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Genotype by Environment Interaction for Holstein Milk Yield in Colombia, Mexico, and Puerto Rico¹

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ABSTRACT

Components of (co)variance and genetic parameters were estimated by REML procedures from first lactation mature equivalent Holstein milk records from 54,604 Colombian, Mexican, and Puerto Rican cows and 198,079 US cows. The objective was to determine the cause of heterogeneous daughter response to sire selection for milk yield between the regions. Data from Latin America were partitioned by country and by herd-year SD class for milk to obtain five joint analyses between the US and Latin America, low herd-year SD, high herd-year SD, Colombia, and Mexico. Sire and residual variances for milk were 41 and 29% smaller in Latin America than in the US, 47 and 58% smaller for low than for high herd-year SD, and 31 and 49% smaller for Colombia than for Mexico. Resultant heritabilities ranged from .20 to .29. Genetic correlations for milk yield between the US and Latin America, low and high herd-year SD, Colombia, and Mexico were .91, .82, .89, .78, and .90. Expected correlated responses for milk in

Latin America, low and high herd-year SD, Colombia, and Mexico were 70, 53, 79, 56, and 78% of the direct response in the US. The scaling effects of heterogeneous variance resulted in smaller daughter milk responses in Latin America compared with the US even when herd-year SD was similar.

(Key words: heterogeneous variance, genotype by environment interaction, Latin America)

Abbreviation key: ETA = estimated transmitting abilities, HYSD = herd-year standard deviations, ME = mature equivalent, PV\$ = net present value.

INTRODUCTION

Widespread importation of North American Holstein germplasm raises important questions about its relative performance in Latin American herds. Genetic and phenotypic relationships between Holstein milk yield in these two regions must be assessed to determine the impact of this gene migration on the productivity of Latin American Holstein populations. For example, Mexico, a substantial importer of both Canadian and US Holstein germplasm, purchased 406,305 units of Holstein semen from US bull studs in 1987 [Mexican Secretariat of Agriculture and Water Resources, 1988, unpublished data; (10)]. This amount of semen was sufficient to breed approximately seven times as many cows as were in the Mexican Holstein

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DHI population, assuming 2.5 services per conception, which implies substantial confidence in North American germplasm.

Stanton et al. (18) discovered that Holstein daughter milk responses to sire selection in Colombia, Mexico, and Puerto Rico were less than in lowest yielding or least variable US herds (9, 12). Milk response for Latin American daughters was calculated as the daughter's mature equivalent (ME) milk yield, expressed as a deviation from the corresponding herd-year mean, regressed on sire's published USDA PD for milk. These regression coefficients described the correlated response in milk in Latin America based on selection for milk yield in the US. Daughter milk response was found to increase with increasing herd-year standard deviation for ME milk (HYSD) in each country, but average coefficients for first and all parities were only .47 and .31, .65 and .54, and .30 and .32 in Colombia, Mexico, and Puerto Rico compared with average daughter response coefficients of 1.0 in the US (9, 12).

Blake et al. (3) found that an expected daughter milk response coefficient of .75 instead of 1.00 changed net present value (PV\$) sire rankings under Mexican conditions. Holmann et al. (8) obtained negative average economic returns on US semen investment for herds with low HYSD in Colombia, Mexico, and Venezuela when the PV\$ of Holstein bulls were calculated using realistic within-country values for conception rate, real interest rate, milk price, semen cost, and daughter milk response (18). That study showed that the dominant reason for less profit in Latin America was smaller daughter response than in the US. Economic returns from positive PV\$ bulls decreased as much as 45, 72, and 81% in Mexico, Colombia, and Venezuela when daughter milk response coefficients in Mexico were .55 (56% of the herd-years in Mexico) rather than .75 (7% of the herd-years in Mexico) and when these coefficients in Colombia and Venezuela were .30 (36% of the herd-years in Colombia) rather than .60 (3% of the herd-years in Colombia). Given this substantial influence, it is important to determine the cause of different daughter milk responses between the US and Latin America and among Latin American herds with differing HYSD.

Different selection responses between environments are generally attributed to two types

of genotype by environment interaction. The first type occurs when the genetic correlation between performance in two environments is substantially less than 1.0, indicating a different genetic basis for the trait in the two environments. As a result, daughter response varies from the one predicted by the estimated transmitting abilities (ETA) of sires in the alternate environment. In this study, the term environment comprises not only physical and climatic factors but also the economic constraints, prevailing agricultural policies, and the management decisions that these combined conditions help to bring about in Latin American herds.

The second type of genotype by environment interaction results from heterogeneous variances. For single trait evaluations, bulls will rank the same in each environment, but differences among daughter responses and among breeding values of their sires will be smaller in the less variable environment. Reranking of sires may occur for multitrait indices because relative weights of traits with heterogeneous variances may vary across the environments. Sire ranking in an economic index for a single trait also may change if daughter responses differ between the environments (3).

The primary objective of this study was to determine the cause of heterogeneous daughter milk responses of Holstein sires in the US and Latin America. This objective was met by estimating genetic (co)variances, environmental variances, and genetic parameters of milk yield between the US and Latin America and among different herd environments in Latin America. A secondary objective was to use this information to evaluate the implications of heterogeneous daughter milk responses on breeding management decisions and breeding policies for Latin American dairy producers.

MATERIALS AND METHODS

Data

The US data were 198,079 305-d ME milk records from primiparous grade Holstein cows calving in California, New York, and Texas from 1970 to 1985. Records were restricted to those accepted for the USDA genetic evaluation if from California or Texas and to those accepted for the Northeast evaluation if from

TABLE 1. Numbers of records, herd-years (HY), and means for mature equivalent (ME) milk yield and for HY standard deviation for ME milk yield (HYSD) across records and across HY for the data sets used in the analyses.

