

GENOTYPE-ENVIRONMENT INTERACTIONS ON THE WEIGHT OF TABAPUA CATTLE IN THE NORTHEAST OF BRAZIL¹

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ABSTRACT – The objective of this work was to verify the presence of genotype-environment interactions (GEI) on the weight adjusted to 365 days of age (W365) for Tabapua cattle in the Northeast of Brazil, using reaction norm (RN) models. The reaction norm model with homogeneous residual variance and 1-step provided the best fit to the data by the criteria information of deviance, deviance based on the conditional predictive ordinate and deviance based on the Bayes factors. Direct and maternal heritability estimates for the animal model were 0.17 ± 0.04 and 0.07 ± 0.03 , respectively. The direct heritability for model reaction norm in the low and high management environment were 0.21 ± 0.06 and 0.70 ± 0.04 , respectively. The correlations between the slope and intercept of the reaction norm were 0.68 ± 0.10 and 0.96 ± 0.06 for the direct and maternal effect, indicating that the animals with high genetic values respond positively to environment improvements, especially for the maternal effect. The Spearman correlations between the sire classifications ranged from 0.14 to 0.94 in the different environments and models. Genetic values of most animals were robust to environmental variation, however, considering the sires with the highest number of progeny, there is the presence of GEI.

Key words: Environmental gradient. Reaction norms. Random regression. Zebu.

INTERAÇÕES GENÓTIPOS AMBIENTES NO PESO AO ANO DE BOVINOS TABAPUÃ NA REGIÃO NORDESTE DO BRASIL

RESUMO – Objetivou-se verificar a presença das interações genótipos ambientes (IGA) para o peso ajustado aos 365 dias de idade (P365) na raça Tabapuã na região Nordeste do Brasil usando modelos de normas de reação (NR). O modelo normas de reação com variância residual homogênea e um passo proporcionou melhor ajuste aos dados pelos critérios de informação da *deviance*, *deviance* baseada na ordenada preditiva condicional e da *deviance* baseada nos fatores de Bayes. As estimativas de herdabilidade direta e materna, para o modelo animal, foram $0,17 \pm 0,04$ e $0,07 \pm 0,03$, respectivamente. As herdabilidades diretas para modelo normas de reação no ambiente de baixo e alto manejo foram de $0,21 \pm 0,06$ e $0,70 \pm 0,04$, respectivamente. As correlações entre a inclinação e o intercepto da norma de reação foram de $0,68 \pm 0,10$ e $0,96 \pm 0,06$, para o efeito direto e materno, indicando que os animais com maiores valores genéticos respondem positivamente à melhoria do ambiente, especialmente para o efeito materno. As correlações de *Spearman* entre as classificações dos reprodutores variaram de 0,14 a 0,94 nos diferentes ambientes e modelos. Os valores genéticos da maioria dos animais apresentam-se robustos à variação ambiental, no entanto quando considera os reprodutores com maior número de filhos, verifica-se a presença de IGA.

Palavras-chave: Gradiente ambiental. Normas de reação. Regressão aleatória. Zebuínos.

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INTRODUCTION

In Brazil, cattle production systems are very heterogeneous due to the large biomes diversity, which is a challenge to the effective definition of selection criteria to assist in the choice of suitable sires to each production system, especially when the genetic evaluation of the herd is carried nationally (NEPOMUCENO et al., 2013).

The genetic merit of an animal can be significantly influenced by changes in the breeding environment, and the progenies of a sire may not repeat the performance of their progenitors if they are raised in a different micro-regions or farms, denoting the need for care when buying sires or semen due to the presence of genotype-environment interactions (GEI). (NOBRE et al., 1987).

GEI exist when the relative merit of two or more genotypes is dependent on the environments in which they are compared (MASCIOLI et al., 2006). According to Streit et al. (2012), if the GEI is disregarded, the predicted genetic values may be biased and the response to selection reduced.

The use of a multi-character approach is a logical choice if the environment may be considered as a distinct variable, however, the use of reaction norms may be more suitable if the environment changes gradually and can be measured on a continuous scale. Thus, there are less parameters to be estimated and there is no need for grouping individuals into different classes (STREIT et al., 2012).

