Factors that Cause Genotype by Environment Interaction and Use of a Multiple-Trait Herd-Cluster Model for Milk Yield of Holstein Cattle from Brazil and Colombia

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ABSTRACT

Descriptive herd variables (DVHE) were used to explain genotype by environment interactions ($G \times E$) for milk yield (MY) in Brazilian and Colombian production environments and to develop a herd-cluster model to estimate covariance components and genetic parameters for each herd environment group. Data consisted of 180,522 lactation records of 94,558 Holstein cows from 937 Brazilian and 400 Colombian herds. Herds in both countries were jointly grouped in thirds according to 8 DVHE: production level, phenotypic variability, age at first calving, calving interval, percentage of imported semen, lactation length, and herd size. For each DVHE, REML bivariate animal model analyses were used to estimate genetic correlations for MY between upper and lower thirds of the data. Based on estimates of genetic correlations, weights were assigned to each DVHE to group herds in a cluster analysis using the FASTCLUS procedure in SAS. Three clusters were defined, and genetic and residual variance components were heterogeneous among herd clusters. Estimates of heritability in clusters 1 and 3 were 0.28 and 0.29, respectively, but the estimate was larger (0.39) in Cluster 2. The genetic correlations of MY from different clusters ranged from 0.89 to 0.97. The herd-cluster model based on DVHE properly takes into account $G \times E$ by grouping similar environments accordingly and seems to be an alternative to simply considering country borders to distinguish between environments.

(Key words: milk yield, genotype by environment, dairy cattle, cluster analysis)

Abbreviation key: AFC = age at first calving, CI = calving interval, DVHE = descriptive herd variable, G

$\times E$ = genotype by environment interaction, HS = herd size, HY = herd-year of calving, IS = percentage imported semen, LL = lactation length, MY = milk yield, PL = production level, YV = MY variability.

INTRODUCTION

In Latin America, which is characterized as a net importer of genetic material, a comparison of the sires used would allow evaluation of genetic resources and the development of genetic improvement strategies that fit the current socioeconomic conditions and, thus, increase the potential of Holstein cattle in pan-American countries (Stanton, 1990; Costa et al., 2001).

For Banos and Smith (1991), selection of sires under international evaluation increases the genetic progress of the countries involved, especially when they present similar selection objectives, and the countries with small populations, low genetic progress, or both would benefit most. This type of genetic evaluation increases the number of sires used, increases the confidence of farms, and allows for the realization of national and regional selection objectives (Fikse, 2002).

According to Costa (1998), joint genetic evaluation involving multiple Latin American countries would be one more tool to complement the national genetic evaluations; however, results from research in these countries indicated the existence of large environmental influences between herds, which is a critical study point before implementing such joint evaluations. Among these studies, there is an urgent need to determine the genotype $\times$ environment interaction ($G \times E$) among the countries involved.

The international genetic evaluations done by the Interbull Center have considered the existence of $G \times E$, attributed to the location of the herds, using country borders as the criterion (Schaeffer, 1994; Mocquot, 2001). However, herds of different countries can be more similar to each other in management, production system, climate, and genetic composition than herds

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within the same country (Weigel and Rekaya, 2000; Fikse, 2002; Zwald, 2003b).

Weigel and Rekaya (2000) proposed ignoring country borders and grouping herds by descriptive herd variables (**DVHE**) that would allow the characterization of management systems, climate, and genetic composition. This herd stratification criterion, in addition to grouping similar herds in different countries, would detect the existence of heterogeneous variances between environments and $G \times E$. However, it would be time consuming and expensive to do genetic evaluation of milk yield (**MY**) for each descriptor variable. Therefore, Weigel and Rekaya (2000) proposed the use of cluster analyses, which would allow the simultaneous evaluation of several DVHE to group the herds.

A cluster scheme organizes and groups similar observations (herds), assuring homogeneity within groups and heterogeneity between groups for the pool of considered variables (Bussab et al., 1990; Everitt, 1993).

According to Weigel and Rekaya (2000), Fikse (2002), Lohuis and Dekkers (1998), and Zwald et al. (2003a), cluster analysis in international genetic evaluation would increase reliability and trustworthiness of joint genetic evaluations and would allow the use of dairy sires adequate for the various environments, consequently increasing genetic progress at each production environment.

This study had as objectives 1) to identify environment descriptor variables, 2) to apply cluster analysis to group herds with similar production systems, 3) to estimate (co)variance components for MY, and 4) to determine the existence of $G \times E$ for MY in Brazilian and Colombian herds.

MATERIALS AND METHODS

Information on 180,522 lactations of 94,558 cows (parities 1 to 6) of Holstein herds from Colombia and Brazil, between 1980 and 1997, from the datasets of the Associação Brasileira de Criadores de Bovinos da Raça Holandesa and from the datasets from the "Asociación Holstein de Colombia" was used. Milk yield was adjusted to 305 d and for age, calving order, and season using adjustment factors suggested by Torres (1998) for Brazil and by Cerón-Muñoz et al. (2003) for Colombia.

