

Investigation on Genotype by Environment Interaction for Milk Yield of Holstein Cows in Luxembourg and Tunisia

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Introduction

Genotype by environment interaction (GxE) occurs when there are differences in expression of genotypes between different environments and would lead to a scaling effect across environment or to a change in actual ranking of sires in different environments.

Many studies investigating genotype by environment interaction were summarized by König *et al.*, (2005) and have been focused mostly on the correlations between great countries (USA, Canada, Australia) and mainly Latin American countries (Brazil, Mexico, Costa Rica). Also the within countries environments correlations were reported mostly in developed countries having their proper progeny testing programs. Studies on genotype by environment interaction on countries with breeding strategy based exclusively on semen importation are rarely reported.

Since the 1970s, Tunisia has imported germplasm (heifers and semen) from different countries to improve milk production (Djemali *et al.*, 1992). Holsteins were and are still imported from Canada, the United States, and some European countries. Continuous importation of semen and temporarily heifers from these countries is maintained using about imported 300,000 straws of frozen semen.

The Luxembourg breeding scheme is similar and also based on imported semen of tested sires and some heifer imports. Obviously, there are major management differences between Luxembourg and Tunisia.

The identical size population in Luxembourg and Tunisia are similar which could be an another asset for the investigation of the GxE interaction.

The objectives of this study were 1) to estimate (co)variance components for milk in Luxembourg and Tunisia (2) to quantify differences of genetic parameters in different environments and (3) to estimate the correlations between performances of daughters sired by the same bulls in Luxembourg and Tunisia considering milk production as separate traits.

Materials and Methods

For this study data were provided by the Luxembourg Herd-book Federation (CONVIS–Herd-Books, Service Elevage et Génétique, Ettelbruck/Luxembourg) and the Tunisian centre for Genetic Improvement “Livestock and Pasture Office, OEP/ Tunisia”. Original Tunisian data comprised 1,229,990 test-day yields records from 59,949 Holstein cows calving between 1990 and 2004 (parities 1 to 10). Original Luxembourg data consisted of 1,175,342 test-day records of 70,374 cows (parities 1 to 3) produced from 1990 and 2000.

Data were edited to include only first lactation test-day records and milk yield was only analyzed in this study for the same period in each country (1990 to 2000). The final data compromised 496,524 Luxembourgian test-day records from 55,882 daughters of 2,023 sires in 500 herds and 177,218 Tunisian test-day records from 15,372 daughters of 1,234 sires in 156 herds. A total of 168 sires have daughters in both countries, Luxembourg and Tunisia.

In order to avoid the heterogeneity of variance across herd environments, milk yields used to define them were adjusted to a 305-d in length of lactation, age-season-parity of calving and milking frequency and using mature equivalent adjustment factors estimated by Djemali *et al.*

(1992). A similar method was used for Luxembourg data.

For Tunisia, data were separated by herd-year means (HYM) equivalent mature into three environment classes: High HYM (> 7360 kg), medium HYM (>5500 and <7360) and low HYM (< 5500 kg). For Luxembourg data, the mean herd test-day yield was less than 20, 20 to 24, > 24 kg/d for herd production levels low, medium and high respectively.

Within Country Models

The equation for the single trait linear model was:

$$Y_{ijklm} = \text{HTD}_i + (\text{SA} \times \text{DIM})_j + \sum_{n=1}^3 \text{hy}_{mn} z_{ln} + \sum_{n=1}^3 \text{a}_{kn} z_{ln} + \sum_{n=1}^3 \text{p}_{kn} z_{ln} + e_{ijklm}$$

where: Y_{ijklm} = milk yield of cow k on day l within the herd-test day effect i , belonging to season of calving, age at calving and DIM interval subclass j and belonging to herd-year period m .

HTD_i is the fixed effect of herd test-day;

$(\text{SA} \times \text{DIM})_j$ = fixed season of calving, age at calving, DIM interval effect.

hy_{mn} = random regression herd-year coefficients;

a_{kn} = random regression genetic coefficients for cow k ;

p_{kn} = random regression coefficients for permanent environment for cow k ;

e_{ijklm} = residual effect;

z_{ln} = covariates.

Age at first calving was assigned to three joint class (<26 months, 26-29 mo and ≥ 30 mo). Four seasons of calving (fall, winter, spring and summer) were defined for Tunisia and three for Luxembourg (January to march; April-august and September to December). 10-d intervals for DIM from 5 to 330 were formed.