Data set ¹	No. of records	No. of HY	Records per HY	Mean					
				ME Milk		HYSD ²		HYSD ³	
				(kg)					
				\bar{X}	SD	\bar{X}		\bar{X}	
US	198,079	12,735	15.6	8672	1756	1465	215	1378	253
LA	54,604	1779	30.7	6321	1733	1309	286	1193	286
LOW	19,818	961	20.6	5385	1340	1018	141	985	152
HIGH	27,689	577	48	7041	1723	1532	190	1517	189
COL	8347	549	15.2	5452	1473	1024	236	1008	240
MEX	39,075	871	44.9	6724	1700	1413	245	1359	251
PR	7182	359	20	5138	1196	1076	161	1074	174

¹Data sets include the United States (US), Latin America (LA), Colombia (COL), Mexico (MEX), Puerto Rico (PR), records from HY in Latin America with HYSD <1200 kg (LOW), and records from HY in Latin America with HYSD ≥1300 kg (HIGH).

²Averaged across records.

³Averaged across HY.

New York. Herd-year standard deviations for ME milk of US cows were calculated previously by Short et al. (16) from all grade cows in a herd-year regardless of parity. The subset of data used in this study was restricted to records of first parity daughters of 607 bulls that also had daughters represented in the Latin American data set. The US daughters were grouped by herd-year-season, where seasons were January through April, May through August, and September through December. Herd-year-seasons were required to include daughters of at least two sires, at least six milk records in California and Texas, and two records in New York. Mature equivalent milk yield and HYSD averaged 8672 kg and 1465 kg (Table 1).

Data from Latin America were 54,604 305-d ME milk records for primiparous Holstein cows calving from 1975 to 1987 in Colombia (8347 records), from 1970 to 1987 in Mexico (39,075 records), and from 1971 to 1987 in Puerto Rico (7182 records). Cows were a subset of the herds described by Stanton et al. (18) and were restricted to daughters of 997 sires with at least 10 daughters represented in at least two herds and 2 yr in any country. As with the US data, HYSD for the Latin American data were calculated previously (18), using all cows within a herd regardless of sire identification or parity. This estimate of HYSD was expected to reflect more accurately herd management levels than would estimates of HYSD

derived solely from the subset of herd members used in the current study. Herd-years remaining in this subset were required to include at least 6 milk records and daughters of two sires. Edits were for records 1) initiated by abortion, 2) DIM less than 60, 3) missing official DHI identification or cow "barn number", 4) missing dates of birth or calving or both, 5) ME milk yield less than 1361 kg, or 6) from herd-years with average ME milk yield of less than 2268 kg for all cows. These edits and the within-country ME adjustment factors were explained previously (18). The resulting ME milk yields and HYSD averaged 2351 kg and 156 kg less (\bar{X} = 6321 kg, HYSD = 1309 kg) for records in the Latin American data set compared with the US data set (Table 1).

Average ME milk yield and average HYSD were greater for Mexican records (\bar{X} = 6724 kg, HYSD = 1413 kg; Table 1), which provided 71.6% of the Latin American data, than for Colombian (\bar{X} = 5452 kg, HYSD = 1024 kg) or for Puerto Rican records (\bar{X} = 5138 kg, HYSD = 1076 kg). However, earlier work (18) showed that daughter responses in milk yield were about the same for each Latin American country at corresponding HYSD. Therefore, these data were pooled.

Latin American data also were subdivided into subsets by HYSD class and by country to permit comparisons between the US and various Latin American herd environments.

Records were in the low HYSD class if HYSD was less than 1200 kg ME milk and in the high HYSD class if HYSD was ≥ 1300 kg ME milk. Standard deviations of the HYSD were larger in Latin America than in the US when averaged either across records or across herd-years (Table 1). When Latin American records were classified by HYSD, average ME milk and HYSD were 81 and 105% as much for the high HYSD class as for the US and 30.8 and 50.5% larger than for the low HYSD class. Herd-year size averaged 48 cows in the high HYSD class and 20.6 cows in the low HYSD class. This positive association between herd size and HYSD resulted in larger mean HYSD when averaged across records compared with averaging across herd-years in all data sets (Table 1). The HYSD tended to increase with ME milk across the data subsets, although HYSD was slightly larger in Puerto Rico than in Colombia despite lower ME milk in Puerto Rico. Correlations between HYSD and herd-year mean had been estimated previously to be .64, .38, and .53 in Colombia, Mexico, and Puerto Rico (18).

Records from Colombia, Mexico, and Puerto Rico made up 33.3, 37.3, and 29.4% of the low HYSD class. However, 93% of records in the high HYSD class were from Mexico. This subset of Mexican records represented 66.5% of the Mexican data.

Because of larger milk yields and HYSD, Mexican data were partitioned separately to determine whether variances and genetic correlations between the US and Mexico differed from those between the US and the other Latin American countries with lower average ME milk yields and HYSD. Colombian cows also were studied separately because of the small heritability (about 7%) reported for Holstein milk yield in Colombia (2) compared with 32% in Mexico (2) and 24% in Puerto Rico (15). The Colombian data were of interest because 66% of records were sire identified compared with 40% in Mexico and 12% in Puerto Rico.

Consequently, five comparisons were made in the form of joint analyses of ME milk records between US daughters of bulls used in Latin America and 1) all cows in the Latin American data set, 2) Latin American cows in the low HYSD class, 3) Latin American cows in the high HYSD class, 4) Colombian cows, and 5) Mexican cows.

Model and Methodology

Two variables for milk yield, ME milk, and weighted milk were analyzed separately. Weighted milk was calculated as (ME milk/HYSD) \times 1000). Division by HYSD expressed ME milk in terms of SD units and standardized the HYSD to 1. Multiplication by 1000 adjusted weighted milk to a scale similar to ME milk. Thus, weighted milk was the amount of ME milk expected given a HYSD of 1000 and a constant heritability. It was hypothesized that standardizing ME milk by the HYSD associated with the milk record might help adjust for changes in daughter milk response between different environments because daughter response appears to increase with HYSD (9, 18). If differing daughter responses are caused by heterogeneous variances, standardizing HYSD would serve as a proxy to standardize genetic variance.

