



Reaction norms models in the adjusted weight at 550 days of age for Polled Nellore cattle in Northeast Brazil

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ABSTRACT - The objective of this study was to evaluate the genotype-environment interaction (GEI) in the body weight adjusted to 550 days of age (W550) of Polled Nellore cattle raised in Northeastern Brazil using reaction norms (RN) models. Hierarchical RN models included fixed effects for age of cow (linear and quadratic) and random effects for contemporary groups (CG) and additive genetic RN level and slope. Four RN hierarchical models (RNHM) were used. The RNHM_{2S} uses the solutions of contemporary groups estimated by the standard animal model (AM) and considers them as environmental level for predicting the reaction norms and the RNHM_{1S}, which jointly estimate these two sets of unknowns. Two versions were considered for both models, one with a homogeneous (Hm) and another with a heterogeneous (He) residual variance. The one-step homogeneous residual variance model (RNHM_{1S}Hm) offered better adjustment to the data when compared with other models. For the RNHM_{1S}Hm model, estimates of additive genetic variance and heritability increased with environment improvement (260.75±75.80 kg² to 4298.39±356.56 kg² and 0.22±0.05 to 0.82±0.01, for low- and high-performance environments, respectively). High correlation (0.97±0.01) between the intercept and the slope of RN shows that animals with higher genetic values respond better to environment improvement. In the evaluation of breeding sires with higher genetic values in the various environments using Spearman's correlation, values between 0 and 0.98 were observed, pointing to high reclassification, especially among genetic values obtained by the animal model in comparison with those obtained via RNHM_{1S}Hm. The existence of GEI is confirmed, and so is the need for specific evaluations for low, medium and high level production environments.

Key Words: Bayesian inference, environmental gradient, genetic value, random regression, Zebu cattle

Introduction

Production environments in Brazil may vary considerably between regions as well as the average yield of herds, the feeding, and climatic variations such as rainfall, temperature and humidity. The phenomenon whereby genotypes respond differently to changes in their environment is known as genotype-environment interaction (GEI) or as differences in sensitivity of genotypes to environmental variation (Falconer and Mackay, 1996). An alternative study on this differential response is the analysis of reaction norms, which can describe the variation of genotypes as a function of an environmental gradient (Lynch and Walsh, 1998).

The use of reproductive technology such as artificial insemination, embryo transfer, among others, allows breeders to have progenies in different production systems and geographical areas. The inclusion of GEI in statistical models should be considered during genetic evaluation of cattle in Brazil since the progenies are often raised in environments which are very different from those where the progenies of bulls were kept to generate their breeding values. The genotype-environment interaction needs to be evaluated in Zebu herds, because it can cause animal ranking changes or even scaling (Lynch and Walsh, 1998).

An alternative to the reaction-norms study is the use of random regression models (RRM), which allow the adjustment of one random trajectory for each animal and thereby allow each animal to have a different form from their performance trajectory, in genetic terms, in the various production environments (Mercadante et al., 2002; Schaeffer, 2004).

Studies with European breeds in Southern Brazil using Bayesian inference as a tool to characterize and quantify

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GEI by RN were described by Corrêa et al. (2010), Cardoso et al. (2011) and Cardoso and Tempelman (2012). These authors demonstrated the importance of including this effect in genetic evaluation programs, since a breeding sire can have superior performance in a given stratum of the environmental gradient and much less than expected in another.

Northeast Brazil has a wide diversity of climates and production systems, where the farming of Zebu breeds predominates. Nevertheless, GEI studies with Zebu breeds are rare in this region (Ambrosini et al., 2012). Therefore, the objectives of this study were to verify the existence of genotype-environment interaction and to quantify its effect on weight adjusted to 550 days of age (W550) of Polled Nellore cattle in Northeast Brazil.

Material and Methods

The data used in this study is from field records collected by the Brazilian Association of Zebu Breeders (ABCZ), pertaining to Polled Nellore animals born between 1975 and 2007 in the Northeast region of Brazil.

The contemporary groups (CG) were formed so that all animals shared a common production environment, including herd, year, diet, farm, gender, and birth period. The birth periods were grouped into four classes (period 1: May, June and July; period 2: August, September and October; period 3: November, December and January; and period 4: February, March and April) so that each period was represented by the climatic conditions observed in the northeast region.

In order to prepare the dataset for RN analyses, we used routines created by Cardoso (2008) in SAS (Statistical Analysis System, version 9.2) language. Moreover, the AMC Program (Roso and Schenkel, 2006) was used to test the connectivity of CG based on the number of genetic ties to the main population group (minimum of 10). After the connectivity analysis, the main archipelago had 731 connected CG and another 20 CG were disconnected.

The initial dataset consisted of 35,221 records, of which 21,955 were excluded due to lack of W550 records. Additionally, 123 records were deleted because they were disconnected, 248 that had W550 measurements outside the 150-280 kg interval, 171 whose dams were aged less than 1.9 or over 25 years, 566 pertaining to sires that had less than five calves, and 3,703 animals that were in contemporary groups (CG) with less than five observations or their weight was outside the range of ± 3 standard deviations from their CG mean. The remaining 8,455 animals were used in the W550 analyses.

The INTERGEN program (Cardoso, 2008) was used to adjust Bayesian hierarchical models, that is, with parameters defined in structured levels or stages, which contemplate the diversity of common situations in animal performance data. In the case of RN models, the genetic value of the animal is obtained by a function of the average environmental level corresponding to the solution of the GC to which the record belongs, that is, for each environmental level there is a specific genetic value for each animal (Cardoso and Tempelman, 2012).

