

Genotype x environment interaction for milk yield in buffaloes

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ABSTRACT: The milk yield at 270 days (MY270) of 1,004 first lactations of Buffaloes Murrah was analyzed. For MY270 analysis, a random regression (RRM) univariate model was performed. In the reaction norm model, the variance components were regressed on the environmental gradient (EG). In RRM linear Legendre polynomials were used, regressed on MY270 average adjusted for each EG. The attainment of the covariance components was performed by Bayesian inference. Estimates of additive genetic, phenotypic and residual variance ranged from 36,562 to 100,426 (kg²), 96,116 to 245,094 (kg²) and from 59,553 to 144,667 (kg²), respectively. The heritabilities ranged from 0.20 to 0.41. The genetic correlations between different EGs were higher as EGs were closer or similar. Based on the criteria used to define the EG, it can be noted the presence of genotype-environment interaction for MY270.

Keywords: dairy cattle; breeding; bayesian inference

Introduction

In dairy cattle, several studies have been developed aiming to verify the presence of genotype by environment interaction (GxE) through the estimation of genetic correlation of the same trait in different environments or by the correlation value between sire breeding values in the considered environments (Kolmodin et al. (2002); Fikse et al. (2003)). In the reaction norm model (RxN), the expression of a genotype in different environments is described as a linear function of a value or environmental gradient. On the other hand, the random regression models (RRM) allow that GxE effect may be systematically assessed by regression of breeding values of sires on some measure of environments where their offspring is grown (Calus and Veerkamp, (2003); Hammami et al. (2009)). The buffalo milk yield has high commercial demand in South America, especially in Brazil. Although farms adopt several technologies against the environmental effect imposed by subtropical conditions, there is great influence on milk yield (Tonhati et al. (2000)). The objective of this study was to verify GxE presence for MY270 using reaction norms of environment, through RRM by Bayesian approach in buffaloes raised in Brazil.

Materials and Methods

Data. The milk yield at 270 days (MY270) of 1,004 first lactations of Buffaloes Murrah, with age ranging from 24 to 48 months, daughters of 203 sires, from 12 herds from São Paulo State, Brazil and calving from 1985 to 2007 were analyzed. The MY270 was calculated by interpolation method and being included in the analysis animals with at

least four controls. Contemporary groups were defined by herd and calving year (at least three animals). Environmental gradients (EG) were defined as groups (EG1 to EG6) the standard deviation of the contemporary groups (CG) of MY270. A pedigree file containing 2,074 animals was used.

Model. For MY270 analysis, a RRM univariate model was performed. The additive genetic random, environment and residual effects were adjusted. The CG, milking frequency (1 or 2 milkings) and age at calving (quadratic effect) and lactation curve mean of the population modeled by an order second orthogonal polynomial were considered as fixed effects. In the RxN, the variance components were regressed on the EG. Subsequently, the EG with similar MY270 average were grouped into 6 classes (Table 1). In RRM, Linear Legendre Polynomials (LLP) were used, regressed on MY270 average adjusted for each EG class. The LLP were also used to model the fixed effect of population average tendency. In addition, as fixed effects the EG and as random effects, animal additive genetic and residual effects were included. The residual variance was modeled into 6 homogenous classes.

Table 1. Number of observations (N°) and descriptive statistics for the MY270 (kg) according to the environmental gradient (EG).

EG	N°	Means (kg)	SD	CV	Min	Max
1	210	866.93	120.58	13.91	621.68	1011.76
2	243	1193.00	64.05	5.37	1023.03	1251.49
3	172	1309.37	38.81	2.96	1259.88	1379.05
4	215	1497.59	69.68	4.65	1393.21	1593.54
5	224	1664.78	43.99	2.64	1605.16	1727.32
6	211	1973.85	183.63	9.30	1728.42	2422.19

