Environmental sensitivity for milk yield in Luxembourg and Tunisian Holsteins by herd management level

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ABSTRACT

Milk production data of Luxembourg and Tunisian Holstein cows were analyzed using herd management (HM) level. Herds in each country were clustered into high, medium, and low HM levels based on solutions of herd-test-date and herd-year of calving effects from national evaluations. Data from both populations included 730,810 test-day (TD) milk yield records from 87,734 first-lactation cows. A multi-trait, random regression TD model was used to estimate (co)variance components for milk yield within and across country HM levels. Additive genetic and permanent environmental variances of TD milk yields varied with management level in Tunisia and Luxembourg. Additive variances were smaller across HM levels in Tunisia than in Luxembourg, whereas permanent environmental variances were larger in Tunisian HM levels. Highest heritability estimates of 305-d milk yield (0.41 and 0.21) were found in high HM levels, whereas lowest estimates (0.31 and 0.12, respectively) were associated with low HM levels in both countries. Genetic correlations among Luxembourg HM levels were >0.96, whereas those among Tunisian HM levels were below 0.80. Respective rank orders of sires ranged from 0.73 to 0.83 across Luxembourg environments and from 0.33 to 0.42 across Tunisian HM levels indicating high re-ranking of sires in Tunisia and only a scaling effect in Luxembourg. Across-country environment analysis showed that estimates of genetic variance in the high, medium, and low classes of Tunisian environments were 45, 69, and 81% lower, respectively, than the estimate found in the high Luxembourg HM level. Genetic correlations among 305-d milk yields in Tunisian and Luxembourg HM environments ranged from 0.39 to 0.79. The largest estimated genetic correlation was found between the medium Luxembourg and high Tunisian HM levels. Rank correlations for common sires' estimated breeding values among HM environments were low and ranged from 0.19 to 0.39, implying the existence of genotype by environment interaction. These results indicate that daughters of superior sires in Luxembourg have their genetic expression for milk production limited under Tunisian environments. Milk production of cows in the medium and low Luxembourg environments were good predictors of that of their paternal half-sisters in the high Tunisian HM level. Breeding decisions in low-input Tunisian environment should utilize semen from sires with daughters in similar production environments rather than semen of bulls proven in higher management levels.

Key words: environmental sensitivity, genotype by environment interaction, genetic correlation, herd management level

INTRODUCTION

The ability of a genotype to alter phenotypic expression in response to environmental differences is known as phenotypic plasticity or environmental sensitivity (Falconer and MacKay, 1996). In animal breeding, genetic variation in response to environmental differences is used as a definition of genotype by environment interaction ($\mathbf{G} \times \mathbf{E}$). Investigations on $\mathbf{G} \times \mathbf{E}$ within and across countries have been mostly based on the region or country border as a criterion for global environmental definition (Carabaño et al., 1989, 1990; Schaeffer, 1994; Rekaya et al., 2001; Ojango and Pollot, 2002; Fikse et al., 2003a; Hammami et al., 2008). However, environments across countries could be more similar than those within countries, and herds from different countries can share similar environmental characteristics compared with herds within the same country. Clustering of herds across countries using descriptive variables and ignoring country borders has been implemented in other studies (Weigel and Rekaya, 2000; Fikse et al., 2003b; Zwald et al., 2003; Cerón-Muñoz et al., 2004).

Experimental studies investigated G × E in which environments were designed to differ with respect to feeding levels and systems (Veerkamp et al., 1995; Kolver et al., 2002; Beerda et al., 2007). In general, using experimental herds with good quality data to assess G × E is more illustrative but is expensive and difficult to realize especially in developing countries. To overcome the lack of information about environmental characteristics, some proxies to feeding level and management were used to form homogeneous environments in studies on G × E in tropical and temperate regions. Herds were stratified by mean herd milk yield level (Kolmodin et al., 2002; Berry et al., 2003; Hayes et al., 2003) or by within-herd milk yield standard deviation (**HYSD**) (Stanton et al., 1991; Cienfuegos-Rivas et al., 1999; Costa et al., 2000; Raffrenato et al., 2003). Most studies on G × E by character state or reaction norm models (Stanton et al., 1991; Weigel and Rekaya, 2000; Kolmodin et al., 2002; Raffrenato et al., 2003) used lactation records. Computing facilities have led to the use of test-day (**TD**) models worldwide in genetic evaluations. The use of TD records improved the accuracy of EBV. Hayes et al. (2003) reported that TD records are better suited to investigate within- and between-cow variations in different environments than lactation yields because they better account for environmental effects peculiar to each TD throughout the lactation.

