Genotype by Environment Interaction for Milk Production Traits in Holstein Friesian Dairy Cattle in Ireland

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Introduction

Interactions of genotype and environment (G*E) occur when there are differences in expression of genotypes between environments. These G*E interactions can take two forms causing either; (1) a scaling effect across environments or (2) a change in the actual ranking of sires across environments. The scaling effect occurs when the scale of differences in sire proofs is unequal in the two environments. Re-ranking occurs when the trait, e.g., milk yield, has a different genetic basis in the two environments i.e., is controlled by different genes. If the degree of re-ranking is large, the genetic correlation between milk production in the two environments will be substantially less than 1.0, with the implication that proofs made in one environment may not be a reliable predictors of genetic merit in the second environment. It is this form of G*E which is of particular interest to animal breeders.

Numerous studies have found evidence of G*E interaction due to scaling in dairy cattle e.g., McDaniel and Corley (1967), Stanton, Blake, Quaas, Van Fleck and Carabano (1991). In contrast, very few studies have found evidence of G*E interaction due to re-ranking. The notable exceptions have been Peterson (1988), who found evidence of significant re-ranking between Canada and New Zealand for milk production traits and Carabano, Van Fleck, and Wiggans (1989) who found evidence of significant re-ranking for fat yield between Spain and the United States. It is interesting to note that in both of these studies comparisons were across countries as opposed to within a country.

Within Ireland there exists a range of milk production systems. Some herds may be predominantly winter calving and feed relatively high levels of concentrate, while other herds may calve predominantly in spring and feed much lower levels of concentrate. The inevitability of lower prices for milk and milk products as a result of GATT, has resulted in renewed interest towards lower cost systems of milk production. The main variable cost on most Irish dairy farms is the level of concentrates fed (concentrates are about 5 times more expensive in terms of cost per MJ of ME than grazed grass). Therefore, given that bulls are generally proven in high concentrate input environments and that dairy farmers often choose to reduce milk production costs through lower concentrate input, it is of interest at present to investigate whether there is evidence of G*E interaction for milk production traits within Ireland.

The aim of this study was therefore to determine the effect of certain herd environments on the genetic evaluation of dairy sires. The herd environments considered in this paper were average concentrate input and average milk yield.

Materials and Methods

Milk records were obtained from the Department of Agriculture, Food and Forestry, Kildare Street, Dublin and from United Dairy Farmers, Belfast, for cows having calved during the period 1st January 1992 to 31st December 1995. The data consisted of 305-day lactation records for milk, fat and protein yield. Records shorter than 305 days were not extended. Age at first calving was restricted to 20-40 months and all cows were required to have at least a first lactation during the four year period to be included in the analysis. After editing there were 274,384 individual milk records, completed on 4,268 farms, available for analysis.

Information on herd concentrate input was available for 665 of the 4,268 herds (dataset 1). These 665 herds were all participants in recognized dairy herd recording schemes during the 4 year period 1992-1995. Herd environments were defined

initially on the basis of average concentrate input/cow/year (concentrate input/cow/year was calculated within herd-year and then averaged across years for the four years of the study). High concentrate input herds were defined as the top 25% of herds on average concentrate input/cow/year and low input herds as the bottom 25% of herds on average concentrate input/cow/year. The performance of high and low input herds for a number of production traits (including concentrate input) are given in Table 1.

Table 1. Mean performance of high and low input herds for a number of production traits (including concentrate input).

Trait	High Input Herds		Low Input Herds	
	Mean	**SD**	**Mean**	**SD**
Concentrate Input (kgs)	1,514	275	505	119
Milk Yield (kgs)	5,887	851	4,497	552
Fat Yield (kgs)	227.3	34.2	170.3	22.3
Protein Yield (kgs)	289.2	27.6	147.7	18.7

The difference in concentrate input/cow/year between high and low input herds was about one tonne. High input herds produced more milk (about 1,400 kgs) and more solids (about 100 kgs) than herds feeding lower levels of concentrate. Variation in milk production performance was also higher in herds feeding high levels of concentrate. Of the 63,313 milk records from herds with concentrate input information, 20,698 records (from 11,211 animals) were completed in herds defined as high input and 11,572 records (from 6,190 animals) were completed in herds defined as low input.

