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Genotype by environment interaction for Holstein Friesian milk yield between Saudi Arabia and the United States

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Abstract: Co-variance components and genetic parameters of the first and all lactations mature equivalent milk yield for Holstein Friesian were estimated by single and multiple-trait animal model using Method R procedures. The objectives of this study were to determine if genotype by environment interactions for milk yield exist between Saudi Arabia and the United States. The Saudi data included 46,777 records of 20,815 cows as daughters of 255 sires and the US data included 38,293 records of 19,456 cows as daughters of 176 sires. There were 151 sires common to both countries with average number of daughters 260 in the Saudi data and 246 in the USA data. Genetic correlations for milk yield between the two environments in the 1st and pooled lactation data set were 0.68 and 0.17, respectively. In the 1st lactation analysis, additive genetic variances were similar but residual variance was 21% smaller in Saudi Arabia than in the USA. In the pooled lactation analysis additive genetic variance was 20% smaller for Saudi Arabia than for USA but residual variances were similar. The heritability estimate of the first lactation milk yield in Saudi Arabia (0.29) was larger than estimate in USA (0.24) but estimate all lactations in the USA (0.34) was larger than the estimate in Saudi Arabia (0.29). These results substantiate the presence of genotype by environment interaction for milk yield. Therefore, selection from within the Saudi Holstein population may be the best tool to identify the optimal animal for Saudi dairy production.

Keywords: genetic, environment, interaction, heritability, milk yield

INTRODUCTION

Saudi Arabia is one of the driest countries in the world, with an average rainfall of less than 5 inches per year. Traditional livestock production in KSA uses local breeds, which are characterized by low milk yield, slow growth rate and high mortality rate. Because of high population growth rate and improvement in the standard of living, demand for milk and dairy products increased. Therefore, in the late 1970's and early 1980's and with the help of booming oil prices, the government of Saudi Arabia decided to attain self-sufficiency in food production. A massive agricultural development program was started to enhance food production in the kingdom. A five-year target period was set for achieving self-sufficiency in dairy products by motivating private investors through substantial government subsidies and financial incentives to establish modern, successful dairy farms. The fastest way to achieve this goal was through the importation of semen and live animals from highly selected breeds of dairy cattle such as Holstein and Jersey from developed countries, mainly the United States of America. About 39 specialized dairy projects were established by 1996, comprising 58,943 imported and local born Holstein Friesian, Jersey, ….. etc) cows and producing 453,000 tons of milk per year (Mansour, 1992).

The importation of germplasm from a temperate country, namely the United States, to a country with these climatic characteristics raises an important question about the performance of animals not bred for a harsh environment. Relationships between performances of these animals in both environments must be studied to determine the impact of the different environments on production traits. It is widely established that if a genotype is developed under particular environmental conditions but reared under different environmental conditions, then investigation of genotype – environment interaction becomes important (Lytton and Legates, 1966; Taneja and Rao, 1982; Togashi *et al.,* 1999). Thus how much of the genetic superiority of the best bulls in the better environment will be manifested in the poorer environment. If the investigation reveals a violation of any of the two following assumptions, then there is interaction. The first assumption is that different environmental conditions have the same effect on different genotypes, and the second is that phenotypic and genetic variances are homogeneous across environments (Stanton *et al.,* 1991).

The classic example of genotype by environment (G x E) interaction occurs when the first assumption is violated. In this case, the genetic correlation between a trait expressed in one environment and the same trait expressed in another environment is no longer unity. This indicates that different sets of genes control the trait in different environments. Consequently, individual breeding values may change rank from one environment to the other.

If the second assumption is violated then another form of G x E interaction occurs. Breeding values for single trait do not change rank across environments, instead the magnitude of differences between animals is not the same across environments. This form of interaction results from heterogeneous variances. Even if genetic correlations between traits expressed in different countries are equal to unity, genetic and phenotypic variances are likely to vary from temperate to arid countries.

The objectives of the present study were to determine whether interactions between genotype and environment for milk production in daughters of sires

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used in the United States and Saudi Arabia exist by estimating and comparing genetic, residual, and phenotypic co-variances across environments from a multi trait animal model.