In Tunisia, Holsteins are mostly managed on small farms with little to no land. Nevertheless, large-scale farms exist and are located in the north of the country. Farms present a wide range of environments and intensities of production varying from intensive to extensive systems. Herds also differ with respect to health care, feed resources, and feeding system within and across production sectors. Rekik et al. (2003) reported that the effect of production sector was highly significant on lactation curve parameters in Tunisia. Mean milk yield in 305 d ranged from 5,456 kg in cooperative herds to 8,337 kg in private herds.

As in most European countries, dairy farms in Luxembourg can be summarized as high-input production systems. Feed resources are varied and they are supported by relatively high use of fertilizers, buffer feeds (i.e., maize silage and brewers grains), and concentrates, which are usually fed to improve milk production (van Arendonk and Liinamo, 2003). Grazing is widespread in Luxembourg where climatic and pedological conditions favor the development of naturally dominant meadows and pastures. Organic farming, with fodder grass being the organic product of choice, is gaining popularity in Luxembourg as a low-input form of dairy herd management (**HM**), where reduced costs of feeding and equipment may lead to greater net profit even if milk production is decreased.

In a previous study, Hammami et al. (2008) found evidence of a large G × E for milk yield and persistency using Luxembourg and Tunisian Holstein populations where lactation performance in each country was considered as a different trait and the country border delimitation was defined as an environmental criterion. However, these authors did not account for differences between herds in management practices within country or how genotypes respond to HM level within these 2 geographically distinct environments. Calus et al. (2002) suggested that clustering herds in groups of similar production systems or intensity of production might be more effective to investigate G × E effects than only considering sire-herd-year-season differences. Fikse (2004) reiterated that breeding programs should have more advantages when the international genetic evaluation is run using performance records in a production system rather than on a country basis. Furthermore, the environmental definition and the heterogeneity of variance may affect the magnitude of G × E and therefore, genetic evaluation and selection accuracy.

The assumption of homogeneous variance across herds with different management levels has no major effect on the evaluation of sires when the latter are equitably used in those herds and that heritability is greatest in the more variable environment (Vinson, 1987; Boldman and Freeman, 1990). Otherwise, ignoring the heterogeneity of variance can lead to bias in genetic evaluations. This bias may have severe consequences as the intensity of selection increases and might then limit the effectiveness of breeding programs (Hill, 1984; Vinson, 1987). Fahey et al. (2007) investigated the effect of heteroscedasticity on genetic parameter estimates for production traits between grazing and confinement herds in the United States to ascertain if that unmasked underlying G × E effects. They found only modest evidence for G × E that did not arise solely from heteroscedasticity. Raffrenato et al. (2003) reported that clustering Sicilian herds by management level was effective in identifying heterogeneous genetic variance. Breed differences in environmental sensitivity to micro- and macro-environmental change could be detected by the examination of heterogeneity of variance (Lynch and Walsh, 1998). Quantifying the environmental sensitivity of dairy sires in different environments is important for making breeding decisions and implementing efficient selection strategies suitable for each specific environment. This can allow the differentiation of sires ranking similarly (desirable) across different herd environments from those ranking differently in one specific environment versus another.

There are differences in management practices between and within herds in Luxembourg and Tunisia. These within- and across-country differences may be

associated with heterogeneous genetic parameters. It is also important to determine if sires can be used throughout the whole of each country independently of management level. Grouping herds on HM level and ignoring country borders may be advantageous and could better accommodate G × E within and across country environments. Therefore, the main objective of this study was to evaluate the environmental sensitivity for milk yield in Holsteins using HM levels within and between Luxembourg and Tunisian contrasted environments.

MATERIALS AND METHODS

Data

A total of 730,810 TD milk records of 87,767 primiparous Holstein cows collected between 1995 and 2006 were used. Luxembourg data were provided by VIT (Vereinigte Informationssysteme Tierhaltung, Verden, Germany). Tunisian data were provided by the Center for Genetic Improvement of the Livestock and Pasture Office (Tunis, Tunisia). Data included records in herds having at least 4 daughters of sires common to both cow populations. Details on data structure are found in Hammami et al. (2008). A pedigree file dating back to 1927 was obtained for all animals in the analysis. There were 2,546 and 2,035 sires with daughters having records in Luxembourg and Tunisia, respectively. Among those sires with progeny records, 231 bulls had daughters in both countries (14,421 and 6,358 daughters in Luxembourg and Tunisia, respectively).