Milk yields in Latin America and the US were treated as separate traits within each joint analysis, using a multitrait sire model similar to those used by Carabaño et al. (4, 5). Genetic (co)variances and residual variances for milk yields in the US and in one of the Latin American groups were estimated simultaneously. The mathematical model in matrix notation was

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} H_1 & 0 \\ 0 & H_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} S_1 & 0 \\ 0 & S_2 \end{bmatrix} \begin{bmatrix} d_1 \\ d_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_i is the vector of n_i observations for a trait (either ME milk or weighted milk) in region i , with $i = 1$ for the US and $i = 2$ for one of the Latin American data sets; H_i is the known incidence matrix for herd-year-(season) effects in region i associated with b_i , the vector of fixed herd-year-(season) effects for region i ; S_i is the known incidence matrix for sire origin effects in region i associated with d_i , the vector of fixed effects for sire origin in region i , with two sire origin groups nested in the US (US

registered and Canadian registered) and five possible sire origin groups nested in the Latin American settings (US, Canadian, Colombian, Mexican, and Puerto Rican); Z_i is the known incidence matrix for sires associated with daughter records in Y_i (contains null columns corresponding to sires with no daughters in region i but with daughters in the other region of the joint analysis or for base bulls without daughters but with at least two sons in either region with daughters); u_i is the vector of random transmitting abilities for sires in region i (corresponding sire effects may differ between regions even though the same sires are represented in each region); and e_i is the vector of random residual effects for region i .

The distribution of $\begin{bmatrix} u \\ e \end{bmatrix}$ was multivariate normal with

$$\text{mean} \begin{bmatrix} 0 \\ 0 \end{bmatrix} \text{ and variance } \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix},$$

and

$$G = \text{variance} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} g_{11} & g_{12} \\ g_{21} & g_{22} \end{bmatrix} \otimes A = G_0 \otimes A$$

where G_0 is a square matrix of order 2 consisting of (co)variances between sire effects in the two regions (one-fourth of the additive genetic variance-covariance matrix for regions 1 and 2) and A is the numerator relationship matrix among sires.

$$R = \text{variance} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} r_{11}I_1 & 0 \\ 0 & r_{22}I_2 \end{bmatrix} = \begin{bmatrix} R_{11} & 0 \\ 0 & R_{22} \end{bmatrix}$$

where r_{ii} represents a residual variance common to all records in region i and I_i is an identity matrix of order n_i . Residual covariances be-

tween records in different regions were assumed equal to zero because a daughter could not have records in both regions.

Estimates of variance components and solutions for random effects for the mixed model equations were obtained by REML using the expectation-maximization algorithm explained by Carabaño et al. (4, 5). Description of transformations and tridiagonalization of the coefficient matrix to reduce computing demands, starting values for the iterations, and convergence criteria is given by Stanton (17). Genetic correlations of milk yield between the regions were estimated by $r_{g(1,2)} = \hat{g}_{12}/(\hat{g}_{11} \times \hat{g}_{22})^{.5}$. Heritability of milk yield for region i was estimated by $4 \times \hat{g}_{ii}/(\hat{g}_{ii} + \hat{r}_{ii})$. Approximate standard errors were calculated using the method of Robertson (14) for the genetic correlations and the method of Swiger et al. (19) for the heritabilities. The ETA were back-transformed by the procedure of Quaas (13) to obtain sire solutions on the original scale. These solutions were substituted into the mixed model equations retained after absorbing herd-year-(season) effects and prior to absorbing sire origin effects to estimate the sire origin effects. Sire origin effects in each region were expressed as deviations from the US sire group effect, which was set to zero.

Expected correlated response in Latin America to direct selection in the US were estimated for each joint analysis. Coefficients of correlated response were estimated by 1) the genetic regression, $\hat{g}_{12}/\hat{g}_{11}$, where \hat{g}_{12} is the estimate of sire covariance between the US and one of the Latin American data sets and \hat{g}_{11} is the estimate of sire variance for the US and 2) the regression coefficient for the untransformed ETA from a Latin American group regressed on the untransformed ETA in the US. The second method utilized only ETA from US registered sires with daughters in each of the paired data sets.

RESULTS AND DISCUSSION

Joint Analysis Between the US and Latin America

Mature Equivalent Milk. Estimated sire and residual variances for ME milk in Latin America [(280.56 kg)² and (1197.61 kg)²] were 59 and 72% of the corresponding estimates in

the US [(365.60 kg)² and (1416.28 kg)², Tables 2 and 3]. The heritability of milk yield in Latin America (.21) was slightly smaller than in the US (.25) because the sire variance decreased relatively more than the residual variance. The heritability for Latin American was within the range generally reported for the US, and it is certainly adequate to improve milk yield by sire selection. Restricting sires in the US data to only those with daughters in the Latin American data could have restricted variability in ME milk. However, estimates of sire and residual variances in the US were 22 and 7% larger than for California and approximately 19 and 60% larger than for the US in previous studies using similar methods (4, 5). Seventy-one percent of US records in this study were from California. The US daughters in this study were generally in herds with above average HYSD (9), which may help explain the large variances estimated.

The genetic correlation for ME milk between the US and Latin America was .91 (Table 3). Therefore, the probable cause of reduced daughter response in Latin America compared with the US is smaller variance rather than any substantial differences between the regions in sire rank in genetic merit for milk yield.

Mature Equivalent Milk Standardized by Herd-Year SD. Estimates of variance components between the US and Latin America were more homogeneous for weighted milk than for ME milk (Table 3). Heritabilities for weighted milk possibly were slightly larger than heritabilities for ME milk. Standardizing ME milk by HYSD may have adjusted for some effects of

herd-year that were unaccounted by absorbing the herd-year-(season) effects, which contained only the average ME milk effects of the herd-mates included in the subset. In addition to these herd-mates, HYSD contained information from all herd members regardless of sire identification or parity.