MATERIALS AND METHODS

Approximately 66,000 records for twice daily milking, 305-d, mature-equivalent milk (Mk-ME) yield of Holstein cows were available from six large farms located in the central region of the Kingdom of Saudi Arabia. The records available were those of cows calved between 1990 and 1998, allowing for some cows to have more than eight normal parities. All records of a cow were discarded if she had a missing or an invalid sire identification number (i.e. sire name was not considered unique), and or if breed of sire was not Holstein. Sires of cows were identified and then sent to Dairy Records Management System, Raleigh, North Carolina to obtain performance records of daughters of the same sires in the United States. Approximately 916,000 records for ME-Mk of Holstein cows that calved in the United States between 1990 and 1998 were provided. The data files from both countries were merged to form a composite data file with records of up to eight lactations for some cows.

Cows were required to have a sequential data pattern to be included in the analysis (i.e. if the 3rd record is to be used, 1st and 2nd records should be available). If any of a cow's previous records were missing, then all her records were eliminated. This helped to overcome the problem of selection or culling of heifers based on their 1st lactation. All production records were restricted to at least 240 days of milking regardless of milk yield, and herds chosen from the overall data contained 230 dairy cows or more. Those last edits decreased USA data to $\simeq$ 540,000 records but did not significantly reduce the Saudi data. The calendar year was divided into six calving seasons, two months each, and each season was identified separately for first and multiple calving cows to prevent biases that may be due to different management within a herd based on age or time of freshening. Herd-year-seasons were required to have at least five observations. Structure of the data in both countries is presented in Table 1.

Statistical Analysis of Variance:

The Saudi data was first analyzed using a single-trait, multiple random components animal model to investigate wither the effect of sire by herd interaction was large enough to be included in the multi-trait model. If the proportion of the total variation attributed to this effect is more than 2%. Otherwise it can be ignored. The model included mature equivalent milk yield as the dependent variable, herd-year-season as fixed effects, and sire by herd interaction, animal, permanent environment, and residual as random effects. The magnitude of the effect of the interaction of sire by herd was less than 1%, so this effect was not important enough to be considered under Saudi conditions.

Single and multi trait animal model were used to obtain co-variances for ME-Mk in the first and pooled lactation data sets within both two country. Milk yield in the Saudi Arabia and the United States were treated as separate traits in joint analysis. Genetic co-variances and residual variance components were estimated simultaneously.

The first model used single trait animal model from method R procedure (Reverter *et al.,* 1994) to analysis within country for pooled lactation data set. Method R produces estimates of variances from which genetic, environment, and phenotypic parameters can be derived. The mathematical model was

$$Y_{ijk} = \mu + HYS_i + A_k + Pe_k + \varepsilon_{ikl} \text{ .... } 1^{st} \text{ model}$$

Where: Y_{ikl} is the l^{th} record for k^{th} cow of mature equivalent milk production, HYS_i is the fixed effects due to i^{th} herd-year-season of freshening, A_k is the random additive genetic effect due to k^{th} animal, Pe_k is the permanent environment due to k^{th} cow and ε_{ikl} is the random residual effect for the l^{th} record of k^{th} animal in i^{th} herd-year-season. In matrix notation the model can be described as

$$Y = Xb + Za + Wpe + e$$

Where: Y is a vector of observations for production variables, b is a vector of fixed effects for herd-year-season, a is a vector of additive genetic values of individual animals for the trait or traits considered, pe is a vector of random permanent effect, e is a vector of residual effects and X, Z, and W are known incidence matrices that assign fixed, additive random, and permanent effects to records in Y. The mixed model equations (MME) were

Table (1): Summary of the data structure for mature equivalent milk yield by parity and month of calving groups in Saudi Arabia and the United States.

		Lactations						
		1st	**2nd**	**3rd**	**4th**	**5th**	**Total[1]**	**Total[2]**
Saudi Arabia	**Sires**	255	242	198	160	107	255	
	Cows	20,815	12,862	7,636	3,769	1,695	20,815	46,777
	HYS[3]	193	183	179	161	128	376	
United States	**Sires**	176	176	155	152	127	87	176
	Cows	19,456	10,215	5,698	2,247	677	19,456	38,293
	HYS[3]	1,525	1,525	1,100	990	639	283	2,640
		Months of calving						
		Jan- Feb	**Mar - Apr.**	**May - Jun**	**July -Aug**	**Sep - Oct**	**Nov – Dec**	**Total**
Cows	**First Calving**	4,226	4,705	2,895	4,251	3,278	1,460	20,815
	Multiple Calving	4,626	4,597	3,696	4,647	4,597	3,799	25,962