SD= standard Deviation
 CV= Coefficient Variation
 Min= Minimum
 Max= Maximum

Bayesian inference was performed to obtain (co)variance components using GIBBS3F90 program (MISZTAL, (2010)), in which Gibbs sampler is applied. The matrix notation of the complete model of random regression can be presented as:

$$y = X\beta + Za + e$$

where **y** is the vector of observations (MY270), **β**, **a** and **e** are, this order, vectors of fixed effects, direct additive ge-

netic coefficients and residual effects, \mathbf{X} and \mathbf{Z} are respectively, the incidence matrices related to $\boldsymbol{\beta}$ and \mathbf{a} . Uniform a priori distributions were considered for the fixed effects, Gaussian distributions for genetic coefficients and reversed Wishart for genetic variance components, where:

$$\begin{aligned} \boldsymbol{\beta} &\propto \text{constant} \\ \mathbf{a} &| \mathbf{ka} \sim N[0, (\mathbf{ka} \otimes \mathbf{A})] \\ \mathbf{ka} &| S_{a,va} \sim IW[S_{a,va}, v_a] \\ \mathbf{R} &| S_r, v_r \sim IW[S_r, v_r] \end{aligned}$$

Where, \mathbf{ka} is the matrix of (co)variances concerning the random regression coefficients for the genetic effect; \mathbf{A} is the additive relationship matrix. A chain with 1.7 million cycles length were established, with a initial discard of 200,000, and samples collection every 100, totaling 15,000 samples. Subsequently, graphic inspection and Geweke test (1992) were used, in order to ensure that burn-in period used was enough for all parameters. After this step, descriptive statistics were obtained. Through the average of posterior distributions of each parameter, genetic and residual variances and heritability for each environment, and genetic correlations between these were estimated.

Results and Discussion

The average MY270 increased when the environmental conditions were favorable (Table 1). Yield variations in these environments are considered to be associated with specific conditions of the farm management, drop by low production in some years and favorable management conditions for high yield animals. When the differences in phenotypic expression among genotypes are larger in one environment than another, with maintained ranking of genotypes, there is a scaling effect of Gx \times E (Kolmodin et al. (2002)).

Estimates of additive genetic, phenotypic and residual variance components for MY270 are shown in Figure 1. These estimates increased with the environmental conditions were favorable ranging from 36,562 to 100,426 (kg^2), 96,116 to 245,094 (kg^2) and from 59,553 to 144,667 (kg^2), respectively. Probably, in less favorable environments (EG1), animals with high and low yields had similar performance, due to the higher level of environmental restriction, and consequently the genetic variability was lower. On the other hand, in more favorable environments (EG6), animal performance was different, so more productive individuals had greater opportunity or chance to express genetic potential under better environmental conditions; hence the genetic variability was higher.

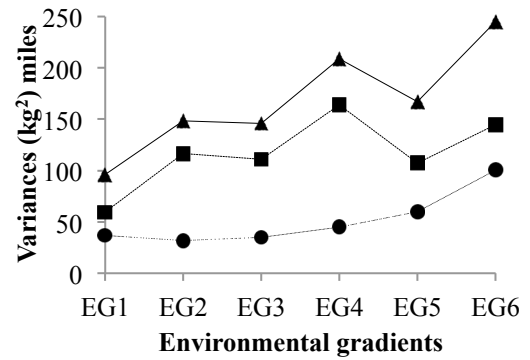


Figure 1: Estimates of additive variance (●), residual (■) and phenotypic (▲) means of MY270 environmental gradients (EG1-EG6).

The phenotypic and residual variances were higher, but displayed the same trend as the genetic variance (figure 1). In dairy cattle, the NxR displayed different phenotypic response in extreme EG, obtaining a response to the scale effect explained by the own effects of each environment (Calus and Veerkamp, (2003); Fikse et al. (2003); Kolmodin et al. (2002)).

