MULTIPLE TRAIT ANALYSIS OF GENOTYPE BY ENVIRONMENT INTERACTION FOR MILK YIELD TRAITS IN SLOVENIAN CATTLE

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Original scientific paper

SUMMARY

The objective of the study was to evaluate genotype by environment interaction (GxEI) for yield traits in Holstein, Simmental and Brown breed cattle in Slovenia using multiple trait analysis. Data from Slovenian milk-recording scheme was used. The lactation records on cows having first to third calving in the period 1990-2004 and milk, protein and fat yield in 305 days were studied. The variables used to characterize the environment were herd-year averages of each trait. The multiple trait analysis was done using the highest and lowest quartiles of the environments. To study the GxEI, animal model methodology and the genetic correlation between the traits were used. GxEI was generally smaller for fat and milk yield than for protein yield. The lowest genetic correlations between high and low environments were estimated for protein yield, especially in Simmental (0.81) and in Brown (0.86) breed. In Holstein the correlation was higher, 0.94. The genetic correlations for fat yield were 0.95 for Brown and Simmental breed and 0.96 for Holstein. For milk yield the estimated genetic correlations were 0.88, 0.92 and 0.96 in Brown, Simmental and Holstein breed, respectively. Differences between variance components obtained in low and high quartile result in the rank of heritabilities from 0.04 to 0.12 in low and from 0.12 to 0.22 in high quartile.

Key-words: cattle, milk yield traits, genotype by environment interaction, genetic correlations

INTRODUCTION

The ability of organisms to respond to changes in the environment is called phenotypic plasticity or environmental sensitivity (Falconer and Mackay, 1996). Genotypes differ in the phenotypic plasticity, which may result in genotype by environment interaction (GxEI). When genotypes react differently in different environments, GxEI is an important parameter to consider (Falconer, 1952); (Falconer and Mackay, 1996). Thus differences between sires in the genetic ability of their daughters to perform in different environments result from interaction between genotype and environment. When difference between genotypes differs in magnitude and not in sign, a scaling effect of GxEI accrues. Accurate genetic evaluation requires consistency of sire rankings across environments. The existence of GxEI might lead to a re-ranking of breeding bulls in different environments which may have consequences for breeding stock selection. A useful way to quantify GxEI is estimation of genetic correlation between the traits expressed in different environments (Falconer and Mackay, 1996). Correlation coefficient below 0.8 gives an indication of genotype by environment interaction (Robertson, 1959). At present, no information is available on the existence of a GxEI in the Slovenian dairy cattle population.
The objective of the study was to evaluate GxEI for 305 days yield of milk, fat and protein in Slovenia dairy cattle breeds using bivariate animal model approach.

MATERIAL AND METHODS

Milk production records and pedigree information was collected for Holstein, Simmental and Brown breed from the database of Slovenian cattle recording scheme (Logar et al., 2005). Milk (MILK), protein (PROT), and fat (FAT) yield in 305 days were studied.

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The first to the third lactation data on cows having the corresponding calvings in the period 1990-2004 were applied. Two levels of data preparing were performed. Criteria for the inclusion of records at the first level were first lactation known, at least 60 kg protein yield, age at first calving within 17-48 months, age at first to third calving within 17-78 months and at least 50 observations of daughters per sire, leaving 85515 records on 49947 cows in Holstein, 58053 records on 37908 cows in Simmental and 37139 records on 22959 cows in Brown breed. The variables used to characterize the environment of each cow were the herd-year averages of each trait. Herd-year classes were excluded if there were less than five observations on dairy traits. At the second stage of data preparing the observations were divided into low and high herd-year classes with regard to MILK, PROT and FAT herd-year averages of each trait. For the herd classes, UNIVARIATE procedure in SAS package (SAS Institute Inc. 2004) was used. The observations in the lowest and highest quartile for each environmental variable were used as production records in a low and high yield environment. At least two observations per herd-year and at least 10 observations per sire in each environment were required. To fulfill those criteria, further elimination of records was done. Descriptive statistics of environmental variables by breeds are shown in Table 1. The number of records fulfilling the criteria at the second level of data preparing is rather lower for low than for high yield environment. The difference is greater in Holstein than in other two breeds. Only 105 to 109 Holstein sires had at least 10 observations of daughters in both quartiles for MILK, PROT and FAT. The number of sires is larger for the other two breeds, 178 to 199 in Simmental and 148 to 153 in Brown. There was a large difference between means in low and high production environments for MILK, PROT and FAT. Environmental variables were more variable in the high than in the low environment and more variable in Brown and Simmental than in Holstein breed. Differences in variability between breeds arise from variability of environments where those breeds are mainly used. In Slovenia Simmental and Brown breed are more traditional dual purpose breeds, which are breed in rather different environmental conditions while, with intensification in the last decades, on bigger dairy farms Holstein has been used.

