

# Interaction Between Milk Yield of Holstein Cows in Mexico and the United States

E. G. CIENFUEGOS-RIVAS,\* P. A. OLTENACU,† R. W. BLAKE,†  
S. J. SCHWAGER,‡ H. CASTILLO-JUAREZ,§ and F. J. RUIZ||

\*Universidad Autónoma de Tamaulipas  
Ciudad Victoria, Tamaulipas, Mexico

†Department of Animal Science and

‡Biometrics Unit,

Cornell University, Ithaca, NY 14853

§Universidad Autónoma Metropolitana, Mexico

||Centro Nacional de Investigación en Fisiología y  
Mejoramiento Animal, Instituto Nacional de Investigaciones Forestales,  
Agrícola y Pecuarias; Secretaría de Agricultura,  
Gauadería y Desarrollo Rulol, Mexico,

## ABSTRACT

Genotype by environment interaction for milk yield was investigated by analyzing 55,162 mature equivalent, first lactation records of daughters from 1339 Holstein sires in Mexico and 499,401 daughters from 663 Holstein sires in the northeastern US. There were 474 US sires in common. Herd-year standard deviation was used to define non-overlapping high ( $\geq 1600$  kg) and low ( $\leq 1300$  kg) Mexican environments and a low ( $\leq 1025$  kg) US environment. Variance components across Mexican environments were about 40% less than those of the US environment. Genetic correlation coefficients between milk yield in various Mexican environments and all US environments ranged from 0.60 to 0.71 and were different from unity ( $P < 0.001$ ). Genetic correlation coefficients with low environment in the US ranged between 0.69 and 0.93; the largest correlation was between the low US and high Mexico environments. Both reductions in the size of genetic variance in Mexican environments relative to the US and genetic correlation coefficients less than unity were indicative of genotype by environment interaction. A significant rank change in estimated breeding values (EBV) of sires in Mexican environments relative to the US was another indicator of genotype by environment interaction. Regression coefficients of EBV of a sire estimated from daughters performances in low and high environments in Mexico were 0.46 and 0.62 against EBV of sires estimated from all data in the US. Against EBV estimated from the low environment in the US they were 0.57 and 0.83. The US low environment was a better predictor of performance in Mexican environments.

**(Key words:** genotype by environment interaction, genetic correlation, Mexico, milk yield)

**Abbreviation key:** **GE** = genotype by environment interaction, **HYSD** = herd-year standard deviation, **ME** = mature equivalent.

## INTRODUCTION

Since the 1950s, Mexico has imported germplasm (mainly animals and semen) especially from the US and Canada to increase domestic milk supplies (22, 23). Although most semen to inseminate Holstein cows in Mexico is from the US (19, 20) and genetic trends in milk in both countries are positive (14), gains in Mexico are less than in the US. Previous studies (13, 14) have shown that daughters of US Holstein sires produced more milk in Mexican herds than did daughters of Canadian or Mexican sires. Also, unequal responses to selection for milk from genotype by environment interaction (**GE**) have been reported in Mexico, other countries of Latin America, and the US (5, 7, 19, 20).

Among various methodologies proposed to evaluate **GE**, bivariate models (two traits measured in two different environments) have been used most often (4, 8, 9, 10, 12, 17). Multivariate models (two or more traits measured in more than two environments) are more appropriate (4, 12) but have been seldom used in situations in which data were limited. For example, in most of Latin America countries the effective number of milk recorded daughters per sire is typically small (19). In this study, a multivariate sire model was used to estimate components of genetic (co)variance for mature equivalent (**ME**) milk yield of Holstein cows in Mexico and US herd environments and to determine correlated responses in different Mexican environments when selection is based on US daughter performance. A complementary objective was to evaluate the hypothesis that predicted response in Mexican herd environments would increase if selection of US sires were to be based

Received June 15, 1998.

Accepted May 28, 1999.

on daughter information from low herd-year standard deviation US environment.

