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Genotype-environment interaction of maternal influence characteristics in Nellore cattle bred in the Brazilian humid tropical regions by reaction norm

Interação genótipo-ambiente de características sob efeito maternal em bovinos Nelore criados no trópico úmido do Brasil por meio de norma de reação

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Abstract

Reaction Norm (RN) is the study of genotype-environment interaction (GxE) that complies with alternative ways of genotypes within different environments. This study was carried out to verify GxE by a reaction norm model of weights at 120 (W120) and 210 (W210) days of age in Nellore cattle raised in the Humid Tropical Regions of Brazil. Environmental gradients were obtained by solutions of contemporary groups which were fitted as co-variables in the random regression model via reaction norms. Mean weight at 120 days of age was 127.97 kg, and environmental gradients ranged between -27 and +26 kg. Average was 185.60 kg at 210 days of age and gradients ranged from -54 to +55 kg. Scale changes in the breeding values and heritability estimates occurred along the gradients for the two weights; the genetic correlations between breeding value breeding values were also similar for both weights. These correlations were high between the close gradients, and low to even negative between extreme environments. Slopes representing the environmental sensitivity were high, with changes of scale and changes in classification of ten bulls with a great numbers of calves for the two traits. When regression slopes of the ten bulls with the highest breeding value breeding values were evaluated, these values were different in W120 from those in W210, perhaps due to the greater influence of maternal effect on W120. These results characterize the influence of GxE on the pre-weaning weights of animals in the humid tropical regions of Brazil. Due to this, it is possible to get greater precision on the predictions of the animals breeding values breeding value. A less biased selection and a greater genetic progress occurred.
Key words: Animal genetic improvement; heritability; zebu cattle

Resumo

Norma de reação (NR) é um estudo de interação genótipo ambiente (IGA) que observa as vias alternativas dos genótipos em diferentes ambientes. Objetivou-se com este trabalho verificar a IGA

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via modelo de norma de reação dos pesos calculados aos 120 (P120) e 210 (P210) dias de idade em bovinos da raça Nelore criados na região do Trópico Úmido do Brasil. As gradientes ambientais foram obtidas por meio das soluções dos grupos de contemporâneos, que serviram de covariáveis no modelo de regressão aleatória via NR. A média para peso aos 120 dias de idade P120 foi de 127,97 Kg, as gradientes ambientais variaram de -27 a +26 kg. Para peso aos 210 dias de idade a média foi de 185,60 Kg, e as gradientes variaram de -54 a +55 kg. Houve alterações de escala dos valores genéticos e das estimativas de herdabilidades entre as gradientes para ambos os pesos, as correlações genéticas entre os valores genéticos foram similares para os dois pesos, as quais apresentaram-se elevadas entre os gradientes próximos e baixas e até negativas entre ambientes extremos. As inclinações que representam a sensibilidade ambiental foram altas, havendo alterações de escala e de classificação dos dez touros com maior número de filhos para ambas as características. Ao avaliar as inclinações das regressões dos dez touros com maiores valores genéticos, observou-se que para P120, estas diferiram das inclinações dos P210, o que pode ser justificado pela maior influência do efeito maternal sobre P120. Os resultados permitiram caracterizar influência da IGA sobre os pesos pré-desmame de animais no trópico úmido do Brasil, assim como permitiu a obtenção de maior precisão sobre as predições dos valores genéticos dos animais, o que resultou em seleção menos viesada e com maior progresso genético.
Palavras-chave: Herdabilidade, melhoramento genético animal, Zebu

Introduction

Cattle breeding systems in Brazil are very heterogeneous and are mainly related to climate, environmental, soil and sociocultural diversity. Diversification implies different circumstances for genotype expression affecting the environment so that it modifies the extension by which the genotype is expressed. Therefore, there is always the possibility that the best genotype in a certain environment fails in a different one (WARWICK; LEGATES, 1980). Knowledge of genetics and the environment is basic for the development and productivity of beef cattle systems since the genotype-environment interaction (GxE) may bring liabilities to the genetic progress of beef cattle populations when there is the inadequate use of breeds.