The genetic correlation between regions for weighted milk was the same as for ME milk. This result substantiates that the genetic correlation as estimated is invariant to heterogeneous variances (7, 14).

Joint Analyses Between the US and Herd-Year SD Classes in Latin America

A wide range in HYSD is represented in Colombia, Mexico, and Puerto Rico (18). Therefore, an important step was to quantify how sire and residual variances changed among Latin American herds with differing HYSD. Also, it was important to determine whether sire and residual variances were the same for US and Latin American herds with same HYSD.

Mature Equivalent Milk. Substantial differences for both sire and residual variances between the low and high HYSD data sets were revealed in joint analyses with the US data (Table 4). The sire and residual variance component estimates for the low HYSD class in Latin America [(232.14 kg)² and (899.18 kg)²] were only 42 and 40% as much as the estimates for the US [(359.46 kg)² and (1416.30 kg)²] and 53 and 42% as much as for the high HYSD class [(319.52 kg)² and (1389.24 kg)²] in Latin America (Tables 2 and 4). Stanton et al. (18) suggested that herds in low HYSD classes were generally lower yielding with less management opportunity to buffer adverse environmental conditions than herds in high HYSD classes. This suggestion of severe environmental constraints was supported by the extremely small residual variance estimated for the low HYSD class. Under conditions of restricted environmental opportunity, the expression of genetic variance could be reduced. This was confirmed by the accompanying decrease in sire variance for the low HYSD data set compared with the US and high HYSD data sets.

Average HYSD was 1532 kg for the high HYSD Latin American data set and 1465 kg for

TABLE 2. Estimated sire and residual variances for mature equivalent (ME) milk yield expressed as a percentage of the paired US data set.

Data set ²	ME Milk		Weighted milk	
	Sire	Residual	Sire	Residual
	(%)			
LA	59	72	76	86
LOW	42	40	85	85
HIGH	79	96	75	88
Colombia	52	42	105	85
Mexico	76	82	81	87

¹Weighted milk = [ME milk/herd-year standard deviation (HYSD) for ME milk] × 1000.

²LA = Latin America, LOW = HYSD <1200 kg, and HIGH = HYSD ≥1300 kg.

TABLE 3. Estimates of sire and residual variances, sire covariances¹ between regions, heritabilities, and genetic correlations for mature equivalent (ME) milk yield in the joint analysis between the US and Latin America (LA).

Data set	Sire	Residual	Cov	h ²	SE	r _{LA,US}	SE
	ME Milk ²						
US	365.60	1416.28	305.90	.25	.014	.91	.007
LA	280.56	1197.61		.21	.012		
	Weighted milk ³						
US	248.92	951.96	221.53	.26	.014	.91	.007
LA	217.71	884.25		.23	.013		

¹(Co)variance components (Cov) are expressed at .5 power.

²ME 305-d lactation yield is in kilograms. (Co)variance units are (kg²)^{.5}.

³Weighted milk = (ME milk/herd-year standard deviation for ME milk) × 1000.

the US data set. Nevertheless, the sire variance calculated from daughters in high HYSD herds in Latin America was only 79% as much as for US daughters (Table 2), although the residual variances were similar. Even under relatively favorable management conditions, it appears that tropical and subtropical environments substantially restrict the expression of genes influencing milk yield.

Previous researchers reported that the heritability of ME milk increases with increasing HYSD and herd-year mean (6, 20). In contrast, changes in sire and residual variances were nearly proportional in the joint analyses between the US and the low HYSD class, resulting in similar heritabilities, .24 for the US and .25 for the low HYSD class. However, the residual variance in Latin America decreased proportionally more than the sire variance for the low compared with the high HYSD class, resulting in slightly larger heritability for the low HYSD class, .25, than for the high HYSD class, .20. The important issue in comparing HYSD classes in Latin America is not that heritability was greater for the low HYSD class but that sire and residual variances were severely compressed in these herd environments compared with variances in the high HYSD class and the US.

The estimated genetic correlation between the high HYSD class and the US (.89) was larger than between the low HYSD class and the US (.82), which suggests that the genetic control of milk yield in high variance herds may be more like that of US herds than that of low variance herds in Latin America (Table 4). However, the genetic correlation coefficients

between low or high HYSD herd-years and the US were large enough (.14) to expect that sires would rank similarly for ME milk across the environments.

Mature Equivalent Milk Standardized by Herd-Year SD. In agreement with the previous joint analyses between regions in this study, standardizing ME milk by HYSD resulted in variance component estimates of more uniform size among the data sets than for ME milk (Table 4). However, the estimated sire variance in the low HYSD herd-years (224.54 kg)², although smaller than the estimates for the US [(243.91 kg)² and (245.29 kg)²], was greater than the sire one estimated from high HYSD herd-years (212.72 kg)². Standardizing ME milk by HYSD may overadjust for sire variances in Latin America, resulting in larger sire variances for less variable herd environments. This overadjustment probably results from disproportionate changes in sire and residual variances between low and high HYSD herds in Latin America. Heritabilities and genetic correlations for weighted milk did not change appreciably from those obtained from the same data sets for ME milk.

Joint Analyses Between the US and Colombia or Mexico

Average ME milk and HYSD varied among Colombia, Mexico, and Puerto Rico. Climate, available forages, economic conditions, and management practices also differ among these countries. Thus, typical herd environments in each country are unlikely to be the same. Variance components for ME milk were much

TABLE 4. Estimates of sire and residual variances, sire covariances¹ between regions, heritabilities, and genetic correlations for mature equivalent (ME) milk yield in the joint analyses between the US and low (LOW)² or high (HIGH)³ variance herd-years in Latin America.