Contemporary groups were formed for lactations recorded in the same herd and the same year. Subsequently, the herds were grouped using as criteria 7 DVHE: production level (**PL**), considered as the average MY of herd-year of calving (**HY**); MY variability (**YV**), considered as the average of the phenotypic standard error of HY; average age at first calving (**AFC**) of the HY; average calving interval (**CI**) of the HY; average percentage of imported semen (**IS**) of the HY; average

lactation length (**LL**) of the HY, and average herd size (**HS**). More than 5 lactations for contemporary groups were considered in each DVHE.

The (co)variance components of first lactation MY in herds grouped in upper and lower thirds of each DVHE were estimated using bivariate animal model analyses and the REML method, using the program MTDFREML (Boldman et al., 1993), considering MY in each group as different traits. The model included the fixed effects of HY, sire genetic group, genetic group of the cow, and the random effects of animal and residual. The MTDFREML software does not indicate the standard errors for variance estimates.

Genetic groups of sires were defined considering origin and birth of sires: Brazilian (before 1979, 1980 to 1984, and 1985 to 1993), Canadian (before 1976, 1977 to 1981, and 1982 to 1993), Colombian (before 1979, 1980 to 1984, and 1985 to 1993), and US (before 1971, 1972 to 1976, 1977 to 1981, and 1982 to 1993). In addition, cows were grouped as Holstein, purebred or grade (genetic composition $\leq 31/32$ Holstein), according to the classification of Holstein Association in each country.

The model for the bivariate analyses of MY between herds grouped in lower and upper thirds for each DVHE is represented in matrix notation as

$$y_i = X_i b_i + Z_i a_i + e_i$$

with

$$y = \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where

y_i = vector of observations for MY in the herds grouped in third i for $i = 1$ (lower) and 2 (upper);

b_i = vector of fixed effects of HY, genetic group of the cow, and genetic group of the sire for MY in the third i ;

a_i = vector of the random additive genetic effect of animal for MY in the third i ;

e_i = vector of random residual effects for MY in the third i ; and

X_i = incidence matrix related to the fixed effects referring to b_i and Z_i is the incidence matrix related to the random additive genetic effect of animal (a_i) in each group $i = 1, 2$.

The assumptions in relation to the first and second moments were

$$\begin{bmatrix} a \\ e \end{bmatrix} \sim NMV \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \right)$$

Table 1. Spearman's correlations between descriptor variables (production level [PL], milk yield variability [YV], age at first calving [AFC], lactation length [LL], calving interval [CI], percentage imported semen [IS], and size [HS]) for Holstein herds in Brazil and Colombia.

Descriptor variable	YV	AFC	LL	CI	IS	HS
PL	0.46**	-0.36**	0.16**	-0.02 ^{NS}	0.15**	0.08**
YV		-0.24**	0.04 ^{NS}	0.018 ^{NS}	0.08**	0.12**
AFC			0.01 ^{NS}	-0.03 ^{NS}	-0.06*	-0.02 ^{NS}
LL				0.24**	0.07**	-0.09**
CI					-0.02 ^{NS}	-0.01 ^{NS}
IS						0.046 ^{NS}

** $P < 0.01$. Level of NS = $P < 0.05$.

where

$G = A \otimes G_0$ is the additive genetic (co)variance

$$\text{matrix for } G_0 = \begin{bmatrix} \sigma_{a_{11}}^2 & \sigma_{a_{12}} \\ \sigma_{a_{21}} & \sigma_{a_{22}}^2 \end{bmatrix},$$

where A = matrix of the additive genetic relationships among animals; $\sigma_{a_{ii}}^2$ = additive genetic variance of for MY in groups $i = 1, 2$; and $\sigma_{a_{12}}^2$ = additive genetic covariance for MY between groups 1 and 2; and

$R = I \otimes R_0$ is the residual (co)variance

$$\text{matrix for } R_0 = \begin{bmatrix} \sigma_{e_{11}}^2 & 0 \\ 0 & \sigma_{e_{22}}^2 \end{bmatrix},$$

where $\sigma_{e_{ii}}^2$ = residual variance for MY in group $i = 1, 2$.

The total number of sires with progeny in herds grouped in upper and lower thirds for each descriptor variable (PL, YV, AFC, LL, CI, IS, and HS) was 1759, 1772, 1725, 1745, 1786, 1776, and 1738, respectively, and the number of sires common to both groups was 1025, 995, 846, 1076, 983, 999, and 1018, respectively.

