INTERACTION BETWEEN GENOTYPE AND GEOGRAPHIC REGION FOR MILK PRODUCTION IN MEXICAN HOLSTEIN CATTLE

INTERACCIÓN ENTRE GENOTIPO Y REGIÓN GEOGRÁFICA PARA PRODUCCIÓN DE LECHE EN GANADO HOLSTEIN MEXICANO

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ADDITIONAL KEYWORDS

PALABRAS CLAVE ADICIONALES

SUMMARY
In order to investigate the presence of genotype-region interactions for milk yield in Holstein cattle in Mexico, first lactation, 305-days mature-equivalent milk production records were used. Data were classified as belonging to three regions of the country: Northern, Central and Southern. Genetic correlations (rG) were estimated for pairs of regions using bivariate animal models. Only data from sires with daughters in two regions were used in each analysis. Models included herd-year-season of calving as fixed effect and animal as random effects. The rG among Northern-Central, Northern-Southern and Central-Southern regions were 0.73, 0.38 and 0.93, respectively. The rG Northern-Southern was significantly smaller than unity (p= 0.002), while for the rG Northern-Central, the test approached significance (p=0.07). These results indicate the existence of genotype-environment interaction which may have several implications for the genetic improvement of Holstein cattle in Mexico. It also encourages further studies oriented toward the identification of specific environmental effects related to these interactions.

RESUMEN
Se utilizaron registros de primera lactancia corregidos a 305 días y equivalente de madurez, para investigar la presencia de interacciones genotipo-regiones para producción de leche en Ganado Holstein en México. Los registros fueron clasificados en tres regiones del país: Norte, Centro y Sur. Las correlaciones genéticas (rG) fueron estimadas por pares de regiones, usando modelos animales bivariados. Sólo se utilizaron registros de sementales con hijas en dos regiones en cada análisis. Los modelos incluyeron el año-estación de parto como efecto fijo, y el efecto de animal como aleatorio. Las rG entre Norte-Centro, Norte-Sur y regiones Centro-Sur fueron de 0.73, 0.38 y 0.93, respectivamente. La rG entre Norte-Sur fue significativamente menor que la unidad (p= 0.002), mientras que la rG entre Norte-Centro tuvo una probabilidad cercana al límite de significancia (p= 0.07). Estos resultados indican la presencia de una interacción genotipo-ambiente, los cuales pueden tener diversas repercusiones para el mejoramiento genético del ganado Holstein en México. Se requieren estudios adicionales orientados a la identificación de factores ambientales específicos relacionados a estas interacciones.

INTRODUCTION
Genotype x environment interaction (GEI) results from the lack of adaptation of
particular genotypes to specific conditions of production systems. It may reduce economic performance of animals when the environmental conditions under which candidates have been selected are different from those of commercial populations (Dickerson, 1977). The effect of GEI reduces selection responses, rendering selection programs or importation of improved germplasm economically less efficient (Dickerson, 1962; Montaldo, 2001).

Since 1950, Mexico has imported Holstein germplasm, (mainly animals and semen) especially from USA and Canada, to increase productivity of its dairy cattle populations. Evidence of genotype-environment interactions among USA, Mexico and other countries from Latin America has been reported (Stanton et al., 1991; Costa et al., 1998; Cienfuegos et al., 1999), when estimated genetic correlations among countries were lower than one. For example, genetic correlations estimated between USA and Colombia and between USA and Mexico for milk production were 0.78 and 0.90, respectively (Stanton et al., 1991). Costa et al. (1998) obtained a genetic correlation of 0.85 for milk production between USA and Brazil, and Cienfuegos et al. (1999) estimated genetic correlations for milk production between Mexico and USA, classifying herd-years according to the standard deviation level, between 0.60 and 0.72.

In another study, Carabaño et al. (1990) estimated genetic correlations for milk production among the states of California, New York and Wisconsin from 0.90 to 0.98, which were regarded as an indication of no GEI. In studies by Van Vleck et al. (1988) and Wade et al. (1989) genetic correlations between milk and fat production were in average 0.70 for the region of California vs. 0.58 for the regions of New York and Wisconsin. The authors interpreted these differences as an indication for the presence of GEI among these regions.

There are no studies on GEI involving estimates of genetic correlations among regions for Holstein cattle in Mexico. Differentiation of environments in Mexico and other countries with tropical and subtropical regions is important, because Holstein herds and production level could be influenced for the environment in different magnitude. Therefore, this type of studies may give some indication of what could happen when selection is performed under several environmental conditions. The objective of this study was to investigate the presence of genotype-geographical region interactions for milk production in Holstein cattle in Mexico.