**MATERIALS AND METHODS**

**Data**

For this study, data were requested from the Mexican Holstein Association (Queretaro, Mexico) and from USDA-Animal Improvement Programs Laboratory (Beltsville, MD). Mexican data comprised 87,920 first calving records of 305-d ME milk yields from Holstein cows calving between 1971 and 1995. The US data comprised 976,477 first calving records of 305-d ME milk yields from Holstein cows calving between 1980 and 1993 in the northeast of US (Maine, New Hampshire, Rhode Island, New York, New Jersey, Pennsylvania, and Vermont). Data were edited to include only first lactation records with known sires; sires were required to have at least three daughters in at least two herds, and herds were required to have at least 5 records. The final data comprised 56,162 Mexican first calving records from daughters of 1339 sires in 164 herds and 499,401 US first calving records from daughters of 663 US and Canadian sires in 3685 herds. From 663 US and Canadian sires, 474 had daughters in both Mexico (32,860 records) and the US (408,894 records). Fifteen genetic groups were defined based on origin and year of birth of sires.

Herd-year subclasses were defined (1254 and 20,761 in the Mexican and the US files), and the herd-year phenotypic standard deviation (**HYSD**) was calculated within each subclass. The HYSD for ME milk yield were used to define non-overlapping high (HYSD ≥1600 kg) and low (HYSD ≤1300 kg) environmental opportunity classes for Mexico and a low (HYSD ≤1025 kg) environmental opportunity class for the US. With these arbitrarily chosen limits, 51% of all herd-year subclasses (with 38.3% of records) and 22.5% (with 32.3% of the records) belonged to low and high Mexican environment class, respectively. For the US, 37.8% of herd-year subclasses (24.9% of the records) represented the low environment class).

**Model and Analysis**

The multivariate sire model for ME milk yield in matrix notation was

$$Y = Xb + Wg + Zu + e,$$

where **Y** = vector of observations; **X** = incidence matrix for the herd-year contemporary group effects; **b** = vector of unknown herd-year contemporary group fixed effects; **Z** = incidence matrix for sire effects; **u** = vector of un-

known random sire effects; **Q** = incidence matrix that relates sires to their respective genetic groups; **W = ZQ** because sires are nested within genetic groups; **g** = vector of unknown genetic-group fixed effects; and **e** = vector of residual effects.

The joint distribution of **u** and **e** was multivariate normal with mean zero and variance

$$\begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix},$$

where **G** and **R** = genetic and residual variance-covariance matrices, respectively.

**Estimation of Variance Components**

For this study, ME milk yield in first lactation was considered as a different trait when measured in different herd environments. Variance components were estimated with multivariate analyses by simultaneously considering four traits. In the first analysis the variance components in **G** for ME milk yield were estimated by considering all data from the US and Mexico and from high and low HYSD Mexican environments. Therefore,

$$G = \text{variance} \begin{bmatrix} u1, \text{US all} \\ u2, \text{Mexico all} \\ u3, \text{Mexico high} \\ u4, \text{Mexico low} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} & g_{13} & g_{14} \\ & g_{22} & 0 & 0 \\ & & g_{33} & g_{34} \\ \text{symm} & & & g_{44} \end{bmatrix} \otimes A = G_0 \otimes A.$$

In the second analysis the variance components in **G** were estimated considering low HYSD US environment and all, high, and low Mexican environments. Therefore,

$$G = \text{variance} \begin{bmatrix} u1, \text{US low} \\ u2, \text{Mexico all} \\ u3, \text{Mexico high} \\ u4, \text{Mexico low} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} & g_{13} & g_{14} \\ & g_{22} & 0 & 0 \\ & & g_{33} & g_{34} \\ \text{symm} & & & g_{44} \end{bmatrix} \otimes A = G_0 \otimes A.$$

In both analyses  $\mathbf{G}_0$  = genetic variance covariance matrix among sire effects in different environments ( $1/4$  additive genetic variance),  $\mathbf{A}$  = numerator relationship matrix among sires, and  $\otimes$  = Kronecker product. Residual covariance among records in different environments was assumed to be zero. Genetic covariances between high and low environments within the same multivariate analysis were restricted to zero.