Definition of Environment

Nearly all studies investigating environmental sensitivity in dairy cattle within or across countries reported that even if no direct measures of nutrition and feeding were available, herd parameters linked to nutrition were the most important for G × E (Calus and Veerkamp, 2003; Zwald et al., 2003; Cerón-Muñoz et al., 2004; Haskell et al., 2007). In this study, because of the lack of information about feeding levels and systems, it was assumed that management group solutions from a genetic analysis of milk yield would reflect general HM level. To assess the environmental sensitivity within and across Luxembourg and Tunisian environments, the following steps were applied to determine environmental (HM) differences.

HM Estimation. Data were analyzed using the following (in matrix notation) random regression (**RR**) TD model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q} \left(\mathbf{Za} + \mathbf{Zp} + \mathbf{Wh} \right) + \mathbf{e},$$

where **y** is a vector of TD milk yield records, **b** is a vector of fixed effects: herd-test-date, age within season of calving and classes of 25 DIM, and stage of lactation classes of 5 DIM, **a** is a vector of RR coefficients for the animal additive genetic (**AG**) effect, **p** is a vector of RR coefficients for permanent environmental (**PE**) effect, **h** is a vector of RR coefficients for herd-year of calving common environmental effect (**HY**), **e** is a vector of residual effects, **Q** is a matrix of Legendre polynomials, and **X**, **Z,** and **W** are incidence matrices relating observations to the various effects. Legendre polynomials were third-order for AG and HY effects and fourth-order for the PE effect. Higher order polynomials for PE effect were used following recommendations by Hammami et al. (2008), who reported that AG and HY in this data are sufficiently modeled by third-order Legendre polynomials, whereas fourth-order polynomials were necessary to better fit the PE effect.

First, solutions for herd-test-date and herd-year of calving effects were obtained for Luxembourg and Tunisian cows. These solutions were then summed for each cow within a herd to define the management level for each TD record, and the average of cows' levels in a herd defined the mean management level for that herd in Luxembourg or in Tunisia. These mean management levels were then the basis for clustering herds into HM levels within country.

Contrasting Herd Environments. Clustering was applied to find similarities between herds within each country environment defined as explained before. The CLUSTER procedure (SAS Institute, 2002) with Ward's minimum variance was used. The standard option was employed to standardize the HM (mean = 0 and standard deviation = 1). Three different levels of management were obtained based on the pseudo F statistic for each country. They will be hereafter referred to as high, medium, and low HM levels. Descriptive statistics on these management classes in addition to other characteristics of Luxembourg and Tunisian environments are in Table 1. Total number of sires used in each of the 2 environments, the number of sires in common, and the total number of common daughters between pairs of HM within and across countries are in Table 2.

Analysis

A multiple-trait RR TD model was used to estimate (co)variance components for milk yield within and across Luxembourg and Tunisian HM levels. Fixed and random effects were similarly defined as in the model used for HM estimation but were nested within contrasted environments. This model was used to estimate genetic parameters and breeding values. The covariance structure was

$$V\begin{bmatrix} a \\ p \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ 0 & P & 0 \\ 0 & 0 & R \end{bmatrix},$$

where $G = A \otimes G_0$, $P = I \otimes P_0$; $\otimes$ denotes the Kronecker product; A = the additive genetic relationship matrix; G_0 = 18×18 covariance matrix for AG regression coefficients; and P_0 = 24×24 covariance matrix for PE regression coefficients. All across-country environmental covariances in P_0 were equal to zero because these effects were considered independent across-country environments; I = identity matrix. The matrix R was considered to be diagonal as $I\sigma_i^2$, where σ_i^2 = residual variances for milk yield for each of the 6 environments ($i = 1$ to 6).