Several authors (AMBROSINI et al., 2012; CARDOSO et al., 2007; CARDOSO; TEMPELMAN, 2012; CORRÊA et al., 2007, 2009; MATTAR et al., 2011; PEGOLO et al., 2011; RODRIGUES 2012; RODRIGUES, 2014; STREIT et al., 2012) have studied GEI through reaction norms (RN). However, there are no studies evaluating this interaction on animals from the Tabapua breed in the Northeast of Brazil, and mainly, including the maternal effect in the valuation model for weight at 365 days of age.

The maternal environment influences the growth of the calf in the pre-birth and post-birth phases, in which the maternal influence can affect the weight of the calf up over one year of age. Biffani et al. (1999) found maternal influence on the weights of calves up to one year of age, and Meyer et al. (1993) found maternal additive genetic effect for weights up to 550 days of age.

Thus, the objective of this work was to verify if there are genotype-environment interactions on the weight fit to 365 days, in animals from the Tabapua breed raised in the Northeast of Brazil, seeking the model that best fits the data of the Tabapua cattle population through reaction norms via Bayesian approach.

MATERIAL AND METHODS

Records from the Brazilian Association of Zebu Breeders (ABCZ) on the Tabapua breed animals, born between 1975 and 2007 in the Northeast of Brazil, were used. The initial database on weight adjusted to 365 days of age had 26,838 entries, from which 19,078 were excluded (12,136 animals with no weight records; 192 disconnected; 266 with measures beyond the established range from 125 kg to 385 kg; 265 cows under 1.9 and more than 25 years of age; 194 sires under 3 progenies; 3,618 cows under 2 progenies; and 2,407 animals contained in contemporary groups, with less than four observations and average weight above and below +2.5 the standard deviations. Thus, 7,760 records were used for the analyzes.

Contemporary groups (CG) were formed to group animals that had an equivalent production environment, including herd, year, birth season, food regime and gender. Three seasons of birth were used, grouping four months each (season 1: July to October, season 2: November to February, and season 3: March to June). The environmental gradient was set in three classes based on the standardized mean and deviations around that mean: standard deviation of -2.17 (-67), zero e standard deviation of +3.66 (113).

The data set was prepared for reaction norm analysis using routines developed by Cardoso et al. (2008) in SAS language (SAS, 2003). The connection of CG was tested, based on the total number of genetic ties (minimum of 10) using the AMC program (ROSO; SCHENKEL, 2006). The reading of the output of the AMC program and the preparation of the pedigree and data files, consisting only of connected CG were performed. The connectivity of CG resulted in a main archipelago (CG with more genetic ties and all CG connected to it) with 7,760 animals in 748 CG and 192 animals in 89 CG disconnected. Only data animal from the main archipelago were used.

The INTERGEN program by Cardoso et al. (2008) was used with a standard animal model (AM), this model ignores the GEI and predicts the animal genetic value, and obtain the average estimates of environmental effects based on the CG, which fits as comparison basis for the analysis of reaction norm models.

The Bayes hierarchical models were adjusted using the INTERGEN program with parameters set at structured levels or stages. In the reaction norm models, the genetic value of the animal was found through a function of the medium environmental level related to the CG solution to which the record belongs. A specific genetic value of each animal was

$$y_{ij} = \mathbf{x}_i'\boldsymbol{\beta} + X_j + a_i + m_i + e_{pi} + e_{ij} \quad (1)$$

predicted for each environmental level according to Cardoso and Tempelman (2012).

Initially, a standard animal model (AM) were used:

In which: y_{ij} = animal record (i) in the environment (j); β = vector of the fixed effects (linear e quadratic to the cow age); x_i' = incidence vector; X_j = random environmental effect of CG; a_i = animal additive genetic value (i); m_i = animal maternal genetic value (i); ep_i = maternal permanent environmental effect, and e_{ij} = random error.

A methodology used to describe the hierarchical reaction norm model (HRNM) was the presupposition of Su et al. (2006), called hierarchical reaction norm model 1-step (HRNM_{1S}), which has simultaneous estimation for CG solutions and the reaction norm (RN) intercept and slope. In this model, the CG effects are considered unknown co-variables in the RN models, in which the environmental effects estimates were used as a co-variable to obtain the slope of the RN of the animals,

$$y_{ij} = \mathbf{x}_i' \boldsymbol{\beta} + X_j + a_i + m_i + ep_i + b_{1i} X_j + b_{2i} X_j + e_{ij} \quad (2)$$

in which X_j and b_i are together estimated as in the model:

Two different presuppositions were used for the residual variance in the models: (a) homoscedasticity for the AM, HRNM_{1S} (HRNMHO_{1S}), with $e_i \sim N(0, \sigma^2_e)$ = residual variance; e (b) heteroscedasticity for the models HRNM_{1S} (HRNMHE_{1S}), com $e_i \sim N(0, \sigma^2_{eij})$.