[1] Total number of unique sire, cow (records) or HYS, [2] Total number of records, [3] Herd-Year –Season

$$\begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + A^{-1}\varphi & Z'W \\ W'X & W'Z & W'W + I_{1\gamma} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{pe} \end{bmatrix} = \begin{bmatrix} X'Y \\ X'Y \\ W'Y \end{bmatrix}$$

$$E\begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \operatorname{var}\begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I_{1\sigma_{pe}^2} & 0 \\ 0 & 0 & I_{2\sigma_e^2} \end{bmatrix}$$

Where: A is the numerator relationship matrix, σ_a^2 is the additive variance, σ_{pe}^2 is the permanent environmental variance, σ_e^2 is the residual variance I_1, I_2 are the identity matrix 1 for cows with records, 2 for all animals in A, $\varphi = \frac{\sigma_e^2}{\sigma_a^2}$ and $\gamma = \frac{\sigma_e^2}{\sigma_{pe}^2}$

The second model was used to analyze ME-Mk in different two data sets either for the 1st parity or for the pooled lactations in a joint analysis using multi-trait animal model of Method R.

The mathematical model was

$$Y_{ikl} = \mu + HYS_i + A_k + \varepsilon_{ikl} \text{ …… (2}^{\text{nd}}\text{ model)}$$

Where: Y_{ikl} is the l^{th} record for k^{th} cow of mature equivalent milk production, HYS_i is the fixed effects due to i^{th} herd-year-season of freshening, A_k is the random additive genetic effect due to k^{th} animal, (Pe_k is the permanent environment due to k^{th} cow of the model 3) and ε_{ikl} is the random residual effect for the l^{th} record of k^{th} animal in i^{th} herd-year-season. In matrix notation the 2nd model can be described as shown for the 1st model.

The third model is similar to the second model with addition of a random effect of permanent environment.

RESULTS AND DISCUSSION

Phenotypic means and standard deviations for milk yield in the first five parities are illustrated in Figure 1.

Means of ME-Mk show little variations across different parities in both countries. Approximately 9.4% mk increment from the 1st to the 2nd lactation in KSA while the corresponding value in USA was 3.6% and declined slightly thereafter in both countries. Romero (1986) reported a decline in milk production after the 2nd lactation from Holstein Friesian in Puerto Rico. American HF was higher than Saudi HF specially across the first three parities and then remain similar. The rates of superiority were 9.7% and 3.6% for USA-HF than KSA-HF during the first two parities, respectively.

Genetic analysis of milk yield within country

Minimum, maximum, median, mean and standard error of the estimates of genetic, permanent environmental, environmental, and phenotypic variation for milk yield in the pooled data set of the first five lactations are presented in Table 2.

The estimates of different variance components do not necessarily correspond to the same sample. Instead they are the values of those parameters from the different subsamples generated by Method R procedure. Estimate of additive genetic variance for KSA-HF was 36% lower than the corresponding estimate for USA-HF. However, environmental variance for KSA-HF was not considerably smaller (85%) than for the United States. The heritability estimate of milk yield in the KSA-HF population (0.29) was smaller by ~ 25% than the estimate for the USA-HF (0.36). This can be attributed to the fact that additive genetic variance in the Saudi data set was reduced relatively more than the residual variance. Coefficients of additive genetic variation (ACV%, Table 2) were calculated by dividing genetic standard deviations by means. The range of coefficients was 6.7 to 7.8% for the Saudi data and 8.2% to 10.2% for the United States data, implying that animals in the United States express more genetic variation relative to the phenotypic mean. It is possible that the smaller additive genetic variance in the Saudi population is due to environmental conditions related to heat stress during most of the year that prevent the genetic potential of superior individual from being expressed, therefore restricting differences in milk production between cows with different genetic values. The ranges of heritability for both countries were similar to the range of 0.18 to 0.51 reported by Van Tassell *et al.* (1999) using Method R procedures. The heritability estimate for ME-Mk of HF-KSA was slightly larger than the estimate of 0.23 to 0.25 by Amin (1998) for Hungarian Holstein Friesian and was smaller than the estimate of 0.34 by Amin *et al.* (2005) for Egyptian Holstein Friesian. But was consistent with reported estimates for Holsteins in the literature (Meinert *et al.*, 1989 and Miglior *et al.*, 1995). The heritability estimate of KSA-HF for ME-Mk (0.29) implies that there is enough genetic variation for milk production under Saudi Arabia environmental conditions for improvement in milk yield to be attained by selection.