Data set	Sire	Residual	Cov	h^2	SE	$r_{LA,US}$	SE
	ME Milk ⁴						
US	359.46	1416.30	262.25	.24	.014	.82	.015
LOW	232.14	899.18		.25	.019		
US	359.62	1416.29	319.36	.24	.014	.89	.010
HIGH	319.52	1389.24		.20	.015		
	Weighted milk ⁵						
US	243.91	951.97	212.84	.25	.014	.83	.015
LOW	224.54	876.06		.25	.019		
US	245.29	951.97	214.77	.25	.014	.88	.010
HIGH	212.72	893.57		.21	.015		

¹(Co)variance components (Cov) are expressed at .5 power.

²Herd-year standard deviation for ME milk <1200 kg.

³Herd-year standard deviation for ME milk ≥1300 kg.

⁴ME 305-d lactation yield is in kilograms. (Co)variance units are (kg²)⁵.

⁵Weighted milk = (ME milk/herd-year standard deviation for ME milk) × 1000.

smaller when calculated from daughters in low HYSD herd-years rather than high HYSD herd-years in Latin America. Seventy-nine percent of the records in the Colombian data set were in the low HYSD class, whereas only 12.8% were in the high HYSD class. In contrast, 18.9 and 66.5% of the Mexican records were represented in the low and high HYSD classes. Therefore, changes in genetic correlations and variance components between Colombia and Mexico should be similar to changes observed between the low and high HYSD data sets, unless country differences that are not reflected in HYSD significantly influence these parameters among Latin American countries.

Mature Equivalent Milk. Estimates of sire and residual variances for Colombia were only 52 and 42% as much as for the US and 69 and 51% as much as for Mexico (Tables 2 and 5). Because the residual component of variance decreased proportionally more than the sire component, the heritability of milk yield for Colombia was slightly larger (.29) than for the US (.24) or for Mexico (.22). The smaller heritability for Mexico compared with the US occurred because the estimate of sire variance in Mexico was only 76% as large as for the US, but the estimate of residual variance was 81% as large. These observations of 1) slightly larger heritability in low HYSD data sets due to

a severe reduction in residual variance and 2) smaller heritability in high HYSD data sets due to proportionally larger reductions in sire variance compared with the US are similar to those reported in the previous section on low and high HYSD classes. Magnitudes of the sire and residual variances reflected the average HYSD of the countries. Estimates of sire and residual variance components in Colombia (average HYSD = 1024 kg) were slightly larger than those reported for the low HYSD data set (average HYSD = 1018 kg), whereas those for Mexico (average HYSD = 1413 kg) were slightly smaller than reported for the high HYSD data set (average HYSD = 1532 kg).

The heritability of milk yield for Colombia is much larger than the estimate of .07 obtained by Abubakar et al. (2) using Henderson's method 3 (Table 4). However, Abubakar's data set was limited to only 4 yr (1980 to 1983) and 60 sires, which gave a much smaller estimate of the sire component of variance [(153.7 kg)²] and a larger residual variance component [(1168.84 kg)²] than found in this study (1). Estimates of variance components for Mexico by Abubakar (1) were similar for residual variance [(1225.73 kg)²] but larger for sire variance [(361.4 kg)²] and heritability (.32) compared with those obtained in the present study.

Genetic correlations were smaller between Colombia and the US (.78) than between Mex-

ico and the US (.90; Table 5). Sires might be expected to rank more similarly between Mexico and the US than between Colombia and the US.

The joint analyses between the US and Colombia had fewer common sires (304) than for the other joint analyses (495 to 607). Also, the average number of daughters per sire was only 21.4 in Colombia, thus reducing accuracy of the sire solutions. Because of this reduction in accuracy and the extreme disparity in the amount of information from the US and Colombia (Table 1), convergence required more rounds of iteration, and C , the measure of the degree of convergence, was larger [although still meeting the criteria for convergence as described previously (4, 17)] than for other joint analyses. Therefore, the standard error for the genetic correlation between Colombia and the US was probably greater than suggested by the approximation (14). Robertson (14) somewhat arbitrarily suggested that important biological differences may be indicated when the genetic correlation between environments decreases to $\leq .80$. Sires in Colombia and the US probably ranked similarly according to this threshold value. There were 82 bulls with at least 20 daughters in both Colombia and the US. Eighty-five percent of the quartile of bulls with largest ETA for ME milk in Colombia were also in the highest quartile for ETA for ME milk in the US. Average ETA for Colom-

bian ME milk was 332 kg for the highest 25% in Colombia and 313 kg for the highest 25% of bulls in the US. Previous studies (11, 15) showed close agreement between expected and calculated correlations for sire values for ME milk in Mexico and the US and in Colombia and the US.

Mature Equivalent Milk Standardized by Herd-Year SD. Standardizing ME milk by HYSD made variance component estimates more uniform among countries. Again, standardizing by HYSD may overcompensate for differences in sire variances for ME milk in Latin America because estimated sire variances for weighted milk were largest for Colombia, intermediate for the US, and smallest for Mexico. Estimates of heritabilities and genetic correlations did not change significantly for weighted milk compared with ME milk (Table 5).

Correlated Responses

Latin America and the US. Coefficients for the expected correlated response for ME milk in Latin America from selection in the US are in Table 6. Due to the large genetic correlations reported for all joint analyses, the second method of estimating correlated responses was expected to overestimate the correlated response for sires with much less information from Latin America than from the US. Howev-

TABLE 5. Estimates of sire and residual variances, sire covariances¹ between regions, heritabilities, and genetic correlations for mature equivalent (ME) milk yield in the joint analyses between the US and Colombia (COL) or Mexico (MEX).

Data set	Sire	Residual	Cov	h^2	SE	$r_{LA,US}$	SE
	ME Milk ²						
US	356.52	1416.29	268.04	.24	.014	.78	.022
COL	257.03	915.37		.29	.032		
US	356.70	1416.30	319.36	.24	.014	.90	.008
MEX	309.97	1282.22		.22	.014		
	Weighted milk ³						
US	242.72	951.96	218.49	.24	.014	.79	.021
COL	248.48	875.55		.30	.032		
US	244.57	951.97	221.00	.25	.014	.91	.008
MEX	220.18	885.67		.23	.015		

¹(Co)variance components (Cov) are expressed at .5 power.