Genetic and nongenetic parameters were estimated with a Bayesian approach via a Gibbs sampling algorithm (Misztal et al., 2002). A chain of 250,000 samples (with 50,000 as burn-in period) was generated. Convergence of Gibbs chains was monitored by inspecting plots of selected realizations. Variances, heritabilities, and correlations for 305-d yields were calculated following Hammami et al. (2008). Genetic correlations were computed among TD milk yields recorded in various HM levels. Rank correlations between EBV of common sires estimated separately in each of the 6 environments were used to assess the level of re-ranking of sires in different environments. Rank correlations were calculated using PROC CORR (SAS Institute, 2002) for common sires that had at least 30 daughters in within-country environments and at least 4 daughters in common in across-country environments. Coefficients of correlated responses in low environments from sire selection in high environments were estimated to evaluate the use of semen from sires proven in high HM herds to improve milk production in low HM levels. They were obtained by regressing EBV of common sires between pairs of contrasted environments within each country.

To investigate the possibilities of using a selection differential and to differentiate between sires ranking similarly across various herd environments (desirable) and those ranking high only in specific environments (undesirable), first a national evaluation was performed for each country, and their top 20 national sires were identified. Second, a separate evaluation for each of the 6 specific environments studied was performed, and the top 20 sires in each specific environment were obtained. Desirable sires were those with similar average EBV from national and country-specific environment evaluations, signaling that when they are the top nationally they are still the top in each of the country-specific environments.

Table 1. Description of data and mean milk yield and standard deviation (in parentheses) for different lactation phases by herd management level (high, medium, or low) in Luxembourg and Tunisia

Item	Luxembourg			Tunisia		
	High	Medium	Low	High	Medium	Low
Test-day records (n)	151,587	192,005	121,430	122,825	57,723	85,240
Cows (n)	18,285	22,446	13,939	15,218	7,324	10,555
Herds (n)	179	106	142	31	29	38
Herd management (kg)	9.6 (2.7)	6.8 (2.6)	4.2 (2.7)	6.8 (4.6)	5.9 (4.1)	4.5 (3.8)
Daily milk yield (kg)	25.5 (2.7)	22.4 (5.3)	19.5 (4.9)	21.6 (6.1)	17.7 (5.3)	13.7 (4.4)
Age at calving (mo)	29.4 (3.6)	30.5 (3.6)	31.5 (3.7)	28.6 (3.5)	30.5 (5.9)	29.3 (3.9)
Milk at DIM 80 (kg)	28.1 (4.7)	25.2 (4.7)	21.7 (4.6)	24.8 (6.0)	19.3 (4.9)	15.6 (3.9)
Milk at DIM 280 (kg)	21.8 (5.0)	18.7 (4.2)	16.1 (4.0)	17.9 (5.4)	14.9 (4.8)	12.0 (3.8)
Test-day records per herd-test-date classes (n)	12.1 (8.7)	8.8 (5.1)	7.5 (4.0)	60.1 (57.6)	26.8 (23.1)	27.8 (16.5)
305-d milk yield[1] (kg)	7,917 (1,248)	7,017 (1,085)	6,086 (969)	7,375 (1,555)	5,462 (1,252)	4,623 (1,027)

[1]Actual 305-d milk yield.

Table 2. Total number of sires used in each herd management level group (on diagonal), sires with at least 4 daughters in common between each pair of environments (above diagonal), and total number of daughters in common across pairs of environments (below diagonal)

Item	Luxembourg			Tunisia		
	High	Medium	Low	High	Medium	Low
Luxembourg						
High	1,663	565	471	126	102	49
Medium	32,242	1,547	614	115	99	45
Low	23,861	42,620	1,175	100	82	37
Tunisia						
High	7,489	5,608	3,982	1,335	208	185
Medium	4,904	4,511	3,402	16,199	763	170
Low	2,593	1,719	1,041	18,000	14,096	648

RESULTS AND DISCUSSION

Within-Country Environmental Analysis

Table 3 has estimated AG and PE variances and heritabilities for 305-d milk yield in contrasted Luxembourg and Tunisian environments. Estimates of AG and PE variances decreased from the high to the low HM level in both countries. The increase in AG and PE variances with HM level found in this study for both populations is in accordance with results in other studies (Stanton et al., 1991; Cienfuegos-Rivas et al., 1999; Costa et al., 2000; Raffrenato et al., 2003) that used HYSD of mature-equivalent milk yield to stratify herds. The TD model used in this study accounts for short-time environmental variation (month-to-month) unlike the herd-year classification of management groups in the lactation model. Moreover, the sum of the herd-TD and herd-year solutions from the TD model may provide an efficient HM level descriptor independent of the other fixed effects in the model.