The environmental direct additive and

$$\sigma_{A|X}^2 = \text{var}(a_i + b_{1i} X_j) = \sigma_a^2 + \sigma_{b1}^2 X^2 + 2\sigma_{a,b} X$$

$$\sigma_{M|X}^2 = \text{var}(a_i + b_{2i} X_j) = \sigma_m^2 + \sigma_{b2}^2 X^2 + 2\sigma_{a,b} X$$

maternal genetic variances X, $\sigma_{A|X}^2$ e $\sigma_{M|X}^2$, were found through:

In which: $\sigma_a^2 = \sigma_a^2|X$ = direct genetic variance component estimates for the intercept of the RN, $\sigma_m^2 = \sigma_m^2|X$ = maternal genetic variance component estimates for the intercept of the RN, $\sigma_b^2 = \sigma_b^2|X$ = variance component estimates for slope of the additive RN, for slope of the RN of the animal maternal effects, and $\sigma_{a,b}$ = co-variance component estimates between the intercept and slope.

$$h_a^2|X = \frac{\sigma_a^2|X}{\sigma_a^2|X + \sigma_m^2|X + \sigma_{pe}^2 + e_e^2|X}$$

$$h_m^2|X = \frac{\sigma_m^2|X}{\sigma_a^2|X + \sigma_m^2|X + \sigma_{pe}^2 + e_e^2|X}$$

The heritability was estimated through the ratio between the genetic variance and phenotypic variance (genetic + environmental):

In which: $\sigma_e^2|X$ = residual variance in the environment X, obtained by $\sigma_e^2|X = \sigma_e^2 \eta^X$ in the heteroscedastic model, and σ_e^2 in the homoscedastic model, in which η is the heterogeneity parameter variance in the environmental gradient (X), following the model structure proposed by Cardoso et al. (2005).

A Bayesian approach (GIANOLA; FERNANDO, 1986) was used to find the parameter estimates, through the Markov Chain Monte Carlo (MCMC) (Blasco, 2001), adapting the following procedure: a) A sample pilot was used with 55,000 cycles, 5,500 for discarding (burn-in) and 5 for the saving interval (thinning); b) using the variance components saved in a) and the Bayesian Output Analysis packet (BOA) from the R program (SMITH, 2007), the Raftery and Lewis (1992) test was applied to assess the new size of the chain and the saving period (thinning); and c) discarding period (burn-in) was evaluated under the criteria of Heidelberger and Welch (1983).

Analyses were performed with the chains that ranged from 330,000 to 440,000 cycles. Means, standard deviations and percentiles (0.025 and 0.975) *a posteriori* of the parameters were obtained from their marginal posterior densities by the KDE Procedure (Kernel Density Estimation) of SAS (SAS, 2003).

The convergence analysis of the chains for the different models was performed using the diagnostic of Geweke (1992), based on Z test for equal means of the logarithm of the conditional distribution of the data, denoted by $l_i^{(j)} = \log p(y|\theta^{(j)}, M_j)$ of the first samples (10% initial) and the last part of the Markov chain (last 50%), similar to that proposed by Brooks and Roberts (1998).

The Spearman correlation was calculated to compare the classification of sires in the animal model (AM) and the hierarchical reaction norm model homoscedastic 1-step (HRNMHO_{1S}) according to the environmental gradient. The values were adjusted with mean zero, so zero represents the environment (medium level), with the minimum and maximum amplitudes representing the environmental levels from low to high management in the environmental gradient, respectively.

The following criteria were used to assess the best fit to the model: Deviance Information Criterion (DIC) (SPIEGELHALTER et al., 2002); Deviance based on conditional predictive ordinate (CPO), as described by Gelfand (1996); and deviance criteria based on Bayes factors (BF), described as the deviation based on the estimate of Monte Carlo, proposed by Newton and Raftery (1994). These

deviations represent the separation level between the evaluated model and a hypothetically perfect fit to the model; and the larger number of criteria with lower values indicates a better fit to the model.