Estimates of (co)variance components and solutions for sire effects were obtained by REML with multivariate, derivative-free REML programs (3). The relationship matrix included sire of sire and maternal grandsire pathways. The initial values for sire and residual variance components were the solutions from univariate analyses for ME milk yield across environments. Convergence was assumed when the variance of the simplex values ( $-2 \log$  likelihood) was  $<10^{-8}$ . A global maximum was achieved when three restarts produced convergence without a change in the first three decimal places of the  $F$  value (3).

### Correlated Responses in Mexico

Correlated responses to selection were estimated by regressing the EBV for ME milk yield from each Mexican data file on the EBV obtained from all US environments and from the low US environment.

### Genetic Correlation

Product-moment genetic correlations between environments were estimated by  $r_{g(i,j)} = g_{ij}/(g_{ii}g_{jj})^{0.5}$ . Standard errors were approximated by using the method of Robertson (16) for genetic correlation and the method of Swiger et al. (21) for heritability. The Spearman rank correlation (18) was used to further examine ranking changes in sire EBV among environments.

### Likelihood Ratio Test

The magnitude of genetic correlation coefficients was tested against unity with the likelihood ratio test (15). Six bivariate analyses (Table 2) were performed to obtain the variance of the simplex value for the test. The likelihood with unitary genetic correlation was obtained by finding the maximum subject to this constraint (reduced model). The likelihood without this constraint was also obtained (full model), and the difference in twice the log likelihood was used to test the result with a chi-square statistic with one degree of freedom.

## RESULTS AND DISCUSSION

Total herds and records and the phenotypic means and standard deviations for ME milk yield in first lactation for all environmental classifications are presented in Table 1. The mean HYSD for high Mexican herd environment was similar to the mean HYSD for the low US environments, 1676 kg vs. 1853 kg, respectively. Note, however, there were substantial differences in the within-herd variance between all US environments and all Mexican herd environments.

### Analysis of All US Environments and Different Herd Environments in Mexico

Estimates of the sire components of (co)variance for milk yield in all US environments and in all, high, and low Mexican herd environments are in Table 2. The genetic variances in Mexico represented 60 to 77% of the genetic variation found in the US. This reduction of the genetic variation indicated that, as HYSD decreased, environmental factors increasingly constrained expression. Similar findings have been re-

TABLE 1. Means and standard deviations for first lactation yield (kilograms) and herd-year standard deviation (HYSD) for mature equivalent milk and number of records in Mexican and US data files.

Data file	Milk yield		HYSD <sup>1</sup>		Records <sup>2</sup>
	$\bar{X}$	SD	$\bar{X}$	SD	
Mexico					
High HYSD <sup>3</sup>	8484	2470	1676	298	18,153
Low HYSD <sup>4</sup>	6565	1542	1102	165	21,524
All data	7454	2134	1453	278	56,162
US					
Low HYSD <sup>5</sup>	9046	2584	1853	237	124,421
All data	9418	2436	2107	205	499,401

<sup>1</sup>Average across herd-years.

<sup>2</sup>Total records within the HYSD quartiles.

<sup>3</sup>Records from herds with HYSD  $\geq 1600$  kg.

<sup>4</sup>Records from herds with HYSD  $\leq 1300$  kg.

<sup>5</sup>Records from herds with HYSD  $\leq 1024$  kg.