GxE features the differentiated response of genotypes to environmental variations (FALCONER; MACKAY, 1996). It is actually a constant challenge for cattle breeders to model or control the effects of the environment on animal breeding since GxE makes difficult the selection and the recommendation of the non-assessed use of genotypes in specific environments. However, GxE inclusion in genetic analyses is, as a rule, highly polemic since the economical niches and cattle selection in Brazil have been developed in different environments. Several methods have been reported for GxE analyses. Studies on reaction norm (RN) models have recently been in the limelight. It is a model that describes the phenotype expressed by a genotype within an environmental gradient. It is useful when phenotypes vary gradually and continually in different environments (DE JONG, 1995).

The environments in Reaction Norms are not merely places where animals are raised, but also comprise temperature, latitude, longitude, feeding, or rather, every factor that may bring about variations in production (AMBROSINI et al., 2012). Linear RN is a co-variance function that attributes to each animal two randomized coefficients of regression (intercept and inclination) to predict the breeding values according to the environment. Each animal has a breeding value breeding value for each environment which may characterize the genotype-environment interaction (GxE) according to slopes. Recent studies on the environmental sensitiveness of cattle in Brazil through RNs have been provided by several researchers, especially Pégolo (2009) for Nellore cattle; Cardoso et al. (2005, 2007) for Angus breeds; Cardoso et al. (2011) for Hereford cattle; Corrêa (2009) for Devon breed; Mattar et al. (2007, 2011) respectively for Caracu and Canchim breeds.

Therefore, RN studies are helpful to identify herds with variability for environmental sensitiveness and, consequently, include adaptive variations in genetic assessments to uniform the prediction of breeding values that have differentiated performances in different environments or privilege genotypes with responses to specific environmental improvements. Studies on the effect of the interaction between genotype and environment in the Brazilian tropical humid environment are rare. Current assay investigates the genotype-environment interaction through the Reaction Norm methodology on weights at 120 and 210 days of age of Nellore cattle in the tropical humid regions of Brazil.

Materials and Methods

Weight records of Nellore cattle, born between 1993 and 2010, which participate in the Genetic Improvement Program of the Nellore Breed (PMGRN) of the National Association of Breeders and Researchers (ANCP) in the Brazilian states of Maranhão, Mato Grosso, Pará, Rondônia and Tocantins, were used. The traits used were weights at 120 (W120) and 210 (W210) days of age.

349 contemporary groups (CG) were formed by animal groupings according to cattle farm, management group and sex. Connection among the CGs was provided by software AMC (ROSO; SCHENKEL, 2006). CGs with less than 10 genetic bonds, less than four animals and bulls with less than three offspring were eliminated. After exclusions, there remained 50,997 weight registers for cattle at 120 days of age and 51,300 weight registers for cattle at 210 days of age.

A first analysis of data was run using Wombat program (MEYER, 2007), in a uni-trait investigation, taking into consideration the entire animal model so that solutions for contemporary groups could be generated. The mathematical model was the following:

$$y = X\beta + Z_1a + Z_2m + Z_3mpe + Z_4cg + \varepsilon$$

where: y = vector of observations (W120 and W210); β = vector of fixed effects (age of the cow at calving as co-variable of the linear and quadratic effects); cg = random effect of the contemporary group (SCHAEFFER, 2009); a = vector of the direct additive genetic effect; m = vector of the maternal additive genetic effect; mpe = vector of the effect of the maternal permanent environment; X = occurrence matrix that associates β with y; Z_1, Z_2 and Z_3 and Z_4 = occurrence matrixes of direct genetic effects, maternal and effect of the maternal permanent environment and contemporary groups, respectively; ε = vector of residual effects, N~(0,σ²).

Solutions of contemporary groups, obtained in the first analysis were used in a second round for analyses by Reaction Norm. Solutions were standardized by taking into consideration the total number of CGs solutions. Henceforth mean, minimum and maximum rates of environmental gradients were calculated. Further, analyses of random regression were performed with the co-variables age of dam at calving (linear and quadratic effects) and standardized environmental gradient (CG solution); the direct additive genetic effect, maternal and maternal permanent environment of the animal and dam were considered randomized effect. The model comprised the heterogeneity of the four classes of residual variances: 1-13, 14-27, 28-41 and 32-64 for W120 and 1-27, 28-54, 55-79 and 80-110 for W210. The randomized regression model used to model the effects of the RN was:

$$y_{ij} = EF + \sum_{m=0}^{k_b-1} b_m \phi_m(t_i) + \sum_{m=0}^{k_A-1} \alpha_{jm}\, \phi_m(t_{ij}) + \sum_{m=0}^{k_M-1} \gamma_{jm}\, \phi(t_{ij}) + \sum_{m=0}^{K_C-1} \delta_{jm}\, \phi_m(t_{ij}) + \sum_{m=0}^{K_Q-1} \rho_{jm}\, \phi(t_{ij}) + e_{ij}$$

where, y_{ij} = i-th measure of the j-th animal (W120 and W P210); EF = set of fixed effect (age of cow at birth as co-variable of linear and quadratic effect); b_m = fixed regression coefficient to model mean curve of the population; $\phi_m(t_i)$ = function of Legendre´s polynomial regression that describes the mean curve of the population according to the environmental gradient; $\phi_m(t_i)$ = function of Legendre polynomial regression that describes the curves of each animal *j*, according to the environmental gradient (t_i), for randomized direct additive genetic effect and maternal, permanent environment of the animal and dam; α_{jm}, γ_{jm}, δ_{jm}, ρ_{jm} = regression coefficients direct additive genetic effect and maternal and permanent environment of animal and dam, respectively for each animal; k_b, k_A, k_M, K_C and K_Q = order of Legendre´s polynomials of effects included in the model; e_{ij} = random error, N~(0,σ²) associated to each environmental gradient *i* of animal *j*.

The components of co-variances were estimated by restricted maximum likelihood using WOMBAT software (MEYER, 2007). Legendre´s orthogonal polynomials were fitted using model direct additive genetic and maternal effects and effects of permanent environment of animal and dam. The components of additive genetic variance and direct heritability will be given by regression quadratic models of estimates of the components according to the environmental gradient. Correlation matrix for W120 and W210 will be given by graphs representing the response surface of correlation estimates according to the environmental gradients.