**MATERIAL AND METHODS**

Data were obtained from the milk recording system of the Mexican Holstein Association. First lactation 305-day mature equivalent records were used. Data were edited by discarding records without lactation number, with less than 18 months of age at first calving, and with codes indicating lactations initiated with abortion, or terminated by sale, illness or lesions, or cows with less than 1500 kg of total milk production. Data from herds with less than 10 records, were also discarded.

Records were classified by location of herd as Northern, Central and Southern regions. Northern region included the arid states of Baja California Norte, Chihuahua, Sinaloa, Coahuila and Durango; the Central region involve mostly arid and temperate states of Aguascalientes, Guanajuato, Michoacán, Jalisco, Querétaro, San Luis Potosí and Zacatecas, and the Southern region included the temperate and subtropical states of Mexico, Hidalgo, Tlaxcala, Puebla and Veracruz. Dominant climatic classification according to the modified Köppen system, average temperature and annual rainfall are presented for each region in table I.

Climates, temperatures and rainfall varied considerably within regions and states. To obtain the average values for
temperature and rainfall given in Table I, climate prevailing in the area where herds were located in each state was considered. Northern region presented the most extreme temperatures, and Southern region was the one with highest rainfall.

Genetic correlations for milk production (r_{ij}) were estimated using records of daughters of sires distributed in several regions, considering only sires with at least 5 daughters in two regions for bivariate analysis (Garrick and Van Vleck, 1987). Numbers of records analyzed are shown in Table II.

Two seasons were defined trying to get a minimum of 10 observations in the combination herd-year-season of calving effects and to have seasons with different average temperature and precipitation effects; season 1 from June to November (warm and rainy); and season 2 from December to May (dry and cold).

Three bivariate animal models were used to estimate the components of (co)variance. Restricted Maximum Likelihood (REML) method and the MTDFREML program (Boldman et al., 1995) were used. Several studies have reported (co)variance estimates from REML-animal model analyses in dairy cattle (Cienfuegos et al., 1999; Dedková and Wolf, 2001; Zwald et al., 2003; Valencia et al., 2004), due to their convenient properties of maintaining estimates within the parametric space taking into account selection bias when complete pedigree is used (Henderson, 1984).

Usual assumptions were made regarding variances and covariances in this type of studies (e.g. Cienfuegos et al., 1999), assuming that the environments for the daughters of each bull were independent, therefore, residual covariance was set to 0. All additive genetic relationships where considered through the numerator additive relationship matrix A with complete pedigree information of each animal and records for several generations. To estimate the (co)variance components, convergence was assumed when the change in -2 log likelihood (L) was equal to or smaller than 10^{-6}. If the model converged to similar values for genetic correlations, using at least three restarts with different initial sets of values for the variances and covariances, a global maximum was assumed to be found (Boldman et al., 1995).

Likelihood ratio statistics were used to

The equations used are represented as:

\[ \begin{bmatrix} y_{1j} \\ y_{2j} \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \]

where:

- subindices 1 and 2 identify the regions where daughters of the sires were,
- \( y \) = vector (nx1) of observations of first lactation milk yields,
- \( X \) = incidence matrix (nxp) of fixed effects, that included the effect of herd-year-season,
- \( b \) = vector (px1) of fixed effects,
- \( Z \) = incidence matrix (nxq) of random effects that included the animal effect,
- \( u \) = vector (qx1) of random effects,
- \( e \) = random vector (nx1) (error).

### Table I. Climates, temperatures (°C) and rainfall (mm) in each region of Mexico. (Climas, temperaturas (°C) y precipitación (mm) en cada región de México).

<table>
<thead>
<tr>
<th>Region</th>
<th>Dominant climate classification</th>
<th>Annual range of temperature (°C)</th>
<th>Annual range of rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern</td>
<td>Arid</td>
<td>14-18</td>
<td>200-400</td>
</tr>
<tr>
<td>Central</td>
<td>Temperate semihumid</td>
<td>18-20</td>
<td>450-900</td>
</tr>
<tr>
<td>Southern</td>
<td>Temperate humid</td>
<td>14-16</td>
<td>600-1200</td>
</tr>
</tbody>
</table>

Adapted from INEGI (2002).

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test if the genetic correlation between two regions was less than one (Robert et al., 1995). Values of L were obtained for two models; in the first model (1) all variances were estimated, while in the second (2), L was obtained restricting \( r_g \) to be equal to one.

**RESULTS**

Number of bulls with daughters in at least two regions were 85, 67 and 236, for Northern-Central, Northern-Southern, and Central-Southern regions, respectively. Total number of daughters for Northern-Central, Northern-Southern and Central-Southern bivariate analyses were 5086, 2854 and 14533 respectively. Estimated correlations between each of these pairs were 0.73, 0.38 and 0.93, respectively (table II).