RESULTS AND DISCUSSION

The results presented were the standard animal model (AM), the hierarchical reaction norm model homoscedastic 1-step (HRNMHO_{1S}) and the hierarchical reaction norm model heteroscedastic 1-step (HRNMHE_{1S}). The HRNMHO_{1S} presented lower values for CPO and BF compared to the

HRNMHE_{1S} (Table 1). The HRNMHO_{1S} model was chosen to present the results discussion because it presented lower values for the adjustment quality evaluators.

Correa et al. (2009), Cardoso et al. (2011), Mattar et al. (2011) and Cardoso Tempelman (2012) used reaction norm models for studies on post-weaning weight gain of breeds Angus, Hereford, Canchim and Devon respectively, comparing the HRNM with the AM, and observed that the adjustment was higher for HRNMHO than for HRNMHE models.

Table 1. Deviance information criterion (DIC), deviance based on conditional predictive ordinate (CPO) and deviance based on Bayes factors (BF) for comparison between the standard animal models and hierarchical reaction norm model homoscedastic 1-step (HRNMHO_{1S}) and heteroscedastic 1-step (HRNMHE_{1S}).

Models	DIC	CPO	BF
AM	72566.13	73042.19	71068.31
HRNMHO _{1S}	71794.68	73920.86	71032.43
HRNMHE _{1S}	62340.13	74305.51	71457.96

The length of Markov chains to the chosen model (HRNMHO_{1S}) was at most 440,000 interactions with 44,000 (burn-in) of heating (discard of 10%) generating subsequent samples every 44 cycles. The convergence of the chain was assessed by the Geweke test (1992) and the indication of the number of chains, burn-in and saving interval were indicated by the Raftery and Lewis test (1992). A convergence of 5% (p>0.05) was observed for all parameters in the AM and HRNMHO_{1S} models within a range between 330,000 and 440,000 cycles.

Cardoso et al. (2011), studying the weight gain at post-weaning of the Hereford breed via reaction norm models, found convergence for all models (standard animal, HRNMHO_{2S}, HRNMHO_{1S},

HRNMHE_{2S} and the HRNMHE_{1S}). Ambrosini et al. (2012) also found a 5% convergence (p>0.05) for all parameters of the models, for the weight per year in Nelore Mocho in the Northeast of Brazil.

The solutions of the environmental gradient for HRNMHO_{1S} model ranged from -67 to 113 kg, thus characterizing low and high environment management levels. Direct and maternal heritability estimates for the animal model were 0.17±0.04 and 0.07±0.03, respectively. The direct heritability for the reaction norm model were 0.21±0.06 in the low environment and 0.58±0.04 in the high; and the maternal heritability in this model ranged from 0.01±0.01 in the low environment and 0.18±0.07 in the high (Figure 1).

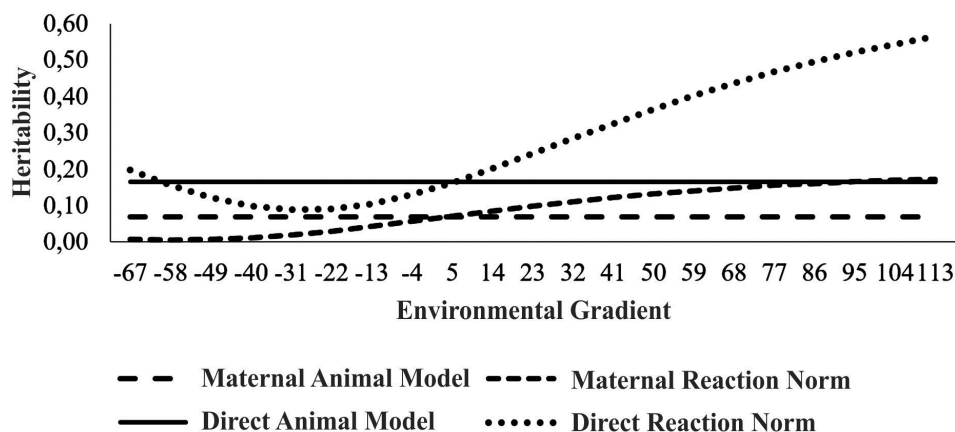


Figure 1. Heritability of the W365 characteristic for the direct and maternal effects in the proposed models.