²ME 305-d lactation yield is in kilograms. (Co)variance units are (kg²)^{.5}.

³Weighted milk = (ME milk/herd-year standard deviation for ME milk) × 1000.

er, estimates for the coefficients of correlated response agreed closely regardless of the procedure (Table 6).

Coefficients for the expected correlated responses for ME milk in first parity cows in Latin America were .70 and .71 (Table 6). Thus, if ETA for two sires in the US differed by 100 kg, differences between their daughters in Latin America would be expected to average 70 kg. Coefficients between the US and either the low HYSD class (.53) or Colombia (.56 and .54) were smaller than between the US and either the high HYSD class (.79 and .80) or Mexico (.78 and .81), thus corroborating our empirical finding (18) that daughter milk response in Latin America increases with increasing HYSD. Therefore, approximately half of the difference in ME milk observed among first lactation daughters of US sires in US herds is expected to be realized from first lactation daughters of the same sires in low variance Latin American herds.

Coefficients for expected correlated responses in ME milk in Colombia and Mexico based on selection in the US were larger than previously reported in Stanton et al. (18). One explanation for this increase is that edits applied in the current study obtained herd-years with slightly larger average HYSD than the original data (52 and 18 kg more for Colom-

bia and Mexico). Also, the previous study used different methods to adjust for herd-year effects and genetic trend, and regressions were on actual USDA PD for milk.

Latin American Data Sets. A second set of correlated response coefficients was approximated by regressing the ETA for the low HYSD class and Colombia on those estimated for the high HYSD class and Mexico, respectively (Table 6). Coefficients for HYSD were estimated using 448 US sires with daughters in both low and high HYSD classes. Coefficients for Colombia regressed on Mexico were based on the 214 US sires represented in both countries. Values were .60 for the low HYSD class regressed on the high one and .61 for Colombia regressed on Mexico. Thus, only about 60% of the difference among sires for ME milk in high HYSD or Mexican herds would be expected in low HYSD or Colombian herds.

Correlated Responses for ME Milk Standardized by Herd-Year SD. Standardizing ME milk by HYSD resulted in larger and more uniform coefficients (.76 to .82) than for ME milk (Table 6). The coefficient for correlated response was .89 in the low HYSD class based on selection in the high HYSD class and .84 in Colombia based on selection in Mexico. Thus, the primary advantage of standardizing ME milk by HYSD is to predict selection responses

TABLE 6. Coefficients for expected correlated response (CR) for mature equivalent (ME) milk yield and for weighted milk¹ in Latin America when selection is on sire performance in the US.

	ME Milk			Weighted milk		
	Method 1	Method 2	SE	Method 1	Method 2	SE
US versus						
LA	.70	.71	.008	.79	.80	.009
LOW ²	.53	.53	.008	.76	.76	.011
HIGH ²	.79	.80	.009	.77	.78	.009
Colombia	.56	.54	.013	.81	.77	.018
Mexico	.78	.81	.009	.82	.83	.009
^b COL,MEX ³		.61	.021		.84	.029
^b LOW,HIGH ⁴		.60	.015		.89	.02

¹Weighted milk = (ME milk/herd-year standard deviation for ME milk) × 1000.

²LOW = Herd-year standard deviation <1200 kg; HIGH = herd-year standard deviation ≥1300 kg.

³The regression coefficient for sire transmitting ability estimated from the Colombian joint analysis regressed on the sire transmitting ability estimated from the Mexican joint analysis.

⁴The regression coefficient for sire transmitting ability estimated from the joint analysis of low variance herds in Latin America regressed on the sire transmitting ability estimated from high variance herds in Latin America.

more uniformly among different HYSD classes and countries. Hence, expectations for ETA based on weighted milk rather than ME milk will be more closely realized between Latin America and the US and among different herd environments of Latin America. However, coefficients for correlated responses in Latin America to direct selection in the US were still less than 1.0, because scaling effects of hetero-

geneous variances for Latin America are more severe at the same HYSD.

Table 7 shows the ETA for ME milk obtained in this study for sires with at least 20 daughters each in Colombia, Mexico, and the US. Sires are ranked from lowest to highest ETA for the US. In general, bulls that ranked low (high) for ETA in the US also ranked low (high) for ETA in the Latin American data sets.

TABLE 7. Predicted Differences for milk [1982 base year (PDM₈₂)] and estimated transmitting abilities (ETA) for 41 sires with ≥ 20 daughters in each of the following data sets: Latin America (LA), Colombia (COL), Mexico (MEX), and the US. Sires are ranked by ETA_{US}.