Heritability estimates for 305-d milk yield were larger in the 3 Luxembourg contrasting environments than estimates in respective Tunisian HM levels (Table 3). The results on heritability estimates in herds with varying milk production levels are in agreement with those reported in other studies (Hill et al., 1983; Boldman and Freeman, 1990; Castillo-Juarez et al., 2000).

Large heritability estimates for milk yield in high HM levels reflect high genetic variation of milk production by cows in this HM class compared with that of their contemporaries in the low HM level.

The high Tunisian HM class included large herds with more milk yield (Table 1) where cows are fed with concentrates, silage, oat hay, and green forage. Large herds were also found to be associated with large AG and PE variances for milk yield in other populations (König et al., 2005; Gernand et al., 2007). On the other hand, the low HM included mostly small herds where cows are fed by-products, low-quality oat hay, and moderate quantities of concentrates bought from the market. High and medium HM levels in Tunisia could be compared with conventional systems found in temperate regions. Thus, high performance levels could be reached when the limiting environmental effects are better controlled, unlike in low HM, where milk production levels as well as AG and PE variances were reduced.

In Luxembourg, feeding resources, heat stress, health care, and financial capacities are not constraining factors for milk production. Dairy farming in Luxembourg varies from conventional to grazing with at least 4 mo outdoors when cows obtain forage from pasture. Heritability estimates for milk yield obtained in Luxembourg for high and low HM levels were in the same range of estimates found in conventional and grazing farms in Canada (Boettcher et al., 2003).

Table 3. Posterior means (and SD) of estimates of 305-d milk additive genetic (AG), permanent environmental (PE) variances, and heritability within country and herd management (HM) levels

HM level	Luxembourg			Tunisia		
	AG variance	PE variance	Heritability	AG variance	PE variance	Heritability
High	496,169	645,987	0.41	272,794	952,796	0.21
	(20,137)	(16,827)	(0.015)	(25,214)	(32,591)	(0.020)
Medium	339,274	537,194	0.37	151,628	764,791	0.15
	(14,079)	(11,730)	(0.014)	(22,947)	(28,154)	(0.031)
Low	203,808	422,877	0.31	96,568	595,144	0.12
	(13,789)	(11,702)	(0.019)	(11,425)	(12,604)	(0.027)

Table 4. Posterior means (and SD) for genetic (above diagonal) and rank correlations[1] (below diagonal) for 305-d milk yield within- and across-country herd management levels in Luxembourg and Tunisia

	Luxembourg			Tunisia		
	High	Medium	Low	High	Medium	Low
Luxembourg						
High		0.98 (0.01)	0.97 (0.01)	0.61 (0.09)	0.43 (0.11)	0.39 (0.12)
Medium	0.82		0.97 (0.01)	0.79 (0.05)	0.70 (0.10)	0.43 (0.10)
Low	0.76	0.83		0.77 (0.06)	0.67 (0.10)	0.55 (0.09)
Tunisia						
High	0.41	0.43	0.26		0.78 (0.04)	0.70 (0.05)
Medium	0.38	0.34	0.23	0.42		0.73 (0.05)
Low	0.26	0.39	0.19	0.33	0.37	

[1]Rank correlation estimated between EBV of common sires of each pair of environments from separate evaluations.

Genetic correlations for milk yield among contrasted environments (Table 4) were different between the 2 countries. In Luxembourg, genetic correlations among all pairs of HM classes were greater than 0.96, suggesting that sires will rank similarly in the 3 HM levels in Luxembourg. Correlation coefficients in Table 4 (from 0.73 to 0.83) indicate minimal reranking of sires among these Luxembourg HM levels. However, differences in variance estimates across these HM classes may lead to scaling effects in sires' EBV, especially between low and high HM levels. Kearney et al. (2004) reported a genetic correlation of 0.94 between lower quartiles in conventional and grazing US herds where mean milk yields (mature equivalent) were 6,435 and 7,925 kg in grazing and conventional herds, respectively, which is in the same range of 305-d yields (6,086 and 7,917 kg) recorded in the low and high HM levels in Luxembourg. Boettcher et al. (2003) also found a genetic correlation of 0.93 between milk yields in conventional and grazing Canadian herds.