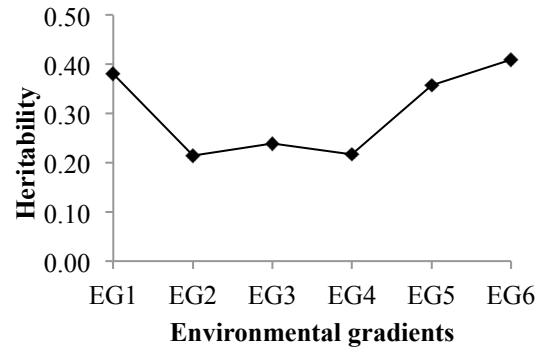


Figure 2: Estimates of heritability of MY270 environmental gradients (EG1-EG6).

The heritabilities ranged from 0.20 to 0.41 (Figure 2). In simulation studies of Su et al. (2006) using bayesian estimators in RxN, heritability trends were similar to those obtained in this study. In buffalo populations the heritabilities for MY270 ranged from 0.14 to 0.20 (Tonhati et al. (2004); Hurtado-Lugo et al. (2011)). Calus et al. (2002) and Kolmodin et al. (2002) reported that in univariate RRM the heritabilities tend to increase as the production level increases, in accordance with that observed in this study. Calus et al. (2002) suggest that the presence of Gx \times E is consequence of the heterogeneity of variances in the environments. It can be observed phenotypic and genetic variations along the EGs, followed by heritability variations, indicating that the genetic component contribution of total variability was considerably over the EGs. Considering that higher heritability estimates were obtained in the environment with low (EG1) and high yield (EG6), environmental conditions in these localities are expected to favor MY270

expression. Although, it would be necessary to consider that the heritability is a population and environment property to which animals are subjected, and that the high heritability in EG1 and EG6 could be associated with environmental uniformities which would lead to increased heritability (Robertson, (1959)).

The estimates of genetic correlation (G_c) to MY270 (Table 2) between different EGs were higher as EGs were closer or similar. Based on the suggestions made by Robertson, (1959) presented GxE between EG with different yields per farm and year of calving. However, similar or close EG did not present GxE (Table 2). It is considered that genes that act in EG1 and EG6 to MY270 are different and phenotypic expression is expected to be different.

Table 2: Genetic correlations of environmental gradients (EG1-EG6) for MY270

	EG1	EG2	EG3	EG4	EG5
EG2	0.86				
EG3	0.75	0.98			
EG4	0.55	0.90	0.97		
EG5	0.40	0.81	0.91	0.99	
EG6	0.20	0.67	0.80	0.93	0.98

One possible explanation is the fact that the data were collected in the farms. Kearney et al. (2004) and Haile-Mariam et al. (2008) suggest that the way husbandry data are collected can lead to considerable heterogenic variances due to specific herd conditions. It should also be considered that in tropical countries there are several strategies to maximize phenotypic and genetic adaptation, as well as animal use in several Agro-Environmental systems (Haile-Mariam et al. (2008); Stinchcombe and Kirkpatrick, (2012); Burrow, (2012)). Although these husbandry practices might not be the most appropriate, in general, they are the most feasible given the system conditions. Milking management gets considerably more complicated during heavy winters (flooding) and summer (drought, discard due to low production) under more intense conditions.

Moreover, the G_c results could possibly be explained as a consequence of environmental adaptation genes (roughness/hardiness) or feeding efficiency (feed conversion rate) which would be triggered under the EG specific conditions. Therefore, as a result of such biological facts, the low G_c between extreme EG indicate that different genes would be acting on the traits of interest. Although it should be remembered that the relationship between biological dynamics may be highly complex as in the case of feeding intake regulation, metabolic routes or genetic architecture (Moczek et al. (2011); Pavlicev and Wagner, (2012)).

Conclusion

The modeling of the reaction norm estimated by using bayesian approaches properly estimated the population parameters according to the expected values for species. Based on the criteria used to define the environmental gradient, it can be noted the presence of genotype-environment interaction for milk yield at 270 days of lactation. Therefore, it can be said that it is necessary to consider or take into account the environmental sensitivity of the genotypes in the selection of the breeding for the next generation to MY270.

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