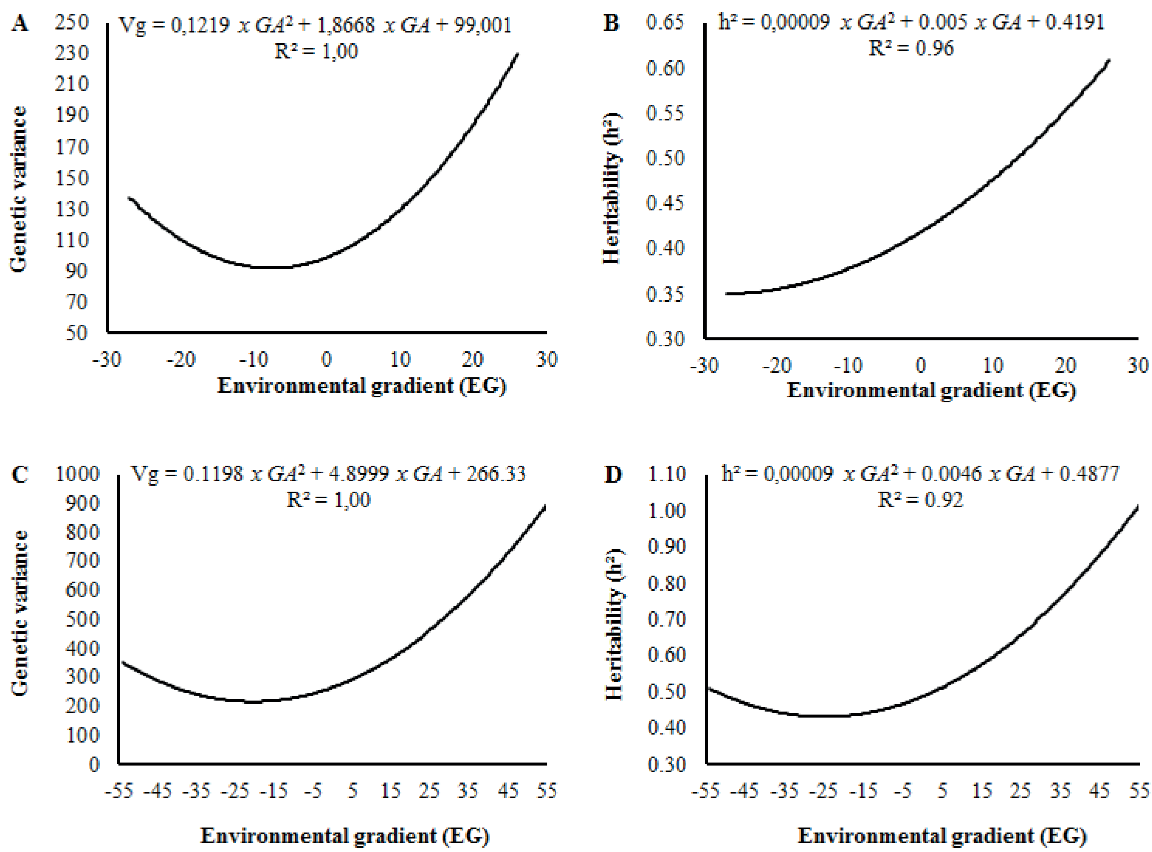
Results and Discussion

Means and standard deviations for weights at 120 and 210 days of age were 127.97±19.63 and 185.60±28.56 kg, respectively. Similar results were given by Lira et al. (2013) in studies on genetic trends in the Brazilian Tropical Humid Region, and Matos et al. (2013) and Nepomuceno et al. (2013) studying GxE using multi-trait model.

There was an increase in estimates of direct additive genetic variance and direct heritability for W120 (respectively Figures 1 A and B) along to environmental gradients. Higher rates were reported in more favorable conditions and showed there were changes in genetic parameters according to the environment, evidenced by the scale effect, which characterizes GxE. Therefore, the best response to the selection for this tratis was also dependent on the environments to which the animals were submitted. The scale effect may be observed throughout all the environmental gradients, with different increase of the breeding values as the environment improved. Kolmodin et al. (2002) showed through RN a scale effect for the production of protein in dairy cows from Northern Europe.

The variations of estimates of direct genetic heritability for W120 (between 0.30 and 0.70) were higher than those reported by Ambrosini et al. (2012) for weight at 205 days of age (0.35±0.03) in Polled Nellore cattle in southern Bahia, Brazil. Nepomuceno et al. (2013) provided lower results (0.34 and 0.18, respectively) for W120 in Nellore cattle in the states of Mato Grosso and Pará, Brazil, using animal model. Standardized solutions of environmental gradients varied between -27 and +26 kg for W120, and between -54 and +55 kg for W210, and characterized environment with low to high management levels. Therefore, variations of estimates of direct additive genetic variances demonstrate dependence on gradient and, consequently, genotype-environment interaction.

Figure 1. Trend of estimates of additive genetic variances (A and C) and direct heritability (B and D) for W120 and W210 of Nellore cattle raise in the Tropical Humid regions of Brazil.



Trends in the estimates of direct genetic variance and direct heritability for W210 were similar to trends of W120 (respectively Figures 1C and D). In other words, higher estimates were proportional to increase or improvement in the environmental gradient. The variability of direct heritability estimates between the worst and the best environmental gradient was high. Since it varied between 0.54 for the less favorable environment and 0.85 for the most favorable, the selection pressure for this trait was great in some herds in the Brazilian Tropical Humid Regions.

In their research with GxE in animal models, Nepomuceno et al. (2013) provided lower weights for Nellore cattle at 210 days in the Brazilian states of Maranhão, Mato Grosso and Pará. These results were higher than those registered by Matos et al. (2013) in the Brazilian Amazon region, and by Ambrosini et al. (2012) in their GxE analysis under RN in Polled Nellore cattle in northeastern Brazil.

Phenotype variance provided a similar behavior for direct genetic additive variance, with higher rates at the extremes of the environmental groups and lower ones at intermediate environments. When each environmental group is analyzed, it may be perceived that the extreme environments were composed by extreme environmental factors, favorable at the extreme right and unfavorable at the extreme left of the environment.

One should underscore that only the direct additive genetic effect has a Reaction Norm, whereas maternal effect and effect of maternal permanent environment do not follow the RN model. Estimates of maternal genetic variance were equal for all levels of environmental gradients, with alterations only in the estimates of heritability that depend on the rates of direct variances and phenotypes, which differ from the gradients.