For cluster analysis, the herds were grouped according to the method of k-averages, using the 7 environmental descriptor variables as previously mentioned (standardized with mean = 0 and variance = 1). A weight for each descriptor variable was included, considering the importance of $G \times E$ on MY, based on the relation of $\sigma_{a_{12}}^2 / \sigma_{a_i}^2$, where i is the group with greater genetic variance of MY. The cluster analysis used the FASTCLUS procedure of SAS (2002). The number of clusters was based on the cubic clustering criterion, where high values of the cubic clustering criterion indicate clearly defined clusters (SAS, 1989).

Genetic and residual (co)variance components of MY from the clusters were estimated using a trivariate ani-

mal model, including the same effects described for the analyses used for DVHE.

RESULTS AND DISCUSSION

As indicated in Table 1, most DVHE variables were relatively independent from each other. However, for the PL, YV, AFC, and LL, there was interdependence among them, as discussed by Zwald et al. (2003b). For example, as the herd PL increased, variability also increased (correlation = 0.46), which was amply discussed by Visscher et al. (1991), who stated that a typical correlation value between the average and the variance is 0.4 to 0.5. Another positive correlation (0.24) among the descriptor variables was found between LL and CI. Negative correlations existed between AFC with PL (-0.36) and YV (-0.24).

The variable with the smallest genetic correlation with MY among groups was the phenotypic variance of the herds (genetic correlation = 0.85), indicating that, among the environmental descriptor variables analyzed in this study, YV was the one that best detected $G \times E$. The herds with large variability presented greater heritability coefficients ($h^2 = 0.33$) than the those with low variability ($h^2 = 0.28$).

In the case of grouping the herds by PL, the genetic correlation was almost unity, indicating that this DVHE did not detect $G \times E$; however, it detected the presence of heterogeneous genetic and residual variances for MY. The discussion about grouping herds by variability or PL has been an issue for several researchers. For Dong and Mao (1990), Boldman and Freeman (1990), and Stanton et al. (1991), grouping the herds by YV can better detect the existence of heterogeneous variances and $G \times E$ than grouping the herds by average yield.

Herds with high MY presented a larger heritability (0.35) than those with low yield (0.28). For Van Vleck (1988) and Boldman and Freeman (1988), genetic and phenotypic variances were, in most cases, different from farm to farm. Greater heritability values for herds with greater MY averages have been observed fre-

Table 2. Mean $\pm$ SD milk yield, estimates of genetic (σ_a^2) and residual variances (σ_e^2), and heritability (h^2) of milk yield for Brazilian and Colombian Holstein cattle within each group of herds located in the group's upper 33% (U) and lower 33% (L) for each descriptor variable. Genetic correlation (r_g) of milk yield between the groupings is also presented.

Descriptor variable ¹	Production records	Herds in Brazil	Herds in Colombia	$\hat{\mu} \pm \text{d.p.}$ Milk yield (kg)	$\hat{\sigma}_a^2$ (kg ²)	$\hat{\sigma}_e^2$ (kg ²)	h ²	ρ_G	
PL	L	21,714	313	223	5141 $\pm$ 1287	259,933	652,440	0.28	0.97
	U	27,618	377	48	7273 $\pm$ 1550	529,531	978,856	0.35	
YV	L	22,489	339	213	5592 $\pm$ 1423	208,021	539,460	0.28	0.85
	U	27,862	308	57	6823 $\pm$ 1715	563,054	1,152,115	0.33	
AFC	L	23,734	383	19	6948 $\pm$ 1658	504,847	1,041,217	0.33	0.87
	U	25,577	209	257	5743 $\pm$ 1205	279,568	650,295	0.30	
LL	L	24,008	437	123	5981 $\pm$ 1570	330,824	822,104	0.29	0.97
	U	25,323	277	110	6630 $\pm$ 1654	493,532	847,015	0.37	
CI	L	21,326	275	149	6132 $\pm$ 1649	386,949	782,104	0.33	0.91
	U	28,934	357	80	6392 $\pm$ 1658	467,440	852,303	0.35	
IS	L	23,799	370	97	6130 $\pm$ 1690	514,285	824,762	0.38	0.92
	U	24,539	298	177	6387 $\pm$ 1692	342,602	891,599	0.28	
HS	L	22,272	695	58	6266 $\pm$ 1690	345,856	838,065	0.29	0.90
	U	25,717	233	45	6422 $\pm$ 1673	490,256	844,529	0.37	

¹PL = production level, YV = milk yield variability, AFC = age at first calving, LL = lactation length, CI = calving interval, IS = percentage imported semen, and HS = herd size.

quently. This difference, possibly, is the result of a more complete expression of the true genetic potential in the best environment (Hill et al., 1983; Powell et al., 1983; Dong and Mao, 1990).