TABLE 2. Estimates of sire components of variance ( $Var_g$ ) and covariance ( $Cov_g$ ), correlations of predicted genetic values ( $r_g$ ), and rank correlations of predicted genetic values ( $r_s$ ) for first lactation mature equivalent milk yield (kilograms) in different herd environments defined by alternative US and Mexican data files.<sup>1</sup>

Data file		$Var_g^2$	$Cov_g$	$r_g$	$r_s$
Trait one	Trait two				
US, all data	Mexico, high HYSD <sup>3</sup>	129,152			
	Mexico, low HYSD <sup>4</sup>	99,079	80,316	0.71 <sup>a</sup>	0.69
	Mexico, all data	77,597	59,894	0.60 <sup>a</sup>	0.57
US, low HYSD <sup>5</sup>		96,722	70,084	0.63 <sup>a</sup>	0.59
		124,732			
	Mexico, high HYSD	99,079	103,386	0.93	0.90
	Mexico, low HYSD	77,597	70,433	0.72 <sup>a</sup>	0.68
	Mexico, all data	96,722	75,788	0.69 <sup>a</sup>	0.65

<sup>a</sup>Coefficient differs from unity ( $P < 0.0001$ ).

<sup>1</sup>Standard errors of correlations ranged from 0.0001 to 0.0009.

<sup>2</sup>Genetic variances were not held constant to estimate covariances; minor differences were found between the two analyses, and so for simplicity were written the same.

<sup>3</sup>Records from herds with herd-year standard deviation (HYSD)  $\geq 1600$  kg.

<sup>4</sup>Records from herds with HYSD  $\leq 1300$  kg.

<sup>5</sup>Records from herds with HYSD  $\leq 1024$  kg.

ported for Brazil, Colombia, Puerto Rico, Mexico, and the US (6, 7, 19, 20).

**Correlated response to selection.** The differences in daughter response in Mexico and the US indicate that US genes have less expression in Mexican environments. Expected daughter responses in Mexican environments based on sire selection with EBV calculated from daughters performing across all US herds are in Table 3. Note that daughter response was always  $>1$  and differed across Mexican environments. Daughter response in Mexico was greatest in the high HYSD environment ( $b = 0.621 \pm 0.001$ ) and lowest in the low HYSD environment ( $b = 0.465 \pm 0.003$ ). Greatest responses also occurred in the highest HYSD environment in other Latin American countries (6, 7, 19, 20).

Substantially lower genetic gains than was predicted from daughter information recorded across all US envi-

ronments were the consequence of the reduction of genetic variance in Mexican environments (Table 2). Note that the size of correlated response was inversely proportional to the difference in mean HYSD between Mexican environments and all US environment (Table 1).

**Genetic correlation.** A trait, such as milk yield, could be measured in two related individuals in two environments, and trait expression would be considered to differ in those environments. Genetic correlation coefficients would describe the differential expression resulting from genes that were identical by descent. Hence, if the trait was under pleiotropic genetic control, and the genes were segregating, then similar variation and unitary genetic correlation would be expected (1). However, the presence of GE disturbs this relationship, as shown by the heterogeneity of genetic (co)variances and correlated responses in Tables 2 and 3. Significant alterations in the genetic variances and correlation coefficients between environments may also result in important rank changes in the EBV of sires between target environments (1, 9, 19).

Table 2 shows that estimates of genetic correlations were significantly less than unity ( $P < 0.0001$ ), ranging from 0.60 in the low HYSD to 0.71 in the high HYSD Mexican herd environments. The estimates of rank correlation coefficients ranged between 0.59 and 0.69, indicating changes in the EBV ranking of sires between US and Mexican environments.

**Analysis of Low US Environment and Different Herd Environments in Mexico**

Estimates of the sire components of (co)variance for milk yield in the low US environment and all, high, and

TABLE 3. Regression coefficients ( $b_{YonX}$ ) of sire EBV for mature equivalent milk yield of first lactation across Mexican herd-year standard deviation (HYSD) environments on sire EBV for milk in all herds and in low HYSD environment in the US.

Data file		$b_{YonX}$	SE
EBV (X)	EBV (Y)		
US, all data	Mexico, high HYSD <sup>1</sup>	0.621	0.001
	Mexico, low HYSD <sup>2</sup>	0.465	0.003
	Mexico, all data	0.545	0.003
US, low HYSD <sup>3</sup>	Mexico, high HYSD <sup>1</sup>	0.828	0.001
	Mexico, low HYSD <sup>2</sup>	0.567	0.007
	Mexico, all data	0.659	0.001

<sup>1</sup>Records from herds with HYSD  $\geq 1600$  kg.