Subsequent analyses of the entire dataset (dataset 2), comprising of 149,691 heifer lactations from 4,268 herds, involved categorization of herds on the basis of average milk yield into high and low yielding groups. Herd average milk yield was calculated as the average heifer yield over the 4 year period.

In the study G*E interaction was investigated in two ways :

(1) Correlation between sires1proofs

Best Linear Unbiased Prediction (BLUP) breeding values were obtained for all sires in high and low input herds separately using PEST (Groeneveld 1990). The model for analysis of milk production traits included; the proportion of Holstein genes as a linear covariate, age at calving within lactation

number as a linear and quadratic covariate, the fixed effects of herd-year-season, month of calving and lactation number and the random effects of animal and permanent environment.

(2) Measuring the genetic correlation (r_g).

(Co)-variance components were estimated using a restricted maximum likelihood procedure applied to bivariate individual animal models on VCE REML version 3.2 (Groeneveld *et al.,* 1996). For each analysis, only heifer lactations were used and the model included; the proportion of Holstein genes as a linear covariate, age at calving as a linear and quadratic covariate, the fixed effects of herd-year-season and month of calving and a random animal effect.

Results and Discussion

1. The effect of herd concentrate input on bull evaluations

Correlation between sires1proofs

Breeding values were obtained for all sires within high and low input herds separately. The proofs of sires which were common to both environments and whose proofs had a reliability of at least 60% in both

high and low categories were then compared to establish if there was evidence of G*E interaction.

Correlation and regression statistics of proofs for milk, fat and protein yield are given in Table 2.

Table 2. Correlation and regression statistics for milk, fat and protein yield in high and low input herds.

	Intercept	b-value	r_{proofs}
Milk (kgs)	+ 91	0.39	0.65
Fat (kgs)	+ 240	0.47	0.67
Protein (kgs)	+ 0.93	0.37	0.62

* Regression of proofs in low input herds on proofs in high input herds.

Product-moment correlations between bulls1 proofs in high and low input herds were 0.65, 0.67 and 0.62 for milk, fat and protein yield respectively. These correlations approximated to the reliability of bull proofs in both high (0.81) and low (0.74) input herds, thus indicating little evidence of re-ranking for milk production traits. However there was evidence of a considerable scaling effect between high and low input herds. Regression coefficients for milk, fat and protein yield were 0.39, 0.47 and 0.37 respectively, indicating that proofs from high input systems over-predict genetic merit for lower concentrate input environments.

Estimation of the genetic correlation (r_g).

Estimates of r_g for milk production traits between high and low input herds were based on 17,301 heifer lactations. Estimates of h^2 and the r_g between performances in high and low input herds are given in Table 3.

Table 3. Heritabilities (h^2) and the genetic correlation (r_g) between performances in high and low input herds.

		High Input	Low Input
Milk (kgs)	h^2	0.43 (.03)	0.29 (.04)
	r_g	**0.92 (.06)**	
Fat (kgs)	h^2	0.32 (.02)	0.32 (.04)
	r_g	**0.89 (.06)**	
Protein (kgs)	h^2	0.38 (.03)	0.24 (.03)
	r_g	**0.91 (.07)**	

Heritabilty estimates for milk and protein yield were higher in herds feeding high levels of concentrate than in herds feeding lower levels of concentrate. The results for milk and protein yield are consistent with those of previous researchers who found evidence of an increase in heritability with mean production and variation in mean production (Dannell, 1982; Hill, Edwards, Ahmed and Thompson, 1983). There was no observed increase in the heritability for fat yield between high and low input herds. Estimates of r_g between herd environments were high (0.92, 0.89 and 0.91 for milk, fat and protein yield respectively) and are in agreement with those obtained from the correlation of proofs analysis. Both analysis would therefore indicate little evidence of re-ranking for milk

production traits for the definition of herd environments considered. The results obtained in these analyses are also consistent with previous researchers who defined environments on the basis of different feeding regimes within a country (McDaniel & Corley, 1967; Wiggans & Van Fleck, 1978).