Herds with a lower AFC presented a greater average, greater genetic and residual variances, and a greater heritability coefficient for MY, indicating that there is a favorable association between MY and AFC. The genetic correlation coefficient for MY between the herds with smaller and greater AFC was 0.87, indicating that after stratifying the herds by variability, stratification by AFC allowed the detection of $G \times E$ on MY. The other DVHE presented coefficients of genetic correlation between 0.90 and 0.97 and heterogeneity of variances (Table 2).

For cluster analysis, weights were attributed to each one of the DVHE as 0.2384, 0.1739, 0.1580, 0.1229, 0.1204, 0.1015, and 0.0849 for YV, AFC, PL, IS, HS, LL, and CI, respectively.

Based on the cubic clustering criterion (Figure 1), 3 clusters were formed: These 3 clusters had an appropriate number of daughters for sire, number of sires and herds by cluster, and sires in common among clusters. Cluster 1 had the greatest number of herds (Table 3), grouping most Brazilian and Colombian herds that were characterized with smaller averages for MY, variability and IS, and greater AFC and CI, showing an

overall situation of production systems of the 2 countries.

Cluster 3, in addition to having the greatest average MY, also had the greatest average of phenotypic standard error of contemporary groups, smaller AFC, smaller CI, and greater IS. Cluster 2 grouped the herds with minor LL and bigger size (Table 3).

Figure 1. Cubic clustering criterion values for 2 to 13 clusters.

Table 3. Distribution of records for milk yield analysis of Holstein cattle and averages of the environment descriptor variables for herds grouped by cluster analysis.

	Cluster 1	Cluster 2	Cluster 3
Milk yield records, no.	41,950	29,268	8958
Brazilian herds, no.	647	70	220
Colombian herds, no.	332	44	24
Production level, kg	5776.00 ± 1054.51	6344.36 ± 800.24	7360.76 ± 935.01
Sires with daughter, ¹ no.	1632	1408	822
Phenotypic standard error, kg	959.91 ± 208.55	1159.42 ± 230.26	1411.90 ± 282.55
Age at first parity, mo	31.13 ± 2.35	30.54 ± 2.04	28.87 ± 1.01
Lactation length, d	312.77 ± 20.00	310.71 ± 15.24	311.28 ± 20.95
Parity interval, d	419.87 ± 29.40	413.19 ± 16.71	405.51 ± 25.05
Percentage imported semen	0.37 ± 0.12	0.39 ± 0.09	0.42 ± 0.07
Herd size, lactations/yr	15.74 ± 9.41	64.49 ± 18.60	16.13 ± 9.85

¹The sires common to the cluster were 654, 512, 96, and 49 among clusters 1, 2, and 3; 1 and 2; 1 and 3; and 2 and 3, respectively.

The genetic and residual variances were heterogeneous among clusters, but the genetic variances of clusters 2 and 3 were similar (Table 4), although greater in cluster 3. The greatest heritability coefficient was estimated for cluster 2 (intermediate MY). Milk yield heritability in the clusters varied from 0.28 to 0.37, indicating that there were differences in this parameter. These differences were also found by Weigel and Rekaya (2000), 0.28 to 0.37 (5 clusters); Zwald et al. (2003a), 0.24 to 0.42 (7 clusters); and Fikse (2002), 0.29 to 0.36 (3 clusters).

The genetic correlation coefficients for MY between clusters varied from 0.89 to 0.97. According to Falconer (1952) and Dickerson (1962), genetic correlations less than unity suggest that, possibly, there was reclassification of animals. In this investigation, the Brazilian and Colombian Holstein cattle populations, presented reclassification of sires among clusters. Also, several values for genetic correlation for MY between clusters were estimated by Weigel and Rekaya (2000), between 0.72 to 0.98, and by Zwald et al. (2003a), between 0.59 to 0.97.

CONCLUSIONS

The herd-grouping criteria using environment descriptor variables and cluster analysis were efficient for stratifying and characterizing production systems within Brazil and Colombia dairy herds. The methods proved that herds of the 2 countries presented similar production conditions, management, and genetic composition. It also estimated the variance components and proved the existence of $G \times E$.

There is a possibility of doing joint genetic evaluations, involving several Latin American countries, always considering the $G \times E$ and variance heterogeneity of the cattle populations of the countries as ongoing.

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Table 4. Estimates of variances, heritabilities, and genetic correlations for milk yield of Holstein herds grouped by cluster analysis.

	Cluster 1	Cluster 2	Cluster 3
Average milk yield, kg	5977.82	6440.37	7359.80
Standard error of milk yield, kg	1596.08	1639.95	1740.26
Additive genetic variance, kg ²	283,923.33	522,015.11	536,554.56
Residual variance, kg ²	717,603.64	896,503.19	1,325,399.24
Heritability	0.28	0.37	0.29
Genetic correlation			
	Cluster 2	Cluster 3	
Cluster 1	0.89	0.97	
Cluster 2		0.95	

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