Maternal heritability for W120 (between 0.05 and 0.03) and W210 (between 0.04 and 0.02) were low. In their study of GxE via animal model, Nepomuceno et al. (2013) reported higher maternal heritability estimates, ranging between 0.12 and 0.19 (W120) and between 0.13 and 0.16 (W210), respectively for the states of Mato Grosso and Pará. Ambrosini et al. (2012) in their analysis on GxE via animal model in Polled Nellore cattle in northeastern Brazil registered maternal heritability estimates (W205) of 0.11±0.02.

Since the genotype x environment interaction presupposes a difference in environmental sensitiveness of the evaluated animals due to environmental gradients, the greatness of the components of (co)variance attributed to the coefficients of regression of the model is relevant to evaluate the effect of the interaction between the genotype and the environment. Current study shows that the correlation estimates between intercept and the slope level of regression are significant (0.72), which indicates genetic variability throughout the environmental gradient. In other words, the classification of animals changed according to GxE variation. Figure 3 also indicates this fact since it presents the response surface of the correlation matrix among the breeding values of the evaluated animals.

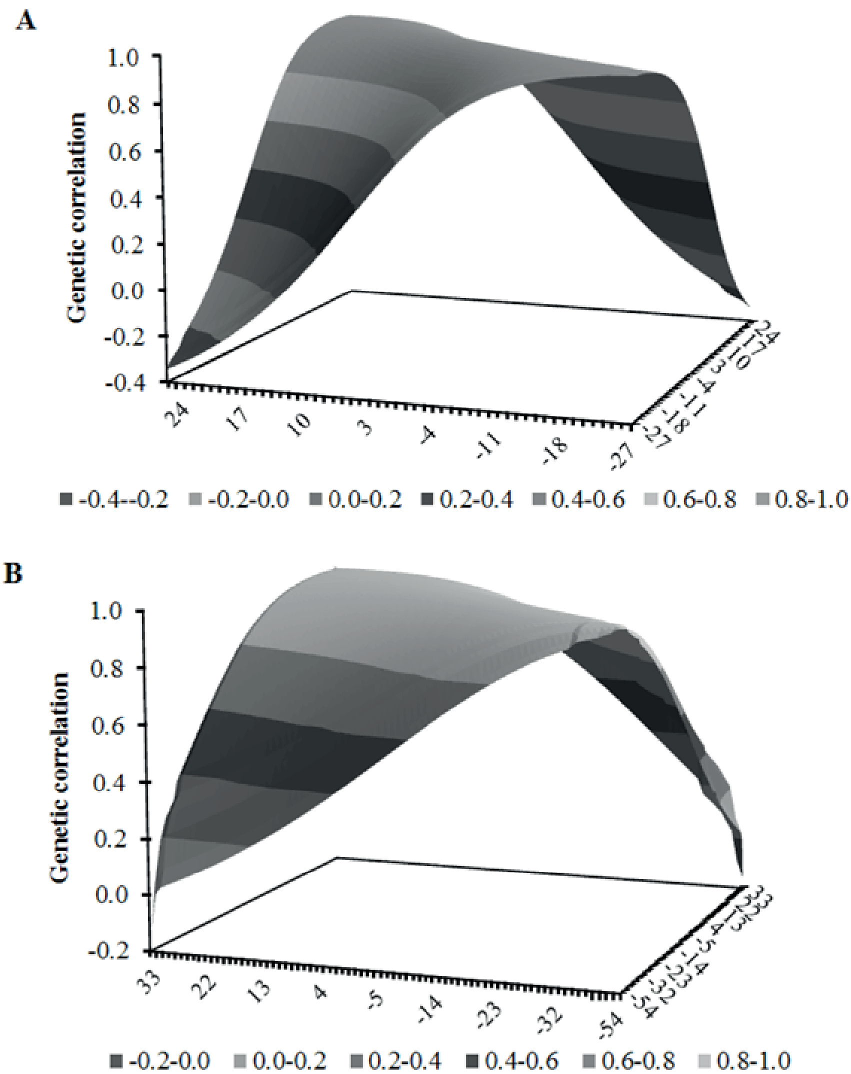
The high rates of this correlation presuppose heterogeneity of sensitiveness, or rather, reaction norms with different slopes. Similar situations show modifications of genetic variance or in the classification of the different environments analyzed. On the other hand, low rates presuppose almost parallel reaction norms to the axes of the environments, without modifications of additive genetic variance and classification order at different points in the interval. Linear regression coefficient, which represents the greatness of the RN slope, is obtained in RN models with randomized regression. According to Ambrosini et al. (2012), higher rates of linear regression rates mean higher slopes and thus greater environmental sensitiveness.