Genetic correlation estimates among milk yields in different HM levels in Tunisia were lower than the threshold of 0.80 suggested by Robertson (1959), indicating the presence of G × E. These coefficients ranged from 0.70 (between high and low HM levels) to 0.78 (high and medium HM levels). Rank correlation coefficients among EBV of common sires in the 3 Tunisian HM levels ranged from 0.33 to 0.42, indicating a high potential for reranking of sires among these 3 contrasted environments. Low genetic correlations for milk yield obtained among Tunisian HM classes are in the same range as those found in high and low environments in the Sicilian region of Italy (Raffrenato et al., 2003). These authors suggested a major reranking of sires among the various environments defined in their study using HYSD of milk yield to classify herds.

Coefficients of correlated response in medium and low HM levels from selection in high or medium HM within Luxembourg and Tunisian environments are in Table 5. Daughter responses in both countries were greatest in high HM and least in low HM levels. However, there were clear differences with respect to the level of genetic response between the 2 countries in favor of selection for milk yield in Luxembourg. In Tunisia, the highest regression coefficient was 56% lower than its corresponding value in Luxembourg. Correlated responses for milk yield in Luxembourg HM classes were consistent with findings from across-country analyses (Stanton et al., 1991; Cienfuegos-Rivas et al., 1999; Castillo-Juarez et al., 2000; Costa et al., 2000; Raffrenato et al., 2003; Verdugo et al., 2004).

Results in Table 6 compare average EBV for the top 20 sires where national data were used for genetic analysis to average EBV for the top 20 sires when data from only one specific environment were considered for genetic analysis. The resulting absolute differences in average merit between the Luxembourg national top 20 sires and the top 20 sires identified in the either high or low Luxembourg specific environment was the lowest. This indicates that the best national 20 sires were also the best ones in this specific environment. Moreover, 18 and 12 of these sires remained in the top 20 identified using specific environment evaluations in high and low HM levels in Luxembourg, respectively. In contrast, ranking of sires in Tunisia changed between national and the 3 specific environment evaluations. Sixteen of the 20 top national sires ranked high in the high HM level evaluation, but only 2 of the top 20 sires ranked by the specific low HM environment were found in the Tunisian national top 20 sires list. Nevertheless, the number of daughters per sire within a specific environment should be taken into account when comparing

Table 5. Estimated correlated response[1] in milk yield from selection within contrasted environments in Luxembourg and in Tunisia

	High (X) – medium (Y)	High (X) – low (Y)	Medium (X) – low (Y)
Luxembourg	0.69	0.53	0.59
Tunisia	0.39	0.16	0.17

[1]Correlated responses to selection were determined by regressing EBV of common sires (Y) in one herd management level (medium or low HM) on EBV of common sires in other HM (high or medium) levels (X) within each country.

between national and specific environment evaluations. Luxembourg breeders may use sires progeny tested in various HM levels without great risks. However, semen exchange among Tunisian HM classes should be used with caution because differences in management practices and resources among those management classes may lead to genetic reranking. By limiting restrictions that foster G × E, it is possible to obtain more benefits from imported semen for use in the high and medium HM environments. Because imported semen is often expensive, it is very difficult to get efficient economic returns from imported germplasm in the low Tunisian HM level. A specific breeding strategy for this large class of herds in the country could be implemented to rely on semen of bulls progeny tested in herds at the same management level, probably requiring reliance on progeny testing in local herds.

Across-Country Environmental Analysis

Genetic correlations of first-lactation milk yield in the high Luxembourg HM level with milk yield in the high, medium, and low Tunisian HM levels were low (Table 4). These coefficients were higher among similar (0.61) than among divergent (0.39) HM levels. Thus, severe reranking of sires of the high HM level in Luxembourg with the 3 Tunisian environments has occurred. These low genetic correlations were the consequence of reduction in genetic variances in the Tunisian environments (Table 3) reflecting differences in HM value and