The wide heritability variation in the environments may be related to the GEI. The high management environments had much higher heritability magnitudes, since the animals could to

express all their productive potential, which generate higher genetic variance estimates and the sires could be best discriminated by their genetic values. Grishkavich and Yanai (2013) reported that the

appearance of the characteristic can change between both genotypes and environments, but the nature of this change can be additive (genotypic and environmental variation). According to these authors, often the environment severely affects the phenotype, which is not an additive effect of the genotype.

Studying GEI characterization and comparing adjustment models for post-weaning weight gain of Devon cattle via reaction norms, Correa et al. 2009 found heritability of 0.13 ± 0.017 for the animal model. The heritability increased as environmental gradient improved in the HRNM and HRNMHE, showing that there is a change in the genetic parameters of the population as a function of the environment in which they are, characterizing the presence of GEI. Ambrosini et al. (2012) found an estimated heritability of 0.29 ± 0.03 to W365 using an animal model, a value higher than the estimate of $HRNMHO_{15}$ at the low environmental level.

The correlations between the slope and the intercept of the reaction norms were 0.68 ± 0.10 and 0.96 ± 0.04 , for the direct and maternal effects, respectively. The medium to high magnitude correlations indicate that animals with higher genetic values for direct and maternal effects respond positively, increasing the estimate of its genetic values in better production environments.

Similar results were found by Mattar et al. (2011) with correlation between intercept and slope of the reaction norm of 0.90 ± 0.03 , indicating the presence of GEI, characterizing the scale effect (FALCONER and MACKAY, 1996). Ribeiro et al. (2010), evaluating reaction norms on estimation of the environmental sensitivity of the genetic merit for weight at weaning in Nelore cattle, observed that the correlation given by the sample averages *a posteriori* between the variance component estimates of the intercept and the slope was 0.75, indicating that

sensitivity to environmental changes increases as the selection for higher genetic values.

Correa et al. (2009) observed that the genetic correlation between level and slope was 0.83 ± 0.01 , higher than that reported through the HRNMHE. These correlations indicated that the animals of greater genetic value on the medium environment were also the ones that better responded to the improved environment.

Phenotypic plasticity is any change triggered by the environment, without requiring genetic changes (BRADSHAW, 1965; SCHEINER, 1993; VIA et al., 1995). Robustness and phenotypic plasticity are related to GEI, and if different genotypes have varied reaction norm, there is occurrence of GEI (DE JONG; BIJMA, 2002). Mattar et al. (2009) used a scale that allowed classifying the genotypes according to the slopes of the reaction norms of the animals. These authors found variation from -0.40 to 0.50 levels and observed high incidence of robust and medium genotypes (13,968 animals) with slopes between -0.20 and 0.20.

The slopes of the reaction norms ranged from -0.45 to +0.45 (direct effect), in which 96.37% of the animals varied between -0.20 and +0.20, characterized as robust genotype; and 3.63% below -0.20 and above +0.20, characterized as plastics genotypes. The change for the maternal effect was -0.20 to +0.24, observing almost all of the robust genotype animals.

Considering the 10 sires with the highest number of progeny (Figures 2 and 3), animals with plastic genotypes and changes on the slopes were observed, which indicates presence of GEI with scale effect and, in some cases, changes in classification over the environmental gradient. This is relevant, since the animals used intensively may be chosen wrongly, depending on the environment in which their progeny will be raised.

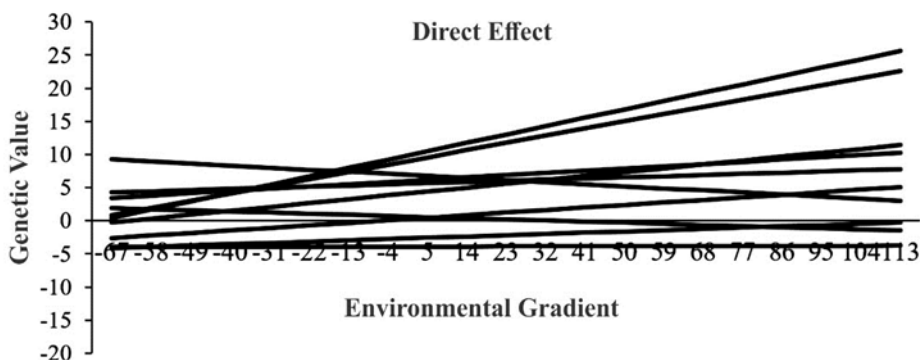


Figure 2. Reaction norm over the environmental gradient to W365 for direct effect found for the 10 sires with the highest number of progeny.