Table 1. Number of records, number of sires with daughters in low and high environment (quartile), means and standard deviations (SD) and corresponding quartile cut-off points for the environmental variables (herd-year average) of milk yield (MILK), protein yield (PROT), and fat yield (FAT) by breeds

Environmental variable	No. of sires	Low quartile			High quartile		
		No. of records	Cut-off point	Mean ± SD	No. of records	Cut-off point	Mean ± SD
				Holstein			
MILK, kg	108	12584	5688	5107 ± 496	25814	7164	7871 ± 605
PROT, kg	105	12562	180.4	159.8±17.2	26009	234.8	260.5 ± 21.6
FAT, kg	109	14434	231.0	205.1 ± 21.3	23563	296.3	328.6 ± 29.5
				Simmental			
MILK, kg	199	10660	3746	3313 ± 550	14853	5007	5622 ± 978
PROT, kg	195	10404	122.6	106.9 ± 18.0	15000	170.7	194.2 ± 33.3
FAT, kg	178	10073	154.6	133.5 ± 24.6	13894	214.4	242.7 ± 45.2
				Brown			
MILK, kg	153	6827	4258	3783 ± 625	10481	5573	6212 ± 1051
PROT, kg	147	6739	137.3	119.9 ± 20.6	10339	188.9	214.9 ± 36.7
FAT, kg	148	6728	173.0	151.5 ± 27.2	10337	235.0	266.8 ± 50.2

Bivariate analyses were performed where the same trait in low and high production environments was treated as different trait. The two yield classes (low quartile as low production environment and high quartile as high production environment) are environmentally independent but they share genes in common. The genetic correlation between the traits was used to study possible effects of GxEI. Data structure and available pedigree allowed animal model. Pedigree included data on two generations of ancestors. Genetic parameters were estimated using residual maximum likelihood (REML) as applied in VCE-5, Version 5.1.2 (Kovač et al., 2002). The following animal model was used:

$$y_{tijkln} = \mu_t + C_{ti} + A_{tj} + S_{tk} + h_{tl} + p_{tn} + a_{tn} + e_{tijkln} \qquad [1]$$

where

y_{tijkln} =   305-days milk, protein or fat yield record of cow n in herd l with calving in season

k, calving age class j, parity i in environment t;

$\mu_t =$ overall mean in environment t (t = 1, 2);

$C_{ti} =$ fixed effect of parity i in environment t (i = 1, 2, 3);

$A_{tj} =$ fixed effect of calving age j (in months) in environment t;

$S_{tk} =$ fixed effect of calving season k (in years) in environment t;

$h_{tl} =$ random effect of herd l in environment t;

$p_{tn} =$ permanent environmental effect of cow n in environment t;

$a_{tn} =$ random additive genetic effect of animal n in environment t;

$e_{tijkln} =$ random residual effect in environment t.

The direct additive genetic effect (a_{tn}) was assumed to be normally distributed with mean zero and variance:

$$\text{var}\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{a_1} & \sigma_{a_{1,2}} \\ \sigma_{a_{1,2}} & \sigma^2_{a_2} \end{bmatrix} \otimes \mathbf{A} \qquad [2]$$

where σ^2_a is the direct additive genetic variance for the trait in low (1) or high (2) production environment, and $\mathbf{A}$ is the additive relationship matrix. For the other random effects it was assumed to be normally distributed with mean zero as well. The variances are:

$$\text{var}\begin{bmatrix} \mathbf{h}_1 \\ \mathbf{h}_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{h_1} & \sigma_{h_{1,2}} \\ \sigma_{h_{1,2}} & \sigma^2_{h_2} \end{bmatrix} \otimes \mathbf{I}_h \qquad [3]$$

$$\text{var}\begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{p_1} & \sigma_{p_{1,2}} \\ \sigma_{p_{1,2}} & \sigma^2_{p_2} \end{bmatrix} \otimes \mathbf{I}_p \qquad [4]$$