Sire number	PDM ₈₂	ETA _{US}	Daughter no.	ETA _{LA}	Daughter no.	ETA _{COL}	Daughter no.	ETA _{MEX}	Daughter no.
	(kg)			(kg)		(kg)		(kg)	
40320891	-555	-786	558	-896	76	-930	42	-1224	64
40328508	-933	-664	28	-874	85	-717	35	-1191	50
1661730	-313	-575	94	-394	78	-323	43	-456	35
1530625	-397	-561	107	-455	111	-331	37	-528	57
1565870	-440	-443	220	-324	186	-342	54	-350	114
40330643	-25	-278	93	-510	58	-399	31	-870	27
1599072	-293	-267	64	-200	49	-132	28	-272	20
1632698	-75	-266	362	-68	137	-255	56	-57	81
40321619	-396	-177	37	-482	41	-634	21	-671	20
1671336	280	-170	359	-166	170	-153	38	-84	53
1590689	-73	-123	253	-93	173	20	42	-138	128
1629120	-24	-112	490	-146	106	79	24	-223	82
1619057	-1	-9	1058	46	104	158	38	-65	63
1483844	-647	23	33	0	137	-152	87	141	38
1563453	27	36	2327	99	97	57	50	80	47
1557246	-216	60	597	104	235	46	24	99	129
1647190	240	70	1036	8	97	-110	51	45	40
1633380	297	111	829	37	101	-331	36	149	26
1672151	41	115	1017	16	138	144	22	-53	114
1685359	303	118	857	141	155	86	71	142	55
1629391	-299	152	415	151	665	12	215	219	432
1450228	96	153	1124	286	308	65	51	292	221
1663720	329	158	1029	36	174	-7	36	61	129
1531866	-109	166	1218	181	244	107	42	173	164
1621881	225	186	218	70	195	336	67	-25	126
1512026	29	189	1680	40	209	31	94	20	102
1441440	22	242	667	169	56	137	30	199	25
1608425	386	302	218	313	195	214	67	310	27
1578139	170	351	1680	365	209	257	94	362	88
1600743	288	404	1123	154	144	68	20	218	98
1458744	-182	424	1144	279	489	154	62	268	378
1635843	424	491	761	389	82	451	53	338	27
1631223	387	543	1235	274	182	284	138	348	40
1626813	402	572	1798	393	121	297	78	456	38
1565026	73	602	103	502	95	360	62	560	33
1629385	87	604	1516	416	289	327	91	429	188
1491007	156	606	1192	413	140	223	49	485	84
1620273	498	639	4250	371	496	291	39	404	428
1642993	539	658	545	471	131	503	56	530	70
1647459	795	686	946	578	254	358	33	635	208
1650414	460	721	927	507	158	392	129	556	24

Fixed Effect of Sire Origin

The US data consisted of 560 US sires averaging 352.8 daughters each and 47 Canadian sires averaging 10.3 daughters each. Thus, prediction error of solutions for sire origin effects are less for US than for Canadian sires. Average ME milk and HYSD were 8425 and 1458 kg for daughters of the Canadian sires and 8672 and 1465 kg for daughters of the US sires. In addition to sires in the US data set, the Latin American data set contained 62 US, 110 Canadian, and 218 Latin American bulls that were not represented in the US data set. Average daughter HYSD was similar for US, Canadian, and Latin American bulls in Latin America, ranging from 1301 to 1320 kg. Distribution of the sire origin groups also did not vary substantially between the low and high HYSD data sets, indicating that use of these sire groups was similar across HYSD classes. Daughters of Latin American bulls and Canadian bulls generally averaged less ME milk (6256 and 6092 kg) than daughters of US bulls (6435 kg).

Sire origin solutions for ME milk as deviations from the US sire origin solutions are in Table 8. Solutions for fixed effects of Puerto Rican sires were not useful because of the large sampling errors with only three sires represented. In the Latin American data sets, solutions for fixed effects of US sires were 315 to 473 kg greater than for Canadian bulls and 350 to 940 kg greater than for Colombian or Mexican bulls. Differences between the US sires and other sire origin groups were larger for the high HYSD class and Mexico than for either the low HYSD class or Colombia.

Differences among sire origin groups were less when ME milk was standardized by HYSD (Table 8). This was particularly true in the joint analysis between the US and Latin America, in which differences between the US and Canadian sire origin groups were not detected for weighted milk. In this analysis, unlike the other ones, a wide range in HYSD was represented in Latin America, permitting more opportunity to standardize for HYSD. In the other Latin American data sets, fixed effects for US sires

TABLE 8. Solutions and standard errors for the fixed effect of sire origin¹ expressed as deviations from the effect of US registered sires on ME milk² and on weighted milk.³

Data sets ⁴	Sire origin															
	Canada				Colombia				Mexico				Puerto Rico			
	ME Milk		Weighted milk		ME Milk		Weighted milk		ME Milk		Weighted milk		ME Milk		Weighted milk	
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
US	-223	77	-53	52
LA	-341	21	-22	15	-474	47	-108	34	-475	21	-100	15	-208	216	-68	159
US	-351	77	-224	52
LOW	-330	32	-313	31	-350	39	-345	38	-389	36	-366	35	-382	205	-259	199
US	-252	77	-161	52
HIGH	-453	31	-303	19	-940	161	-656	104	-585	28	-387	18
US	-502	77	-327	52
Colombia	-315	51	-280	49	-466	36	-424	34
US	-369	77	-250	52
Mexico	-473	23	-331	16	-558	22	-387	15

¹Sire origin groups were US registered, Canadian registered (Canada), Colombian grade (Colombia), Mexican grade (Mexico), and Puerto Rican grade (Puerto Rico).

²ME Milk = 305-d mature equivalent milk yield in kg.

³Weighted milk = (ME milk × 1000)/HYSD, where HYSD = herd-year standard deviation for ME milk.

⁴LA = Latin America, LOW = HYSD <1200 kg in LA, HIGH = HYSD ≥1300 kg.

were 280 to 331 kg greater than for Canadian sires and 345 to 656 kg greater than for Colombian or Mexican sires when weighted milk was the trait considered. It was difficult to ascertain why differences among sire origin groups varied for the different joint analyses. Average daughters per sire were not consistent either among sire groups or Latin American data sets. Indirect ties between US and Canadian sires represented in the US data set varied with the Latin American data set used in the joint analysis. Therefore, the fixed effect of sire origin group should be interpreted with caution.

Implications of Results

On-Farm Breeding Decisions. Results from this study confirmed that the response to US sire selection for ME milk is less in Latin America than in the US and that it is less in low variance herds than in high variance herds in Latin America. Average daughter differences among sire groups of different origin and among sires of varying ETA for ME milk appear to increase with HYSD. Thus, classifying herd environments by HYSD would be a useful tool to help Latin American dairy producers predict benefits from sire selection based on US daughter information. Therefore, dairy record processing centers should consider providing estimates of HYSD to their Latin American clientele. Producers need to consider their probable HYSD status when allocating resources for semen investment compared with other management expenditures. For example, producers with HYSD consistently less than 1200 might expect their first parity cows to achieve roughly half of the daughter response obtained in the US, whereas those who consistently average ≥ 1300 kg HYSD might expect to achieve about 75% of the US daughter response. These differences in response have been shown to affect the profitability and ranking of preferred sire choices in Latin America (8).