Regression curves were modelled by Legendre polynomials of order three:

$$z_{l0} = 1; z_{l1} = 3^{0.5} x \text{ and } z_{l2} = (5/4)^{0.5} (3x^2 - 1) \text{ where } x = -1 + 2((\text{DIM}-1) / (330-1)).$$

Bivariate Between Countries Model

A bivariate TD model was used to obtain estimates of (co)variance components between the two countries. It combined the same within countries model with an appropriate covariance structure between the two countries. In matrix notation the model was:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Q}_h\mathbf{h} + \mathbf{Q}_a\mathbf{a} + \mathbf{Q}_p\mathbf{p} + \mathbf{e}$$

where \mathbf{y} is the vector of 2 traits defined as milk yield within each country; \mathbf{b} is the vector of fixed effects herd-test day, season and age at calving (nested within countries); \mathbf{h} is the vector of random effect for 2-year time within herds; \mathbf{a} is the vector of animal genetic effect; \mathbf{p} is the vector of permanent environment effects. \mathbf{X} matrix incidence that relates \mathbf{y} to \mathbf{b} ; \mathbf{Q}_h , \mathbf{Q}_a and \mathbf{Q}_p are matrices of the third Legendre polynomials that links \mathbf{h} , \mathbf{a} and \mathbf{p} .

The (co)variance structure for the model was:

$$\text{Var} \begin{bmatrix} h \\ a \\ p \\ e \end{bmatrix} \text{ is the } \begin{bmatrix} I_h \otimes H_0 & 0 & 0 & 0 \\ 0 & A \otimes G_0 & 0 & 0 \\ 0 & 0 & I_p \otimes P_0 & 0 \\ 0 & 0 & 0 & I_n \sigma_e^2 \end{bmatrix}$$

where \mathbf{I} is the identity matrix; \mathbf{H}_0 and \mathbf{P}_0 are 6x6 block diagonal matrices for herd period and environment permanent regression coefficients, respectively and \mathbf{G}_0 is 6x6 covariance matrix for genetic regression coefficients. Residual covariance matrix \mathbf{E} is the $\text{diag}(e_{kl})$.

Genetic parameters

Components of (co)variances for milk yield within and between countries were estimated by REMLF90. Heritabilities of the Legendre parameters and genetic, environment permanent correlations between these parameters were estimated.

Genetic correlations between countries were estimated by $r_g(i,j)$ is the $g_{ij} / (g_{ii}g_{jj})^{0.5}$.

Resultats and Discussion

Within countries analysis

Estimates of variance for genetic and environment permanent random regression coefficients are shown in Table 1. Estimates of genetic variance were higher for Luxembourg than for Tunisia, however Tunisia showed the highest variability for permanent environment and residual variances.

Within countries genetic parameters of lactation curve coefficients are presented in Table 2. Heritability estimate for milk in the Tunisian population (0.15 for the intercept) was smaller than the same one in Luxembourg population.

Table 1. Residual variances and variances of genetic and permanent environment (PE) random regression coefficients.

	i_0	i_1	i_2
Genetic RR			
Luxembourg	2.81	0.27	0.09
Tunisia	1.27	0.13	0.04
PE RR			
Luxembourg	3.99	0.89	0.41
Tunisia	6.52	1.43	0.67
Residual variances			
Luxembourg	3.77		
Tunisia	6.32		

This estimate is lower than estimates found in other studies on milk yield for the Holstein populations (Jamrozik *et al.*, 2002). However Tunisian estimates agree with results of Ben Gara *et al.* (2005) who applied Bayesian methods with Gibbs sampling for 305-d milk yield related to the Tunisian population and found a heritability of 0.17. Carabano *et al.* (1989) reported a heritability estimates for milk in Spanish population of 0.16 within country and 0.12 in joint evaluation with US data (0.33 within country and 0.27 jointly). Heritability estimates for Luxembourg data were in the range of heritability estimates in many others countries and especially in Germany and Belgium.

The smaller heritability estimates in Tunisian population could be explained by the limited expression of genetic potential under difficult environment conditions for small dairy holders and a high rate of culling during the first lactation

in large dairy farms, together with a less accurate identity recording in Tunisia.