In the Equations 3 and 4, σ^2_h is herd and σ^2_p is permanent environmental variance of the cow. The $\mathbf{I}_h$ and $\mathbf{I}_p$ are the corresponding identity matrices. The residuals were assumed to be normally independent and identically distributed within environments with mean zero and variances presented in equation 5.

$$\text{var}\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{e_1} & 0 \\ 0 & \sigma^2_{e_2} \end{bmatrix} \otimes \mathbf{I}_e \qquad [5]$$

Heritability for trait in environment t (t = 1, 2) was calculated by equation 6.

$$\text{h}^2_t = \sigma^2_{a_t} / \sigma^2_{total_t} \qquad \sigma^2_{total_t} = \sigma^2_{a_t} + \sigma^2_{h_t} + \sigma^2_{p_t} + \sigma^2_{e_t} \qquad [6]$$

RESULTS AND DISCUSSION

The herd-year average was chosen as environmental variable because of its potential importance for production of dairy cattle. The herd-year averages are easily available from milk recording data, and they have a reasonable variation within the average herd production levels (Table 1). Herd production levels have been shown to be important for GxEI for milk yield traits in several studies ((Cromie et al., 1998); (Strandberg et al., 2000); (Kolmodin et al., 2002); (Petersson et al., 2005); (Carlén et al., 2005)). A bivariate animal model was applied where the same trait in different environments (high and low yield environment) was treated as different trait. Genetic correlations were used to describe GxEI. Estimates of variance components for MILK, PROT, and FAT in low and high environment (Table 2) show differences for genetic and residual variance components. Tendency of enlarged genetic variance from low to high environment was observed. The proportion of herd variance is higher in low than in high quartile and higher in Simmental and brown than in Holstein breed. From descriptive statistics of

environmental variables (Table 1) a large difference between low and high production environments for MILK, PROT and FAT has already been seen. The environments with Simmental and Brown breed are more heterogeneous than those with Holstein breed. The estimated parameters (Table 2) are in agreement with the studies of (Boldman and Freeman, 1990), (Castillo-Juarez et al., 2000), (Raffrenato et al., 2003) where genetic and residual variances for milk yield traits were smaller in the low than in high production environments. Likewise, in organic dairy production system, which could be comparable with low-input production system, slightly lower phenotypic variances than in conventional production system were found (Nauta et al., 2006). It is indicated that environmental changes can modify variance components and genetic parameters of traits (Brotherstone and Hill, 1986). The environmental restrictions in barren environments deflated their genetic expression (Cromie et al., 1998); (Raffrenato et al., 2002); (Raffrenato et al., 2003).

Table 2. Estimates of additive genetic (σ_a^2), herd (σ_h^2), permanent environmental (σ_p^2) and residual variance (σ_e^2) for milk yield (MILK), protein yield (PROT), and fat yield (FAT) in low (L) and high (H) environmental quartiles by breeds

Environment	Low				High			
Variance	σ_a^2	σ_h^2	σ_p^2	σ_e^2	σ_a^2	σ_h^2	σ_p^2	σ_e^2
Trait / Breed				Holstein				
MILK, kg^2	95266	140481	135836	414526	341602	159883	285309	749070
PROT, kg^2	67.3	204.2	127.7	367.7	276.0	227.4	284.6	726.7
FAT, kg^2	167.9	296.6	188.4	765.0	568.9	403.7	433.8	1589.4
				Simmental				
MILK, kg^2	18468	37939	282538	156589	144907	73167	358442	807506
PROT, kg^2	12.2	96.6	298.4	162.7	112.7	172.7	417.7	918.0
FAT, kg^2	32.3	63.9	565.3	324.4	199.4	135.7	899.1	1731.7
				Brown				
MILK, kg^2	27278	53816	346555	185114	175078	95203	880587	404112
PROT, kg^2	20.1	94.2	372.2	182.1	179.9	187.5	1080.0	466.4
FAT, kg^2	66.0	116.9	663.6	358.0	377.8	257.2	2071.8	1084.9

