows during hotter seasons of summer and spring.

Reaction norm of protein yield to THImax. Genetic variances of level (a_0) were higher than variances of the linear term (a_1) for all populations (Table 1). Ratios between level and linear term were low and having a similar range in the 4 regions indicating that magnitude of G x E in terms of hot and cold situations within each country will not be very important.

Table 1. Posterior means of AG variances (diagonal), genetic (above diagonal), and PE (below diagonal) correlations between regression coefficients by country.

Country		a_0	a_1	a_2	a_3
BEL	a_0	26.18	-0.36	-0.56	-0.001
	a_1	-0.12	1.07	0.41	-0.80
	a_2	-0.90	0.28	0.22	-0.07
	a_3	-0.05	-0.98	0.35	0.35
LUX	a_0	25.98	-0.38	0.08	-0.60
	a_1	-0.08	0.71	0.16	-0.30
	a_2	-0.69	0.60	0.54	-0.22
	a_3	0.14	-0.97	-0.72	0.33
SLO	a_0	26.34	-0.18	0.28	0.21
	a_1	-0.08	0.52	0.01	0.12
	a_2	-0.48	0.74	0.14	-0.60
	a_3	-0.08	-0.93	-0.55	0.34
SPA	a_0	47.79	-0.26	-0.34	-0.22
	a_1	-0.20	0.82	0.64	-0.65
	a_2	-0.28	-0.04	0.78	-0.46
	a_3	0.05	-0.87	-0.36	0.74

Antagonistic relationships between genetic level (a_0) and linear term (a_1) effect concerned all populations with lower correlations observed for SLO. However, other countries correlations were more moderate and in the same range of estimates advanced by Aguilar et al. (2009). These results show that selection for high protein yield ignoring heat tolerance (linear term) would impair adaptation of individuals to heat stress.

Averaged AG variances estimates across THI trajectory (Figure 1) showed a tendency towards a decrease of variance estimates at high THI values. Decrease was more evident for the case of the studied sub-population of SPA regions. The decrease was also more pronounced for BEL and LUX. By contrast, a slight increase of variance estimates as THI increases was observed for SLO. Shapes of production trait variances as a function of THI were different in the literature among authors (Ravagnolo and Misztal, 2000; Brügemann et al., 2011). It is difficult to compare estimates from different studies disregarding data, models, and assumptions used. However, the decrease observed in this study could indicate that heat stress

conditions hampered individuals from expressing their genetic potential, especially for highly selected populations.

Rank correlations between sire (with more than 30 daughters) EBVs for the three measures of heat tolerance from within-country models are shown in Table 2. For most measures, high correlations approaching 0.80 were observed between several pairs of regions (BEL-LUX, BEL-SLO, and LUX-SLO). These results suggest that measures of heat tolerance proposed here will result in only minor re-ranking of sires in those pairs of regions. However, the lowest correlations observed between SPA and all other regions indicate changes of ranking of sires.

Table 2. Rank correlations between estimated breeding values for 3 measures of heat tolerance of sires having more than 30 daughters in common in both pairs of country.

	BEL-LUX	BEL-SLO	BEL-SPA	LUX-SLO	LUX-SPA	SLO-SPA
HT_1	0.80	0.75	0.74	0.75	0.66	0.56
HT_2	0.81	0.75	0.59	0.77	0.62	0.59
HT_3	0.81	0.74	0.63	0.78	0.66	0.58

Figure 1. Estimates of genetic variances of protein yield across THI trajectory.
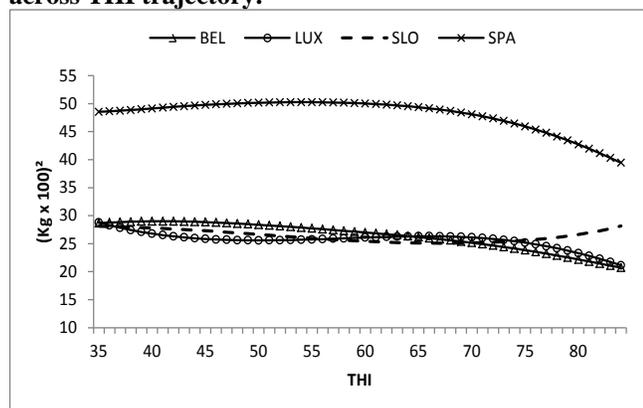
Conclusion

Among the production traits, protein yield was considered in the literature as the most sensitive trait to heat stress under tropical and Mediterranean conditions. In this study, daily protein yield varies both phenotypically and genetically throughout THI scale of each region and was characterized by a decrease at high THI levels. Antagonistic relationships between level and linear term genetic effects indicate that consideration of sensitivity to heat stress in the breeding programmes should be prioritized for highly intensive selected populations to advance towards more sustainable and robust individuals to deal with risks of extreme climate events. The magnitude of genotype by climate was quantified here indirectly from within-region evaluation. However, for better consolidation an across-country analysis, similar to the approach of international genetic evaluation, should be applied.

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