Results from this study suggest that the primary impediments to realizing substantial gains from genetic selection in low variance Latin American herds are environmental restrictions that are reflected in greatly reduced environmental variances. Therefore, a logical investment for producers in low HYSD solutions (i.e., most of the Latin American producers) is

to identify and possibly alleviate environmental restrictions and to seek management practices that benefit milking performance in their herds, thereby permitting greater phenotypic expression of sire effects.

Regional Genetic Evaluations. Latin American countries could make more rapid genetic gains from collaborating in a regional sire evaluation than from investing their scarce resources in national evaluations. Scaling down of genetic expression in the low HYSD environments of most Latin American herds makes it more difficult to distinguish between bulls, thereby necessitating more daughters for sire evaluation. In this study, common US and Canadian sires in Colombia, Mexico, and Puerto Rico increased the effective number of daughters per sire to 54.8 when the countries were combined compared with 21.4, 49.2, and 18.0 daughters per sire for Colombia, Mexico, and Puerto Rico. Confounding of sires within herds and years in Latin America also reduces the effective number of daughters (2). Bulls that are represented across different Latin American countries and, hence, different HYSD classes could serve as reference sires to evaluate more accurately grade bulls that are represented in only one country or HYSD class. Realistic ETA across collaborating countries could be obtained either 1) by evaluating sires for weighted milk rather than ME milk or 2) by classifying herds by HYSD class and then adjusting differences among ETA by the expected daughter response for that HYSD class.

This information sharing among countries would be computationally more efficient for organizations contracted to do the evaluations. Recording of lactation information and sire identification is relatively uniform among Colombia, Mexico, and Puerto Rico because they all follow a DHI format. Thus, edits to combine information from these countries are minor. However, this may not be the case for other countries that are not following a DHI format. Other problems may arise if cooperation is poor, if monetary exchange among the countries is difficult, or if cooperating countries lack the infrastructure to coordinate a regional evaluation.

Use of ME Milk Standardized by Herd-Year SD in Genetic Evaluations. Different selection responses in low and high HYSD environments in Latin America will result in under- or over-

estimation of ETA for bulls and cows represented predominantly in low or high HYSD herds, especially if there are few reference sires to provide ties among the different herd settings. Evaluating animals for weighted milk rather than ME milk would help alleviate this problem. Weighted milk did an excellent job of standardizing residual variance in Latin America. It overcompensated slightly for small sire variances for ME milk in low HYSD environments, resulting in possibly slightly larger sire variances in these environments. Standardizing ME milk by HYSD should help to rank bulls and cows accurately across different Latin American herd environments. Care would need to be exercised in using this standardization with regard to sampling variance in small herds. To aid managing sire selection, predicted responses in daughter ME milk yield could be provided to farmers from a bull's ETA for weighted milk by regressing daughter ME milk yield on sire's standardized ETA within various HYSD classes.

CONCLUSIONS

Differences in variance for ME milk were substantial between the US and Latin America and among different Latin American herd environments. Sire and residual variance estimates were 59 and 72% as much for Latin America as for the US (Table 2), 53 and 42% as much for low HYSD as for high HYSD herds in Latin America, and 69 and 51% as large for Colombia as for Mexico. In contrast with previous reports, smaller sire and residual variances were not necessarily associated with smaller heritabilities. The Latin American data sets with similar HYSD to the US (high HYSD class and Mexico) appeared to have proportionally smaller sire variances and, hence, smaller heritability than the US. However, within Latin America data sets with low average HYSD (low HYSD class and Colombia) had larger heritability than did more variable data sets because residual variances were compressed proportionally more in the less variable data sets.

In spite of restricted sire and residual variances, heritability estimates in all Latin American data sets were .20 to .29 and were within the range of most reports for milk yield in temperate regions. Therefore, sire selection

would be successful to improve ME milk or weighted milk in Latin America. It should be noted that accurately differentiating among sires based on Latin American performance rather than US performance will be more difficult because of fewer daughters per bull and the scaling effects of reduced variances.

Estimates of genetic correlations for Holstein milk between the US and the Latin American data sets in this study were relatively large, suggesting that sires will rank similarly for ME milk in the two regions. However, resources are more limited and costly in Latin America, and profit margins are often austere and risky. Therefore, it may be useful in Latin America to evaluate sires with a multitrait index combining ME milk and other economically important characters such as stayability and reproductive traits. Genes that are inconsequential for survival in the US may express important differences in Latin America, thereby influencing genetic variability for stayability and reproduction, especially relative to genetic variation in milk yield. Under these conditions, sire rankings in pertinent multitrait indices might differ between Latin America and the US.

In agreement with our empirical results (18), coefficients for correlated selection responses were smaller than unity between the US and Latin America and among different Latin American herd environments. Changes in heritabilities and genetic correlations were insufficient to explain these differences. Instead, a genotype by environment interaction associated with the scaling effects of reduced sire and residual variances appeared to be the primary cause of less selection response in Latin America than in the US and in low versus high variance Latin American herds.

Further research is needed to identify the most effective management practices to circumvent the environmental constraints on genetic expression of milk yield in Latin America. Producers and consultants need to acknowledge that optimal sire choices are affected by environmental influences on daughter milk response (8). Simulation studies may be useful to determine how much differing genetic correlation coefficients alter sire rankings for milk and for multiple trait indices. Research to utilize multitrait indices in Latin America includes 1) determining the economically important traits

(e.g., stayability and reproductive performance) and how their variances, heritabilities, and relationships with ME milk vary among US and Latin American herd environments (e.g., by HYS in milk) and 2) developing economic methods to combine genetic information for multiple traits into a useful sire selection index.

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