Estimates of genetic co-variances and genetic correlations showed the effect of GxE for W120 and W210, due to the environmental gradients, with antagonism between the extreme environments (Figures 2 A and B). The saddle shape is a graphic configuration of the correlation matrix between the breeding values of the animals, spaced due to the environmental gradients. In other words, it presents a symmetric shape since the correlation matrix is both square and symmetric. The higher section is the diagonal of the correlation matrix whose rates are equal to 1; decline from the center to the extremities shows that, as the environmental gradients become more and more distant, the estimates of correlations become smaller and, between extremes, antagonistic.

In a RN model with linear random regression, the presupposition is that RN is linear. In other words, animals respond linearly to a continuous environmental gradient. According to Valente (2007), two coefficients of randomized regression (intercept and slop) are attributed to each animal under analysis, which is used to predict the breeding value in accordance to the quality of environment. Higher coefficients of linear regression mean greater sensitiveness to environmental changes.

In the case of W120, animals shown slopes between -7.5 and 3.98, whereas in the case of W210, there were slopes between -7.93 and 23.7, with relatively high positive rates. The above reveals that the bulls have greater differences between the environments (Figure 3). Similar results were provided by Mattar et al. (2011) on Canchim cattle; Cardoso and Tempelman (2012) on Angus strain in southern Brazil and Rodrigues (2012) on Polled Nellore cattle in northeastern Brazil.

Figure 2. Response surfaces of the correlation matrix between the breeding values along to environmental gradients for W120 (**A**) and W210 (**B**).

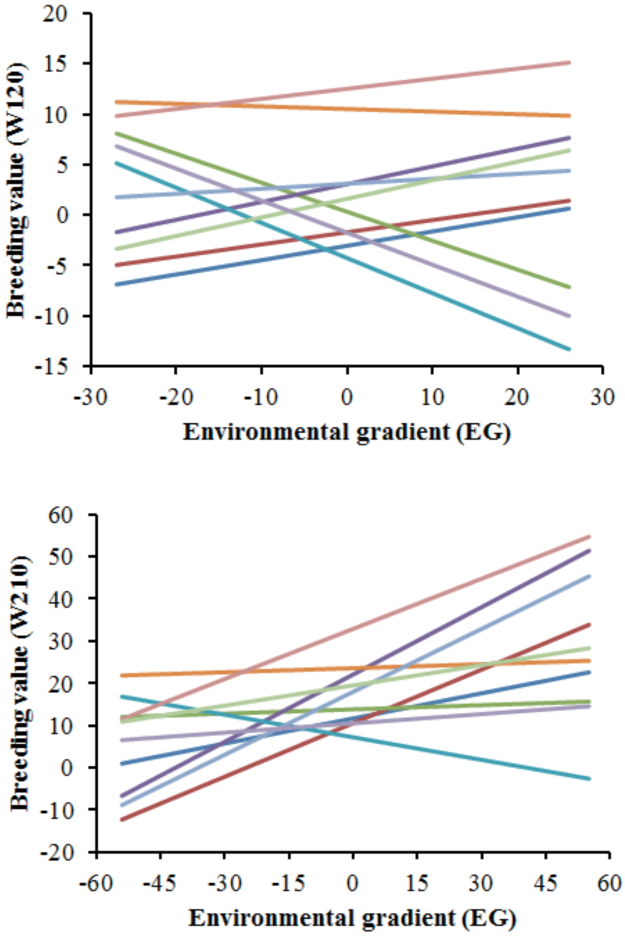


According to several authors (JONG; BIJMA, 2002; KOLMODIN, 2003; BIJMA, 2004; MATTAR et al., 2011), there is an ideal environment to obtain a greater selection response since the slope level of the RN should be maintained so that plastic genotypes could be selected in environments that would provide a better response.

When the breeding values of the ten best bulls are analyzed, the slopes for W120 vary between -39.29 and -21.62, and reveal the genotype - environment interaction (Figure 4) mainly represented by the decrease of breeding values as improvement in the environment increased, with changes in animal classification observed by variations of the animals´ breeding values due to environmental gradients.