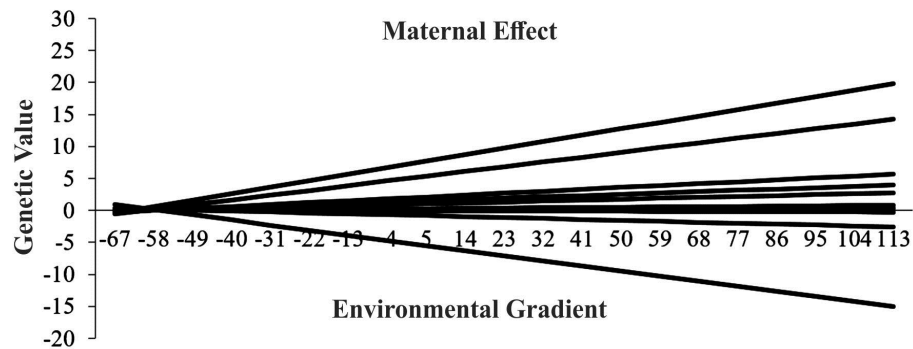


Figure 3. Reaction norm over the environmental gradient to W365 for maternal effect found for the 10 sires with the highest number of progeny.

Ambrosini et al. (2012) found slope of the reaction norms ranging from -0.80 to 0.67. Most animals (80.96%) were classified as robust and medium with slopes between -0.20 and 0.20. Plastic genotypes were observed only for 19.03% of the animals of the kinship matrix.

The Spearman correlation between the sire classifications ranged from -0.35 to 0.95 in the different environments and models (Table 2).

The correlation between the AM and HRNM (medium and high levels), considering all the sires,

were high, indicating that the AM selects animals that can be used in these environments but not in low management environment, common in the Northeast of Brazil. Correlations between HRNMHO_{1S} (medium level) with HRNMHO_{1S} (high level) were also high. The other low correlations (positive and negative) indicate that selection in an environment does not necessarily imply genetic gain in the other. The selection of animals in the medium and high management environments will not result in gain if they are used in low management environments.

Table 2. Spearman correlations between the classifications of Tabapua sires in the Northeast of Brazil, found for the animal model (AM) and the hierarchical reaction norm model homoscedastic 1-step (HRNMHO_{1S}) for the different environmental levels.

Models	HRNMHO _{1S} (Low)		HRNMHO _{1S} (Medium)		HRNMHO _{1S} (High)	
AM	0.1416	(0.0375)	0.9519	(0.0001)	0.8162	(0.0007)
HRNMHO _{1S} (Low)			-0.0513	(0.4531)	-0.3549	(0.0001)
HRNMHO _{1S} (Medium)					0.9362	(0.0001)

Numbers between parentheses = p-value

Correa et al. (2010) found similar results, with Spearman correlation between classifications ranging from 0.12 to 0.99, considered a moderate to high ordering change. They stated that these results indicate the need to consider the GEI in the selection process, especially in low individual performance levels conditions, in which most of ordering inversions were found. However, scale effect was observed in the high performance levels, therefore, the higher average genetic value individuals were the ones that better responded to environmental changes.

Mattar et al. (2011) evaluated GEI for weight per year in cattle Canchim via reaction norms and observed high Spearman correlations, with values greater than 0.90 compared to the animal model,

with HRNMHO in three levels (low, medium and high).

Ambrosini et al. (2012) observed that the Spearman correlations between sire classifications with greater genetic value ranged from 0.73 to 0.99 in the different environments and models when the 5% of sires with the highest genetic values were chosen, and 0.71 to 0.99 when 10% of these sires were chosen. The lower correlations were observed in the animal model compared to reaction norm models, confirming the presence of GEI.

The correlations between the genetic values of the sires in the different environmental gradients ranged from -0.61 to 1.00 for the direct effect, and from -0.41 to 1.00 for the maternal effect on the HRNMHO_{1S}. (Figures 4 and 5).