Whilst the present study indicated little evidence of re-ranking for milk production traits, the environments considered were not dramatically different, i.e., the difference in average concentrate input/cow/year between high and low input herds was less than 1 tonne. Plotting published estimates of genetic correlations for milk yield between environments, Cunningham and O'Byrne (1975) observed a linear decline in the r_g between environments as the difference in environments became more pronounced. A further analysis was therefore undertaken using the complete dataset (dataset 2) and defining herds on the basis of herd average milk yield, to investigate the effect of increasing the difference in environment on the r_g for milk production traits.

2. The effect of herd average milk yield on the r_g for milk production traits

In the second study of 149,691 heifer lactations from 4,268 herds (dataset 2), high yielding herds were defined initially as the top 25% of herds on herd average milk yield (H_{25}) and low yielding herds as the bottom 25% of herds on herd average milk yield (L_{25}). Subsequent analyses considered the top and bottom 20% of herds (H_{20} vs. L_{20}), the top and bottom 15% of herds (H_{15} vs. L_{15}) and the top and bottom 10% of herds (H_{10} vs. L_{10}) on herd average milk yield to establish the effect of increasing the difference in herd environment on the r_g for milk production traits. The results from this study are given in Table 4.

Table 4. Means, and heritabilities (h^2) for milk, fat and protein yield in high and low yielding herds and the genetic correlation (r_g) between expression of the same trait between high and low yielding herds.

		H_{25}	L_{25}	H_{20}	L_{20}	H_{15}	L_{15}	H_{10}	L_{10}
Milk (kgs)	h^2	0.44	0.33	0.44	0.30	0.44	0.28	0.44	0.26
	r_g	**0.96 (.02)**		**0.95 (.03)**		**0.94 (.05)**		**0.82 (.08)**	
Fat (kgs)	h^2	0.38	0.37	0.37	0.34	0.38	0.40	0.38	0.39
	r_g	**0.96 (.02)**		**0.90 (.03)**		**0.94 (.07)**		**1.00 (00)**	
Protein (kgs)	h^2	0.39	0.33	0.38	0.28	0.39	0.28	0.40	0.26
	r_g	**0.95 (.02)**		**0.95 (.02)**		**0.94 (.07)**		**0.85 (.09)**	

s.errors for h^2 range from .01 - .04

As with the previous analyses of dataset 1, heritability estimates were consistently higher for milk and protein yield in high yielding herds than in low yielding herds. Estimates of heritability for fat yield were similar in high and low yielding herds. Regardless of the extent of difference in herd average milk yield, heritability estimates remained remarkably consistent for all three traits. However, there was a decline in the r_g for both milk and protein yield as the difference in herd average milk yield increased i.e., when differences in environments are relatively small i.e., H_{25} vs. L_{25}, the genetic correlation (r_g) between the environments is high (>0.95). However, at greater differences in herd environment, i.e., H_{10} vs. L_{10}, estimates of r_g for both milk and protein yield approached the value of 0.80 suggested by Robertson (1959) as indicative of a G*E interaction of biological and agricultural importance. This trend of declining r_g with increasing difference in environment was also obtained from analyses of dataset 1, albeit with much larger standard errors (resulting from lower numbers of records).

Conclusions

The results from this study indicate that there is evidence of a considerable scaling effect between high and low concentrate input herds within Ireland. Proofs made in high concentrate input environments will over-predict genetic merit for lower concentrate input systems. However, for both definitions of herd environment, there appears to be little evidence of serious re-ranking of bulls with regard to milk, fat and protein yield for the majority of milk production systems within Ireland. Nevertheless, there is some evidence of re-ranking for milk and protein yield in very low yielding herds and therefore farmers in these herds would be advised to consider the environment in which a bull was tested when selecting sires for use on these herds.

Acknowledgements

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