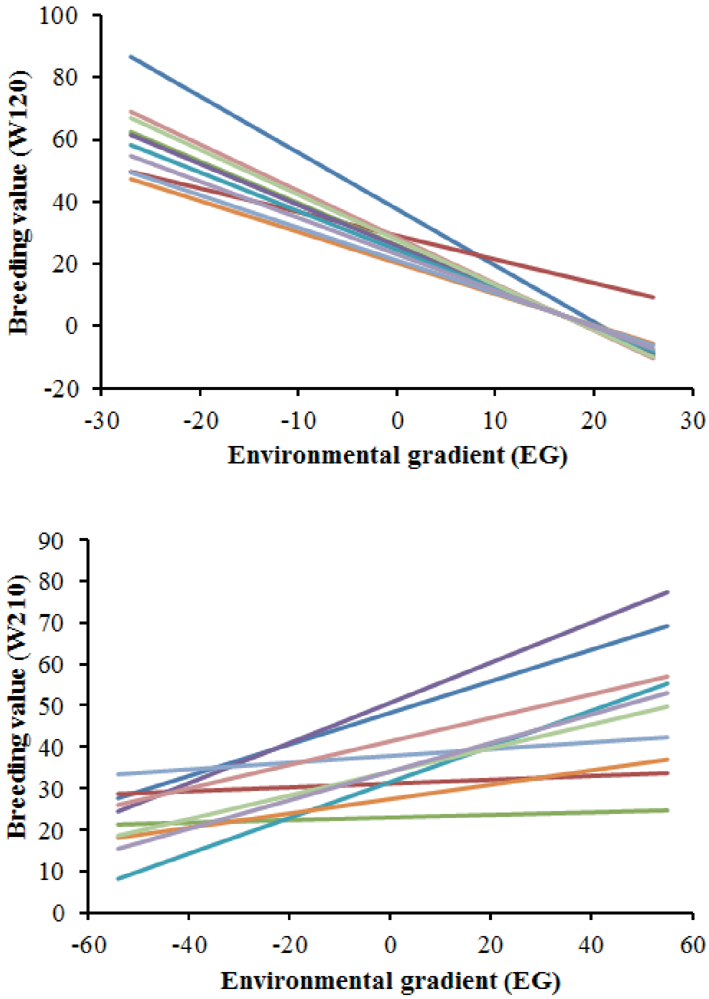
In the case of W210, the ten animals with the highest breeding values had positive slopes, varying between 1.39 and 21.59, and also showed GxE (Figure 4). When both traits are compared, a discrepancy may be noted with regard to change in animal classification and the greatness of degrees of the slope, due to a greater influence of maternal effect and of maternal permanent environment on the weight at 120 days of age, with a lower impact on the bull´s reclassification. Although the maternal effect of weight at 210 days is substantially lower than that for W120, the effect of the genotype and environment interaction was more evident for W210. Consequently, the effect of GxE should be included in the animals´ genetic evaluations to have more precise prediction of the breeding values for the animals under selection.

Figure 3. Reaction Norm of breeding values of ten bulls with the greatest number of young, according to environmental gradient for W120 and W210.



RN models for the analysis of the genotype and environment interaction presupposes that the environment may be classified on any scale and that the traits have a physiological continuity on the environment (JONG; BIJMA, 2002), distinguishing the capacity of the genotypes in being more or less sensitive to environmental changes. When current analysis takes into account the animals with greater representativeness within a set of data, or rather, ten bulls with a great number of young, there was a change in their genetic classification in weight at 120 and 210 days of age, following changes in the environmental gradient (Figure 4).

Figure 4. Reaction Norm of breeding values of 10 best bulls according to the environmental gradient for W120 and W210.



Conclusions

The genotype-environment interaction using reaction norm models occurred for weights calculated at 120 and 210 days of age in Nellore Cattle in the Tropical Humid regions of Brazil. Estimates of heritability coefficients for W120 and W210 varied according to an environmental gradient which resulted, which can result in selection response dependent on environmental gradient.

Animal evaluation with regard to environmental sensitiveness should be included to prediction of breeding values, because it is an important tool capable of distinguishing genotypes susceptible to changes in their expression and consequently in the animals´ performance, in accordance to environmental level. Animal breeding programs should take into account the interaction between genotype and environment to improve both the predictions of breeding values of animals and the genetic progress livestock production system.

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