<sup>2</sup>Records from herds with HYSD  $\leq 1300$  kg.

<sup>3</sup>Records from herds with HYSD  $\leq 1024$  kg.

low Mexico environments are in Table 2. The genetic variances in Mexican environments were from 62 to 80% as large as the genetic variation found in the low HYSD US environment.

**Correlated response to selection.** Expected daughter responses in Mexico based on EBV of sires estimated from the performance of daughters in low HYSD US environment are shown in Table 3. Response was greatest in the high HYSD environment ( $b = 0.828 \pm 0.001$ ) and was least in the low Mexican environment ( $b = 0.567 \pm 0.007$ ). Note that the differences in mean HYSD between high and low Mexican environments with low HYSD US environment (Table 1) were 177 kg and 751 kg, respectively.

**Genetic correlation.** The genetic correlations between milk yield in first lactation in the low US environment and all, high, and low Mexican environments (Table 2) were smaller than unity and were significantly different ( $P < 0.001$ ) between low US and all or low Mexican environments. However, the correlation was greatest and not significantly different from unity ( $P = 0.174$ ) between the high Mexican herd environment and the low US herd environment. This finding indicated that sire EBV estimated from daughters producing in the low US herd environment were a better predictor of performance of daughters in Mexico.

Our results showed that milk yield expression of US Holstein genes was less in Mexican environments than in US environments, in agreement with reports from other Latin American dairy production environments (6, 7, 13, 14, 19, 20). The proportion of US genetic superiority that was recovered in the high HYSD Mexican environments when the sire selection decision was based on daughter performance in all US environments was 60%. However, it increased to 80% if US sires were evaluated with the daughter information from low US environment, which had a similar mean HYSD to the high Mexican environment. In this study, the only genetic correlation not different from unity was between milk yield of daughters in low HYSD US environment and performance of half-sisters in high HYSD Mexican environment. These results and the rank correlation between the EBV of sires (Table 2) supported our hypothesis that daughter information from the low HYSD US environment improved the prediction of daughter performance across Mexican environments compared with using information from all US environments.

## CONCLUSIONS

In this study, significant GE interaction was found between genotype for milk yield and the dairy production environment. Unequal and smaller daughter responses to US sire selection were detected across Mexi-

can herd environments. Furthermore, genetic correlation coefficients less than unity for ME milk and rank-order correlations  $< 0.7$  in sire EBV indicated that sires were ranked differently in Mexican environments. However, these impediments to genetic gain and net economic returns to the sire selection decision (2, 11) would be alleviated by using information from daughter records from similar HYSD environments to obtain sire EBV. These results support the hypothesis that cows producing in a low HYSD US environment better predict performance of the paternal half-sisters in Mexican herds. Similar findings were reported by Costa et al. (7) for Brazil and by Stanton et al. (19, 20) for Colombia, Mexico, and Puerto Rico. Consequently, we urge exporting countries to provide importing countries with sire information based on production environments defined to match those in the importing country. The GE interaction not only impedes genetic gain but, more importantly, it contributes to severely reduced and unequal net economic benefits from AI biotechnology in importing countries of Latin America (11).