Changes in genetic, residual, and other variance components for MILK, PROT, and FAT in low versus high yield environment (Table 2), lead to higher heritability in the high environment (Table 3). Heritability estimates are higher in Holstein than in Brown and Simmental breed and tend to be higher in the upper quartile. With the exception of Brown breed, the highest heritability was estimated for milk yield, in a range from 0.18 to 0.22 in high and from 0.07 to 0.12 in low production environment. Except Simmental breed in high production environment, the heritabilities for fat yield were slightly lower than those obtained for milk yield. Estimated heritabilities for protein yield ranged from 0.12 to 0.18 in the high and from 0.04 to 0.09 in the low environment. Heritabilities estimated in Holstein breed were higher with smaller differences between quartiles as observed by (Cromie et al., 1998) and (Boettcher et al., 2003). Heritabilities increasing with production level estimated with test-day model were also reported by (Gengler et al., 2005) and (Hammanmi and Croquet, 2006).

Genetic correlation between the two environments was used to describe GxEI. They were rather high for all traits. The lowest genetic correlations were estimated for protein yield; 0.81 in Simmental and 0.86 in Brown breed. The genetic correlations for fat yield were 0.95 for Brown and Simmental breed and 0.96 for Holstein. For milk yield, the estimated genetic correlations were 0.88, 0.92 and 0.96 in Brown, Simmental and Holstein breed, respectively. Some correlations obtained indicated the presence of GxEI, particularly in Simmental and Brown breed and the others, which are closed to unity, indicated that MILK, PROT and FAT are genetically equivalent traits across the environment classes. (Robertson, 1959) proposed that correlation less than 1.0 indicated GxEI, while values below 0.8 already proved the presence of GxEI to be biologically important. Similar high genetic correlation for production traits in low and high production environments by Holstein breed were obtained in the study of (Cromie et al., 1998) and also in those of (Castillo-Juarez et al., 2000), (Castillo-Juareza et al.,

2002), and (Boettcher et al., 2003). However, (Raffrenato et al., 2003) obtained relatively low genetic correlations between low and high production environment. High genetic correlations in Slovenia were expected because of less variation in environments as for example in studies by (Boettcher et al., 2003) and (Kearney et al., 2004) where the estimates were also high. However, the heterogeneity of production conditions between regions in Slovenia could not be negligible.

Table 3. Genetic correlations and heritabilities of milk yield (MILK), protein yield (PROT), and fat yield (FAT) in low and high environmental quartiles by breeds

Breed / trait	Low environment		High environment
Holstein	Heritability	Genetic correlation	Heritability
MILK	0.12	0.96	0.22
PROT	0.09	0.94	0.18
FAT	0.12	0.96	0.19
Simmental			
MILK	0.07	0.92	0.18
PROT	0.04	0.81	0.12
FAT	0.06	0.95	0.12
Brown			
MILK	0.08	0.88	0.20
PROT	0.05	0.86	0.17
FAT	0.10	0.95	0.18