The permanent environmental variance for the United States data set was 80% that for Saudi data which compensates for the reduction in genetic variance from the Saudi data and resulted in estimates of repeatability in both countries that are virtually the same (the median estimates were 0.48 for Saudi Arabia and 0.50 for the United States). These values are consistent with estimates by Van Tassell *et al.* (1999) who reported repeatability estimates of 0.50 using Method R procedures. Our estimate is also within the range of reports in the literature using different procedures (Dematawewa and Berger, 1998, and Romero, 1986), implying that the likelihood of Holstein cows performing under Saudi environmental conditions to persist in their productivity in advanced lactations is as great as in other areas. Hence, it seems there is a considerable potential for cow selection to improve milk production in Saudi Arabia, and culling on the basis of first lactation records should be effective.

Joint analysis between the United States and Saudi Arabia

Parameters for variance components, heritability, and genetic correlation estimates from 20 subsamples of

Method R for mature equivalent first lactation milk yield are shown in Table 3.

The range of genetic variance from those 20 subsamples for KSA-HF was smaller than that of USA-HF but other values for estimates of genetic values of KSA-HF did not differ from those for USA-HF. However; due to the environmental constraints that affect the performance of individuals under a Saudi environment and the fact that these data were drawn from a small number of large-scale farms, estimates of residual variance for Saudi Arabia were smaller than estimates for the United States. The median estimated residual variance for Saudi Arabia was 79% that of the United States. The range of residual variances from those 20 subsamples for Saudi Arabia was less than half that of the United States. Because these changes in genetic and residual variances were disproportional, the estimate of heritability (0.29) for Saudi Arabia was slightly higher than the estimate for the United States (0.24). Castillo-Juarez, *et al.,* 2000 reported a non-proportional change in genetic and residual variances for mature equivalent milk yield in the low versus high environment, leading to higher heritability (0.30 vs. 0.22) in the high environment class.

In all analysis of pooled lactation data set, estimates of genetic variance for Saudi Arabia increased and estimates for United States decreased (Table 4) in comparison with the corresponding estimates of within country analysis (Table 2), but differences were small. Also, coefficients of additive genetic variation for the Saudi data set from all lactations analysis increased slightly and the corresponding estimates for the United States decreased slightly than within country analysis. It is possible to attribute this change in genetic variances to the fact that the breeding values that produce these estimates in both countries are positively genetically correlated. Because of this relationship, greater genetic differences among animals (sires in particular) in the United States data could increase the genetic variance between the same animals in Saudi data. For the same reason, a reduction in genetic variation between animals in the United States is expected as a result of reduced genetic variation among the same animals in the Saudi data set. Estimates of residual variances for the Saudi data set from all lactation joint analysis were also greater than those of within country analysis. However the differences were small.