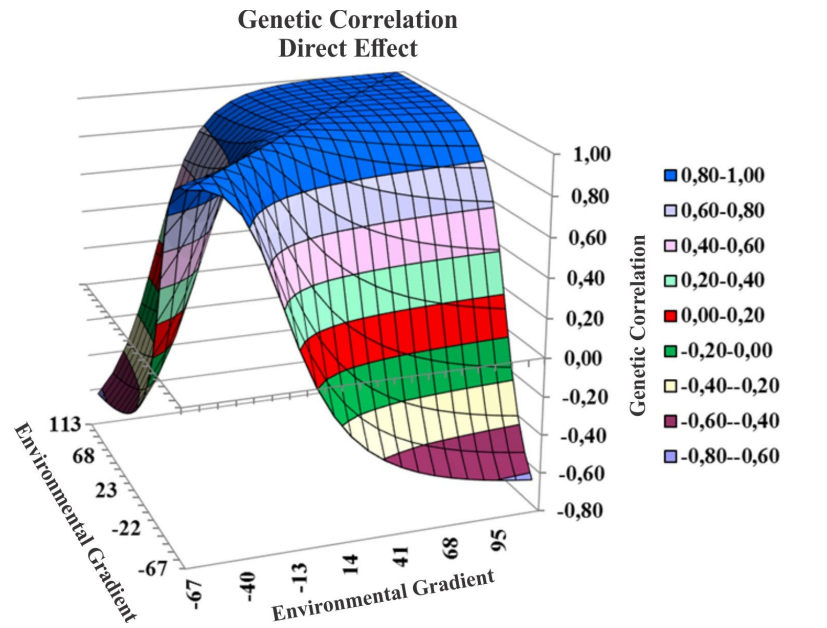


Figure 4. Surface graph of response of correlations between direct genetic values and environmental gradient.

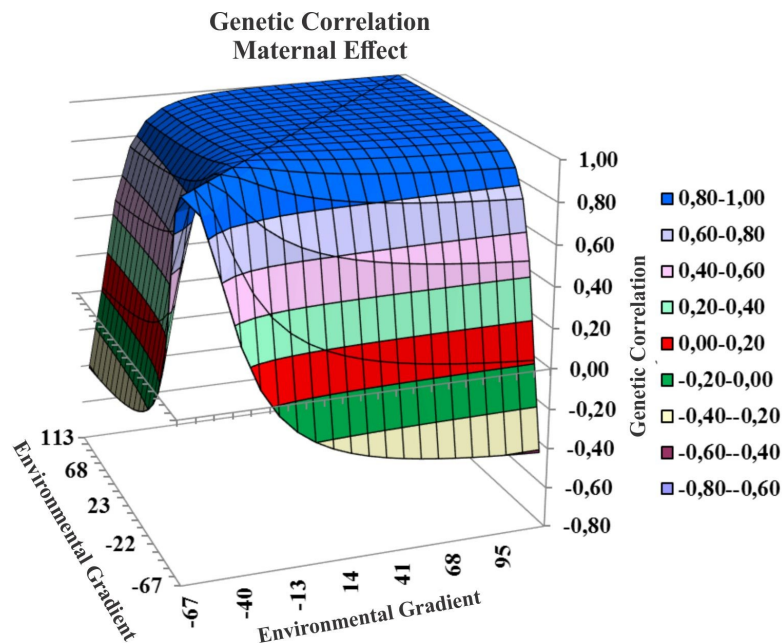


Figure 5. Surface graph of response of correlations between maternal genetic values and environmental gradient.

The Figures 4 and 5 show that the genetic correlation in the medium and high values of the environmental gradient is highly positive, greater than 0.80, however, this correlation decreases as the environment is unfavorable, with negative values between the extremities of the environmental gradient. These results agree with those found by Correa et al. (2009), who stated that the genetic required for production in very adverse environments is different from that which best produces in reasonable and good environments.

Ambrosini et al. (2012) found correlations between genetic values in the environmental gradient

with little difference for the HRNMHO_{1s} (0.78 to 1.00). Regarding the 2-step model, which was the second best model of the study, the correlations showed higher variation (0.50 to 1.00), indicating that there may be GEI.

CONCLUSIONS

The reaction norm model 1-step, which consider the homogeneity of residual variance, is the one that best fits the data in the population of Tabapua cattle of the Northeast of Brazil. Genetic

values of most animals were robust to the environmental variation. However, considering the sires with the highest number of progeny, the presence of GEI is observed.

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