Estimated genetic parameters for Holstein breed indicated that low and high yield environment presented similar production, management and genetic conditions. Using the estimates from the bivariate animal model the breeding values for Holstein breed were predicted. Around hundred sires (Table 1) had at least 10 observations of daughters in both production systems, enabling the estimation of breeding values. Breeding values predicted by multiple trait animal model for the sires with daughters in both environments are graphically presented in Figure 1 for MILK, PROT and FAT. Consequently, if genetic correlations are high, breeding values and ranking of sires are expected to be the same in the two yield environment classes for each trait studied (Castillo-Juarez et al., 2000). Despite high genetic correlation between low and high production environment in Holstein (Table 3), there was an indication of scaling and re-ranking of sires between low and high environments for MILK, PROT and FAT. Some sires have higher breeding value in low environment than in high production environment while others rank higher in rich environment and lower in poor environment. There is a great importance that sire is used under production environments similar to test conditions (Cienfuegos-Rivas et al., 1999) or, in a situation without GxEI, it needs to be considered in low production environments (Kolmodin et al., 2002); (Kearney et al., 2004). However, elite sire tested in rich environment may not be suitable for limited production conditions.
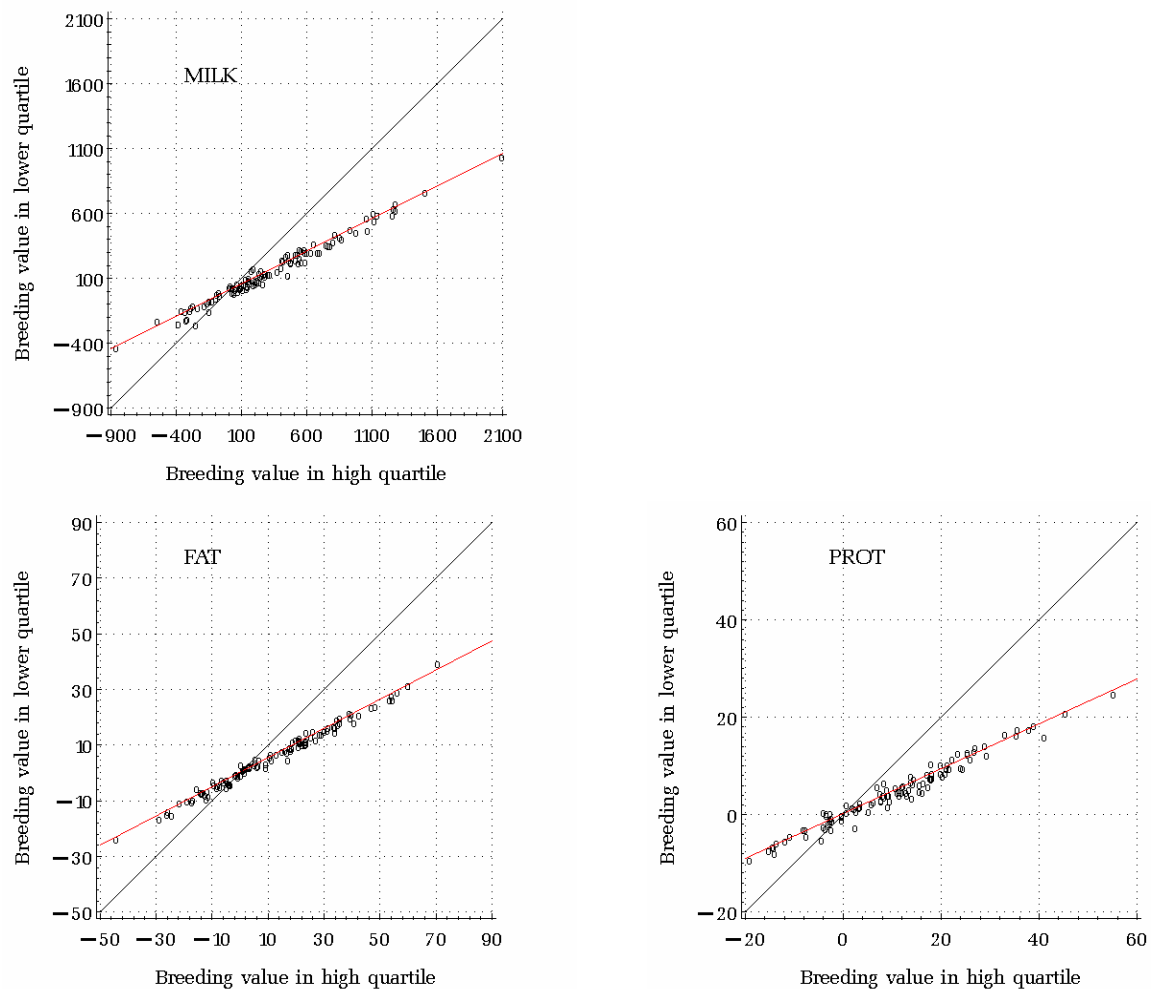
Figure 1. Breeding values of Holstein sires in low and high yield environment (quartile) for milk (MILK), fat (FAT) and protein (PROT) yield

CONCLUSION

Existence of GxEI for dairy traits in Slovenian cattle population was studied using bivariate animal model approach where production in different environments was treated as different traits. Results of this initial study do not provide strong evidence for the existence of GxEI in the environments defined. GxEI was generally smaller for fat and milk yield than for protein yield. The lowest genetic correlations between high and low environments were estimated for protein yield while those for milk and fat yield were higher. Genetic correlations near unity indicated small GxEI effect while those near the border of biological importance require further investigation. Despite high genetic correlations between high and low environments from the predicted genetic parameters some re-ranking and scaling effects of GxEI are evident. Between low and high production environment differences for genetic and other variance components were observed. The aforesaid results in heritabilities higher in the high than in the low environment.

ACKNOWLEDGEMENTS

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