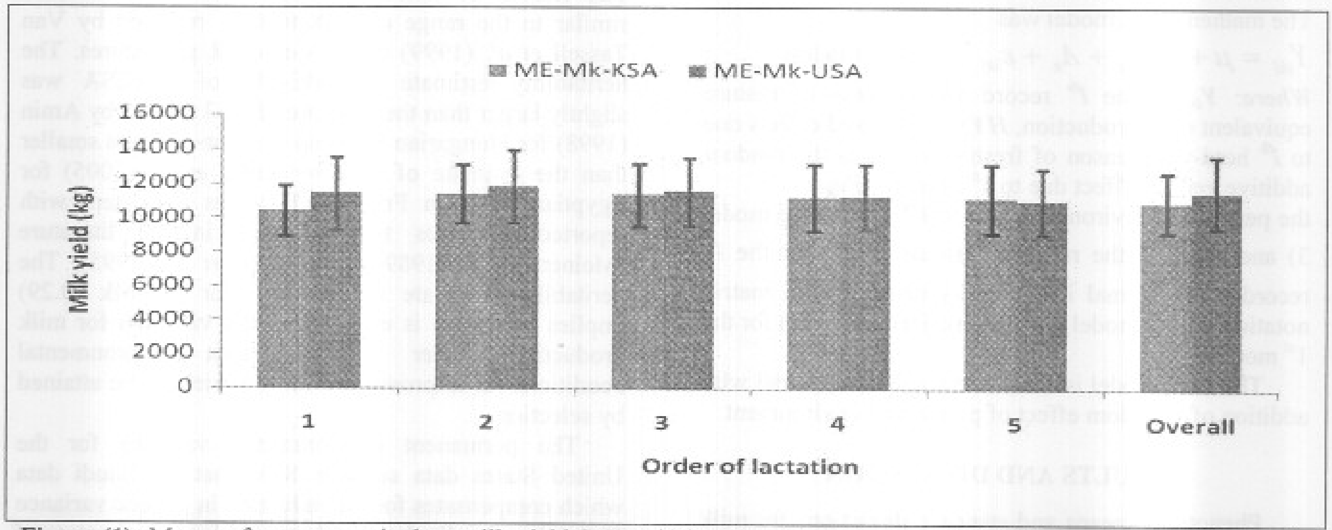

Figure (1): Means of mature-equivalent milk yield (ME-Mk) in Kingdom of Saudi Arabia (KSA) and United States of America (USA) across the first five lactations.

Table (2): Estimates of variance components, heritability (h^2), repeatability (r), additive coefficient of variation (ACV%), and standard errors (SE) for milk yield from within country analysis for Saudi Arabia and United States in pooled lactations data set.

		Variance components				Parameters		
		σ_a^2	σ_{PE}^2	σ_e^2	σ_P^2	h^2	r	ACV%
Saudi Arabia	**Minimum**	601,047	330,203	1,109,590	2,128,928	0.26	0.45	6.7
	Maximum	796,545	532,126	1,305,740	2,497,202	0.33	0.49	7.8
	Median	672,984	438,869	1,257,800	2,345,377	0.29	0.48	7.1
	Mean	681,050	443,216	1,250,475	2,374,742	0.29	0.47	7.2
	SE	2,787	2,260	2,237	4,247	0.001	0.0004	0.0008
United States	**Minimum**	889,425	248,181	1,280,130	2,601,118	0.30	0.47	8.20
	Maximum	1,369,540	532,826	1,530,900	3,168,226	0.43	0.54	10.20
	Median	1,074,375	355,311	1,478,280	2,918,951	0.36	0.50	9.00
	Mean	1,066,176	385,975	1,470,548	2,922,699	0.36	0.50	9.00
	SE	10,603	6,942	5,550	11,265	0.0030	0.0008	0.0004

σ_a^2 : Additive genetic variance, σ_{PE}^2 : permanent environmental variance, σ_e^2 : Environmental variance, σ_P^2 : phenotypic variance

Table (3): Estimates of variance components, heritability (h^2), additive coefficient of variation (ACV%), genetic correlation ($r_{a_{USA.KSA}}$) and standard errors (SE) for milk yield from joint analysis between Saudi Arabia and United States in first lactation.

		Variance components			Parameters		
		σ_a^2	σ_e^2	σ_P^2	h^2	$r_{a_{USA.KSA}}$	ACV%
Saudi Arabia	**Minimum**	569,851	1,445,580	2,028,114	0.26	0.25	7.3
	Maximum	736,608	1,727,080	2,417,409	0.33	0.84	8.3
	Median	641,391	1,553370	2,195,963	0.29	0.68	7.7
	Mean	642,398	1,557,823	2,200,222	0.29	0.60	7.7
	SE	3,248	6,079	6,553	0.11	0.01	0.0002
United States	**Minimum**	425,880	1,674,200	2,184,672	0.16		5.7
	Maximum	986,325	2,277,600	2,943,945	0.34		8.6
	Median	631,668	1,954090	2,630,332	0.24		7.0
	Mean	643,525	1,961,191	2,604,716	0.24		7.0
	SE	11,208	9,390	12,580	0.003		0.0006

σ_a^2 : Additive genetic variance, σ_e^2 : Environmental variance, σ_P^2 : phenotypic variance

Table (4): Estimates of variance components, heritability (h^2), repeatability (r), additive coefficient of variation (ACV%), genetic correlation ($r_{a_{USA.KSA}}$) and standard errors (SE) for milk yield from joint analysis between Saudi Arabia and United States in all lactations.