Table 2. Within countries estimates of heritability (diagonal), genetic (above diagonal) and permanent environment (below diagonal) correlations between regression coefficients.

Country	i_0	i_1	i_2
Luxembourg			
i_0	0.39	0.08	-0.51
i_1	-0.08	0.36	0.41
i_2	-0.05	0.01	0.35
Tunisia			
i_0	0.15	0.22	-0.26
i_1	0.04	0.13	-0.05
i_2	-0.13	-0.11	0.13

Genetic and PE correlations between the intercept (i_0), the linear (i_1) and the quadratic (i_2) terms of the lactation curve were small with a superiority of genetic parameters compared to environment permanent terms.

Stratification according to production level

Figures 1 and 2 show variances components and heritabilities for herd level production respectively for Luxembourg and Tunisia. Variances were highest in herds with high levels production. In Luxembourg, there was a substantial increase of additive genetic variances with increasing production level associated with a small variation of PE and residual components from high to low production level and let's seeing highest heritabilities observed in the three production levels.

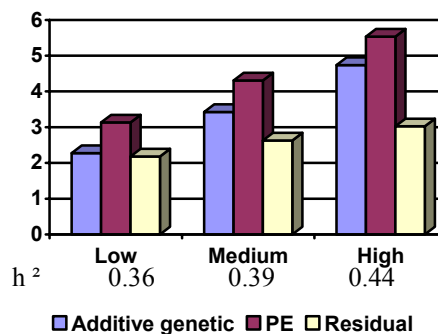


Figure 1. Estimated variance components for milk yield in different herd level production in Luxembourg.

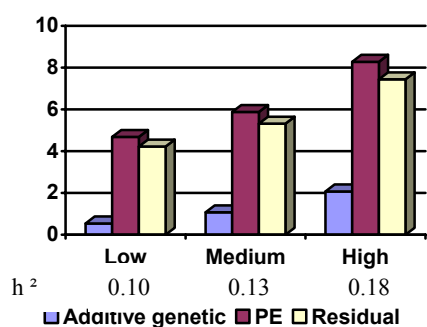


Figure 2. Estimated variance components for milk yield in different herd level production in Tunisia.

For the Tunisian population, an increase of additive genetic variances from low to high production was observed but was simultaneously accompanied by a considerable increase of the PE and residual variances enabling an increase of heritabilities (0.10 to 0.18) respectively in low and high production levels but still more low than the (0.36 to 0.44) observed with Luxembourg data. Increasing heritabilities with increasing production level were also reported by Gengler *et al.* (2005).

Between countries analysis

Estimates of variance components, heritabilities and genetic correlation between Luxembourg and Tunisia in the joint analysis are shown in Table 3. An increase in the genetic additive variance and PE variance and a decrease in residual variance of the intercept over single-trait estimates were observed in Luxembourg data, whereas, a decrease in the genetic additive variance was obtained with the Tunisian data. This situation has led to an increase on the heritability in Luxembourg against a decrease of this parameter in Tunisia from within-country to joint analyses.

Table 3. Estimates of variances components, heritabilities and genetic correlation between Luxembourg and Tunisia.

Components	Luxembourg	Tunisia
Genetic additive	3.09	1.16
Permanent environment	4.09	7.05
Residual variances	2.59	6.42
Heritability	0.42	0.14
Genetic correlation (Luxembourg, Tunisia)	0.79	

Genetic correlation between countries is relatively higher than reported by Jamrozik *et al.*, (2002) for countries as far apart as Canada and New Zealand. The estimates however are similar to the correlation between Spain and US (0.79) obtained by Carabano *et al.* (1989). INTERBULL results for the closest participating country (Israel) were all similar (INTERBULL, 2006).

Conclusion

Genetic parameters estimates in Tunisia were relatively small. Size of the data set, accuracy of recording and sampling for the period studied perhaps have participate to this situation, but the management conditions that limit expression of genetic potential of superior cows could be the major affecting factor.

Preliminary results show a high correlation between the two countries and also an heterogeneity of variances. Correlation coefficient < 0.8 gives an indication of the existence of genotype x environment interaction. Rankings of bulls in Luxembourg and Tunisia are expected to be similar with a scaling effect due to the differences on genetic additive variances. Further investigations are needed to consolidate these results incorporating modelisation of milk components and functional traits.

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