milk yield observed between the high Luxembourg and high Tunisian HM levels (Table 1). Similar declines in genetic correlation estimates with increased differences in management levels were reported in other studies (Cromie et al., 1998; Kearney et al., 2004). Genetic correlations between medium Luxembourg and high, medium, and low Tunisian HM levels (Table 4) were below 0.80. The highest correlation (0.79) was observed between the medium Luxembourg and high Tunisian HM levels. Moreover, AG variance of milk yield in the medium Luxembourg HM level was only 21% larger than that found in the high HM environment in Tunisia (Table 3). Nevertheless, given the low rank correlations between EBV of common sires in the contrasted environments (Table 4), reranking of sires on EBV has occurred even between the medium Luxembourg and high HM classes. Cienfuegos-Rivas et al. (1999) found that the largest genetic correlation was obtained between the low US and high Mexican environments that had similar mean HYDS. They also reported that the proportion of US genetic superiority that was recovered in the high HYSD Mexican environments when sires were selected on their daughters' performances in all US environments were only 80% effective when US sires were evaluated in the US low-opportunity environment. Genetic correlations for milk yield between low Luxembourg HM and high, medium, and low Tunisian HM levels (Table 4) were similar to those obtained between the medium in Luxembourg and the 3 Tunisian HM levels. Generally, results in this study suggest that daughter performances in the medium and low Luxembourg HM levels could be considered good predictors of their paternal half-sister performances in the high HM levels in Tunisia. Genetic correlation estimates for across-country HM levels from the current data should be used with caution because of the low number of common bulls with more than 20 daughters in the different contrasted environments within country.

Genetic correlations of milk yield estimated across-country and environments were below 0.80. Correlations found between the medium and low Luxembourg and

Table 6. Average EBV of the national[1] top 20 sires, the specific environment[2] (SPE) top 20 sires, and the average number of daughters per sire for the 2 extreme herd management (HM) environments in Luxembourg and Tunisia

	Luxembourg				Tunisia			
	National top 20		SPE top 20		National top 20		SPE top 20	
Environment	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire	EBV (kg)	Daughters per sire
High HM	1,689	91	1,731	88	836	90	990	104
Low HM	1,233	76	1,098	71	613	93	309	92

[1]Average EBV of the top 20 sires evaluated using the whole performance data of each country.

[2]Average EBV of the top 20 sires evaluated using performance data specific to each herd management within each country.

the high Tunisian environments were approximately 0.80. On the other hand, genetic correlations among all of the Luxembourg environments and the low Tunisian environment were below 0.60, suggested by Mulder et al. (2006) as a break-even point for separate breeding schemes for similarly defined environments. Milk yield genetic correlations among various HM levels indicate that sires will rank differently between Luxembourg and Tunisian environments. Hammami et al. (2008) found evidence for G × E for milk yield using within- and across-country analyses of Luxembourg and Tunisian data where each country was treated as a unique and constant production environment. Genetic correlations for 305-d milk yield and persistency between countries were 0.60 and 0.36. It was not possible from that study to compare genotypes' performances in across- and within-country specific environments with varying HM levels to explore possibilities for semen exchange among production systems rather than between populations. Results from Hammami et al. (2008) and the present study suggest that management levels in addition to climatic conditions are potential sources of G × E effects.

In addition to differences in management resources between Luxembourg and Tunisia, Holsteins may not tolerate extended heat stress in Tunisia. Furthermore, low HM herds are frequent in Tunisia. Locally evaluated Tunisian bulls should be more suitable for this group of herds. Vargas and van Arendonk (2004) compared genetic gain of a local progeny-testing scheme in Costa Rica with genetic gain of semen importation from the United States. They concluded that given the genetic correlation between the 2 countries of around 0.60, a local breeding program based on a nucleus herd could be more profitable than a strategy based on continuous semen importation.

CONCLUSIONS

The emphasis in this study was on milk yield of first-lactation Holstein cows in response to management levels within and across Luxembourg and Tunisian production environments. Genetic parameters were dependent on HM levels in Luxembourg and Tunisia. Within-country-environment genetic correlations of milk yield suggest that there was insufficient sire ranking in Luxembourg to warrant formation of separate breeding schemes for their contrasted environments. However, low genetic and rank correlations within the Tunisian environments indicate serious reranking of sires among HM levels. Genetic correlations between medium and low Luxembourg and high Tunisian HM levels were close to 0.80, supporting the hypothesis that daughters producing in those 2 Luxembourg environments could

be considered a good performance predictor of their paternal half-sisters in the high Tunisian HM herds.

Largest AG and PE variances were found in high HM classes in both populations. The high HM levels were identified as being the most environmentally sensitive among the different contrasted environments. Under unlimited feeding resources and no stressful conditions, a high degree of environmental sensitivity is desired. This postulate can be applied for the case of nearly all the Luxembourg and the high Tunisian HM classes. However, for the other 2 Tunisian environments, a stable production level should be preferred more than a high phenotypic plasticity.

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