		Variance components				Parameters			
		σ_a^2	σ_{PE}^2	σ_e^2	σ_P^2	h^2	r	$r_{a_{USA.KSA}}$	ACV%
Saudi Arabia	**Minimum**	671,522	417,996	1,344,020	2,5356987	0.24	0.45	0.03	7.5
	Maximum	949,970	607,998	1,554,220	2,915,927	0.33	0.50	0.38	8.9
	Median	795,955	488,154	1,435,625	2,719,432	0.29	0.47	0.17	8.0
	Mean	798,335	487,194	1,439,878	2,725,408	0.29	0.47	0.18	8.2
	SE	3,343	1,913	2,260	4,495	0.00	0.00	0.00	0.00
United States	**Minimum**	725,801	277,357	1,392,440	2,788,619	0.24	0.47		7.4
	Maximum	1,319,790	746,645	1,627,120	3,287,506	0.42	0.52		9.9
	Median	991,195	454,484	1,508,385	3,016,286	0.34	0.50		8.6
	Mean	1,007,032	479,234	1,508,759	2,995,026	0.34	0.50		8..7
	SE	6,754	5,426	2,764	5,438	0.002	0.00		0.007

σ_a^2 : Additive genetic variance, σ_e^2 : Environmental variance, σ_P^2 : phenotypic variance, σ_{PE}^2 : permanent environmental variance

Because the proportion of changes in genetic and phenotypic variances was relatively equal in both countries, heritability estimates from both within and across environmental analysis for all lactations were similar. This result is in contrast to the report by Hammami *et al.* (2008) who reported lower heritability estimate for milk from within-country analyses than those from the joint analysis from Tunisian data using test-day analysis. Substantial differences for additive genetic variance for the United States were revealed between joint first and all-lactations analysis. While all parameters for phenotypic variance estimates for the United States from across-parity analysis were only 15% greater than those estimates from the first lactation analysis, estimates of additive genetic variance from across-parity analysis were 56% greater than those estimates of the first lactation analysis. Dairymen usually select cows based on their first lactation records. This implies that individuals in later lactations are selected genotypes which would be expected to be more homogeneity resulting in reduced additive genetic variance and heritability. However, this is not the case in this study because, again, the edits of records in the present study assume no culling (sequential records are required). In fact both genetic and phenotypic variances increased in both countries, but residual variances for the United States in all lactation data set decreased by an approximately 22% of that in the 1st lactation. It seems that younger cows are under the stress of production and growing at the same time, but as they get older and approach mature weight, they are more able to express their potential in milk production. Repeatability estimates from joint analysis were similar in both countries were similar in both countries and did not differ from those within-country analysis.

Median and mean estimates of genetic correlations in the first and all lactations are listed in Tables 3 and 4, respectively. Median and mean estimates from first lactation analysis were in moderate values and ranged from 0.68 to 0.60, but estimates from pooled lactation analysis were substantially lower (0.17 and 0.18). This suggests the existence of a significant genotype be environment interaction and a considerable change in rank of sires across environments, because if the genetic correlation is low "then the characters are to a great extent different, and high performance requires a different set of genes" (Falconer, 1993). It becomes obvious that progeny of some sires selected in temperate areas are more susceptible to heat than progeny of other temperate area's sires. The results agree with those of Abubaker (1985) who investigated the genotype by environment interaction between Mexico and Colombia and reported a considerable interaction between sires and environments as indicated by the rank correlation between sire values of 0.26. Several studies reported small correlations, suggesting a considerable genotype by environment interaction (Bar Anan *et al.,* 1987; Cunnungham and O'Byrne, 1977; Holmes, 1995, Romero, 1986; Schneeberger *et al.,* 1982).

CONCLUSION

Results from the present study indicate that high yielding breeds could perform well with respect to production under arid environmental conditions provided good management. However, these results also substantiate the presence of highly significant genotype by environment interactions for milk yield between KSA and USA. Estimates of genetic correlations reported herein for Holstein milk yield were 0.68 for 1st lactation and 0.17 for all lactations between KSA and USA, suggesting that sires with daughters in USA are significantly re-ranked for Me-Mk for daughters in KSA. The two environments involved were widely divergent, thus genetic adaptability to local environmental conditions seems to be of permanent importance for production. There is evidence of enough genetic variation in milk yield under KSA environment conditions. Therefore, it may be useful for herds in KSA to participate in a national sire evaluation program to predict the merit of those sires with daughters with high performance under the KSA environmental conditions.

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