Table II shows that genetic variances estimated for Northern region were larger than those for Central and Southern regions. Additive genetic variance estimated for Northern region was 2.24 and 2.34 times those for Central and Southern regions, respectively.

**DISCUSSION**

The reduced value of the genetic correlation between the Northern and Southern regions estimated in this study for milk yield (0.38), significantly less than one, Table III shows the values of -2 log likelihood of complete and restricted models for each analysis and the results of likelihood ratio tests.

The \( \chi^2 \) value calculated for the Northern-Southern regions analysis was 3.84, then the \( Ho \) was rejected (\( p=0.002 \)) indicating the presence of GEI between these two regions. The \( r_g \) obtained between Northern and Central regions was 0.73 and was close to significance (\( p=0.07 \)). Average milk yields varied among regions in this study. The largest environmental differences, estimated as the average milk yields minus the average breeding value of sires, were found between Northern and Central regions (778 kg), followed by the Northern and Southern (511 kg) and Central and Southern regions (141 kg).

**Table II.** Additive genetic and residual (co)variances and genetic correlations among Northern (N), Central (C) and Southern (S) regions of Mexico. ((Co)varianzas genéticas aditivas y residuales y correlaciones genéticas entre regiones Norte (N), Centro (C) y Sur (S) de México).

<table>
<thead>
<tr>
<th>Pairs of regions</th>
<th>N-C</th>
<th>N-S</th>
<th>C-S</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of sires</td>
<td>85</td>
<td>67</td>
<td>236</td>
</tr>
<tr>
<td>Total number of daughters</td>
<td>5,086</td>
<td>2,854</td>
<td>14,533</td>
</tr>
<tr>
<td>Number of daughters N region</td>
<td>1,479</td>
<td>1,805</td>
<td>-</td>
</tr>
<tr>
<td>Number of daughters C region</td>
<td>3,807</td>
<td>-</td>
<td>9,382</td>
</tr>
<tr>
<td>Number of daughters S region</td>
<td>-</td>
<td>1,049</td>
<td>5,151</td>
</tr>
<tr>
<td>Milk yield (kg) N region</td>
<td>8,116</td>
<td>8,242</td>
<td>-</td>
</tr>
<tr>
<td>Milk yield (kg) C region</td>
<td>7,298</td>
<td>-</td>
<td>8,124</td>
</tr>
<tr>
<td>Milk yield (kg) S region</td>
<td>-</td>
<td>7,696</td>
<td>7,979</td>
</tr>
<tr>
<td>Additive genetic variance N region</td>
<td>656.276</td>
<td>873.666</td>
<td>-</td>
</tr>
<tr>
<td>Additive genetic variance C region</td>
<td>293.458</td>
<td>-</td>
<td>381.297</td>
</tr>
<tr>
<td>Additive genetic variance S region</td>
<td>-</td>
<td>373.614</td>
<td>416.098</td>
</tr>
<tr>
<td>Additive genetic covariance</td>
<td>319.390</td>
<td>216.238</td>
<td>369.897</td>
</tr>
<tr>
<td>Residual variance N region</td>
<td>1,374.478</td>
<td>1,161.085</td>
<td>-</td>
</tr>
<tr>
<td>Residual variance C region</td>
<td>1,159.599</td>
<td>-</td>
<td>1,414.212</td>
</tr>
<tr>
<td>Residual variance S region</td>
<td>-</td>
<td>1,327.986</td>
<td>1,381.565</td>
</tr>
<tr>
<td>Genetic correlation</td>
<td>0.73</td>
<td>0.38</td>
<td>0.93</td>
</tr>
</tbody>
</table>

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indicates an important genotype-environment interaction, and therefore, a different expression of the same genes in the daughters of the same sire on each environment (Aasteveit and Aasteveit, 1993). Genetic correlation obtained for Northern-Central regions was 0.73 and was close to significance. In other studies, authors had considered genetic correlations below 0.80, as having important negative effects in the efficiency of selection programs and reducing selection responses (Robertson, 1959; Carabaño et al., 1989; Cienfuegos et al., 1999, Muñoz et al., 2001).

Larger additive genetic variances was found for the Northern than for Central or Southern regions. Differences between residual variances were low (table II). These trends are similar to previous findings by Valencia et al. (2004). Heritability estimated for the Northern region was higher than the value obtained for other regions in Northern-Central (0.32 vs. 0.20) and Northern-Southern (0.43 vs. 0.22) analysis, while heritabilities estimated in Central-Southern region analysis (0.21 vs. 0.23) were similar. These heritability values indicates that in spite of the existence of an important additive genetic variance in all three regions which make selection potentially effective at each region, selection of sires across regions deserves further analysis. If herds included in this study represents well all herds in each region, the ranking of bulls by their breeding values for milk yield will be very different in Northern and Southern regions. Selection response in Southern region and possibly in Central regions, will be lowered if sire selection is based on genetic evaluation done only with data of herds in Northern region (Cienfuegos et al., 1999; Montaldo et al., 2001).