## REFERENCES

- 1 Aasteveit, A. H., and K. Aasteveit. 1993. Effects of genotype-environment interactions on genetic correlations. *Theor. Appl. Genet.* 86:1007-1013.
- 2 Blake, R. W., F. J. Holmann, J. Gutierrez, and G. F. Cevallos. 1988. Comparative profitability of United States Holstein artificial insemination sires in Mexico. *J. Dairy Sci.* 71:1378-1388.
- 3 Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassel, and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variance and covariances. Draft. Revised. USDA-ARS, Roman L. Hruska US Meat Animal Research Center, Clay Center, NE.
- 4 Cameron, N. D. 1993. Methodologies for estimation of genotype with environment interaction. *Lives. Prod. Sci.* 35:237-249.
- 5 Carabaño, M. J., K. M. Wade, and L. D. Van Vleck. 1990. Genotype by environment interactions for milk and fat production across regions of the United States. *J. Dairy Sci.* 73:173-180.
- 6 Carvalheira, J.G.V., R. W. Blake, E. J. Pollak, R. L. Quaas, and C. V. Duran-Castro. 1998. Application of an autoregressive process to estimate genetic parameters and breeding values for dairy milk yield in a tropical herd of Lucerna cattle and in US Holstein herds. *J. Dairy Sci.* 81:2738-2751.
- 7 Costa, C. N., R. W. Blake, E. J. Pollak, and P. A. Oltenacu. 1998. Genetic relationships for milk and fat between Holstein populations in Brazil and the United States. 6th WCGALP World Congress on Genet. Applied Livest. Prod. 23:323-326.
- 8 Danell, B. 1982. Interaction between genotype and environment in sire evaluation for milk production. *Acta Agric. Scand.* 32:33-46.
- 9 Eisen, E. J., and A. M. Saxton. 1983. Genotype by environment interactions and genetic correlations involving two environmental factors. *Theor. Appl. Genet.* 67:75-86.
- 10 Falconer, D. S. 1952. The problem of environment and selection. *The Am. Nat.* 86:293-298.
- 11 Holmann, F., R. W. Blake, R. A. Milligan, R. Barker, P. A. Oltenacu, and M. V. Hahn. 1990. Economic returns from United States artificial insemination sires in Holstein herds in Colombia, Mexico, and Venezuela. *J. Dairy Sci.* 73:2179-2189.
- 12 Mathur, P. K., and W. Schlote. 1995. Univariate or multivariate approach for estimating genotype-environment interactions? *Arch. Tierz. Dummerstorf* 38:577-586.

- 13 Powell, R. L., and F. N. Dickinson. 1977. Progeny Tests in the United States and in Mexico. *J. Dairy Sci.* 66:1768–1772.
- 14 Powell, R. L., and G. R. Wiggans. 1991. Animal Model Evaluations for Mexican Holsteins. *J. Dairy Sci.* 74:1420–1427.
- 15 Robert, C., J. L. Foulley, and V. Ducrocq. 1995. Genetic variation of traits measured in several environments. I. Estimation and testing of homogeneous genetic and intra-class correlations between environments. *Genet. Sel. Evol.* 27:111–123.
- 16 Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469–485.
- 17 Sahota, R. S., and G. S. Gill. 1991. Genotype  $\times$  environment interaction for some traits of economic importance of dairy cattle. *J. Res. Punjab Univ.* 28:395–409.
- 18 Siegel, S., and N. J. Castellan. 1988. *Non-parametric Statistics for the behavioral sciences*. 2nd ed. McGraw-Hill Int. Editions, Singapore, Singapore.
- 19 Stanton, T. L., R. W. Blake, R. L. Quaas, L. D. Van Vleck, and M. J. Carabaño. 1991. Genotype by environment interaction for Holstein milk yield in Colombia, Mexico, and Puerto Rico. *J. Dairy Sci.* 74:1700–1714.
- 20 Stanton, T. L., R. W. Blake, R. L. Quaas, and L. D. Van Vleck. 1991. Response to selection of United States Holstein sires in Latin America. *J. Dairy Sci.* 74:651–664.
- 21 Swiger, L. A., W. R. Harvey, D. O. Everson, and K. E. Gregory. 1964. The variance of intra-class correlation involving groups with one observation. *Biometrics* 20:818–826.
- 22 US Department of Agriculture. 1997. *Dairy: World Markets and Trade*. Foreign Agricultural Service. Circular Ser. FD 2-97 July 1997. USDA, FAS, Washington, DC.
- 23 US Department of Agriculture. 1997. *Dairy, Livestock, and Poultry: US Trade and Prospects*. Foreign Agricultural Service. Circular Ser. FD 09-97 September 1997. USDA, FAS, Washington, DC.