In another independent analysis performed with this same data, the genetic correlation for records obtained in herds with extremely high or low milk production was 0.40, indicating again the presence of genotype-environmental interactions in this population (Montaldo, 2001).

The lowest values of genetic correlation found in several studies carried out to evaluate GEI in different populations and environments in dairy cattle has been around 0.60 (Stanton et al., 1991; Cienfuegos et al., 1999; Costa et al., 1998; Muñoz et al., 2001; Zwald et al., 2003). Large differences among regions for feeding, climate, herd size level of production and particular management in the present study, probable could explain the low value of genetic correlation estimated between Northern and Southern regions of this study. In Colombia, Muñoz et al. (2001) found evidences of GEI for milk production in Holstein cattle in a study involving four regions. They found a significantly lower than unity (p<0.05) genetic correlation of 0.70 between Cundinamarca and Valle del Cauca regions. Carabaño et al. (1989) estimated an average value of 0.81 for genetic correlations for milk production between United States and Spain. In a study by Cienfuegos et al. (1999), herds in Mexico and United States were classified in high and low categories, based

Table III. -2 log likelihood values (L) obtained for complete and restricted models and results of likelihood ratio test (Ho: r g=1). (Valores obtenidos de -2 log de verosimilitud para los modelos completo y restringido y resultados de la prueba de razón de verosimilitud).

<table>
<thead>
<tr>
<th></th>
<th>Northern-Central</th>
<th>Northern-Southern</th>
<th>Central-Southern</th>
</tr>
</thead>
<tbody>
<tr>
<td>L from restricted model</td>
<td>27.033</td>
<td>15.872</td>
<td>84.078</td>
</tr>
<tr>
<td>L from complete model</td>
<td>27.030</td>
<td>15.863</td>
<td>84.077</td>
</tr>
<tr>
<td>Differences of L</td>
<td>3.23</td>
<td>9.19</td>
<td>1.04</td>
</tr>
<tr>
<td>Observed P-value</td>
<td>0.0723</td>
<td>0.0024</td>
<td>0.3078</td>
</tr>
</tbody>
</table>

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on their phenotypic standard deviation of milk production. Estimates of genetic correlations between both countries varied from 0.60 to 0.72, pointing out the presence of GEI, related to country and to herd environment. In this and other studies with data from Mexico and other Latin American countries with imported bulls, genetic correlations decreased when the management, geographical and climatic differences increase (Stanton et al., 1991; Cienfuegos et al., 1999; Montaldo, 2001). The higher average production of herds in Northern region are probably related to a better and more homogeneous nutritional and management practices than in other regions (Valencia et al., 2004).

Zwald et al. (2003) identified factors that cause genotype by environment interactions in Holstein herds in seventeen countries with temperate climate. They used genetic correlation estimates between records classified by quintiles for all production, reproduction, climate and others evaluated traits. Variables with genetic correlations deviating the most from unity were temperature (0.84), herd size (0.79), sire PTA for milk (0.89), percent of North American Holstein genes (0.83), peak milk yield (0.84) fat:protein ratio (0.90), and standard deviation for milk yield (0.90). In this present study probably any of these factors could be causes of genotype by environment interaction. Any of these factors could be causes of genotype by environment interaction in this study. The lower values found in this study could be attributed to more extreme differences in some of these factors between regions. These may involve feeding, climate, altitude over sea level, herd size, production levels and different management practices.

A minimum number of daughters by sire has been set, following recommendations by Garrick and Van Vleck (1987). Therefore, we can rule out that low value estimated values may result from an inadequate data structure. Further studies on this subject are desirable. Furthermore estimators of variance and covariance components with multivariate animal models are unbiased under REML (Hofer, 1998; Searle et al., 1992), and the number of daughters in each environment may not bias the estimates of genetic correlations in a predictable way.

CONCLUSIONS

Studies oriented to the identifying factors involved in GEI in Mexico may help in the evaluation of restrictive environmental influences so that the genetic superiority can be expressed in improved production environments. This low value of genetic correlation estimated in the present study suggest that genotype-environmental interactions might exists for Holstein sires through regions in Mexico. Its may have an impact for an important proportion of the herds in the country with less intensive production systems, not only for milk yield.

GEI reduces genetic gains and therefore reduce the economic returns from the use of selected artificial insemination sires. Results from this study stimulate the comparison of regional genetic evaluations with national evaluations to better account for these effects in the evaluation procedures.

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estimates of variances and covariances (Draft).