Initially, a standard animal model (AM) ignoring GEI was fit to estimate the genetic value of the animal and obtain the estimates of average environment effects based on CG:

$$y_{ij} = x'_i\beta + X_j + a_i + e_{ij}, \quad (1)$$

in which: y_{ij} = record of animal i in environment j ; β = vector of fixed effects (linear and quadratic for cow age); x'_i = incidence vector; X_j = random CG environmental effect; a_i = additive genetic value of animal i ; and e_{ij} = residual error.

Additionally, two models were implemented to describe hierarchical reaction norms (RNHM): the model proposed by Kolmodin et al. (2002), which uses the AM solutions as co-variables in the RNHM, is called two-step RM model (RNHM_{2S}), and its equations are presented as follows:

$$y_{ij} = x'_i\beta + \phi\hat{X}_j + a_i + b_i\hat{X}_j + e_{ij}, \quad (2)$$

in which: ϕ = fixed regression coefficient; a_i = additive genetic value for the RN intercept or level of animal i ; b_i = random regression coefficient or RN slope of animal i in the environment represented by \hat{X}_j ; $\hat{X}_j = X_j$ predictor obtained in (1); and e_{ij} = residual error.

In addition, we used the assumption of Su et al. (2006), called here one-step hierarchical RN model (RNHM_{1S}), which in spite of its similarity with the previous model (2), presents a different and simultaneous estimating process for the solutions of GC and RN intercepts and slopes. In this model, the GC effects are considered unknown covariates in the RN model, in which the estimates for environmental effects were used as a covariant to obtain the slope of the RN of the animals, that is, X_j and b_i are jointly estimated as follows:

$$y_{ij} = x'_i\beta + X_j + a_i + b_iX_j + e_{ij}, \quad (3)$$

Two different assumptions were adopted for residual variance in the models:

(a) Homoscedasticity for AM, RNHM_{2S} (RNHM_{2S}Hm) and RNHM_{1S} (RNHM_{1S}Hm), with $e_i \sim N(0, \sigma_e^2)$ and σ_e^2 = residual variance; and (b) heteroscedasticity for models RNHM_{2S} (RNHM_{2S}He) and RNHM_{1S} (RNHM_{1S}He), with $e_i \sim N(0, \sigma_{e_j}^2)$ and $\sigma_{e_j}^2 = \sigma_{e_j}^2\eta^{X_j}$, in which η = heterogeneity of variance parameter in the environmental level X_j , following the structural model proposed by Cardoso et al. (2005).

The additive genetic variance in environment X, $\sigma_A^2|X$, was obtained by:

$$\sigma_A^2|X = \text{var}(a_i + b_i X) = \sigma_a^2 + \sigma_b^2 X^2 + 2X\sigma_{ab},$$

in which: σ_a^2 = estimate of the variance component for the intercept of the reaction norm; σ_b^2 = estimate of the variance component for the slope of the reaction norm; and $\sigma_{a,b}^2$ = estimate of the genetic covariance component between the intercept and slope.

The heritability was estimated by the ratio of genetic variance to phenotypical variance (genetic + environmental) as:

$$h^2|X = \frac{\sigma_a^2|X}{\sigma_a^2|X + \sigma_e^2|X},$$

in which: $\sigma_e^2|X$, = residual variance in environment X, obtained by $\sigma_e^2\hat{\eta}^X$ in the heteroscedastic models, and by σ_e^2 in the homoscedastic model.

A Bayesian approach (Gianola and Fernando, 1986) was used to obtain estimates of the parameters, via the Markov Chain Monte Carlo (MCMC) methods (Blasco, 2001), and by adopting the following procedure: 1) running a pilot analysis with 55,000 cycles, 5,500 burn-in and 5 for thinning; 2) using the variance-component samples saved in 1) and the R package (R Development Core Team, 2008) - Bayesian Output Analysis - BOA (Smith, 2007), the Raftery and Lewis (1992) test was applied to determine chain size and thinning; in addition, the burn-in was evaluated using the criterion of Heidelberger and Welch (1983).

The analyses (Figure 1) were rounds with chains that varied from 55,000 to 220,000 cycles. Means, standard deviations and percentiles (0.025 and 0.975) *a posteriori* of the parameters were obtained from their marginal posterior densities through procedure KDE of SAS (Statistical Analysis System, version 9.2).

The diagnosis by Geweke (1992) was used to verify the convergence of the chains to the different models. This is based on a Z-test for equality of means of the conditional data distribution logarithm, denoted by $l_i^{(j)} = \log p(y | \theta^{(j)}, M_i)$,

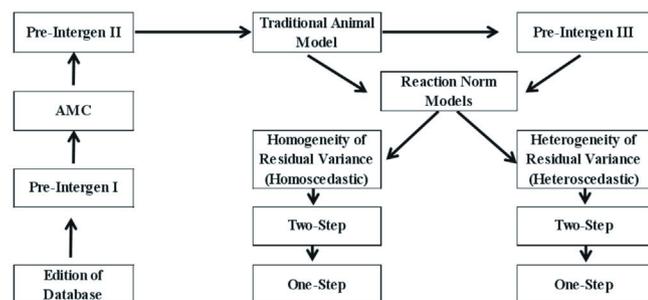


Figure 1 - Illustrative flowchart showing the necessary steps for the analyses in the INTERGEN program.

of the first samples (initial 10%), and of the last part of the Markov chain (last 50%), similar to what was proposed by Brooks and Roberts (1998), using the following statistic:

$$Z_i = \frac{(\bar{l}_i^A - \bar{l}_i^B)}{\sqrt{\frac{1}{n_A} \hat{S}_i^A(0) + \frac{1}{n_B} \hat{S}_i^B(0)}}$$

in which: $\bar{l}_i^A = \frac{1}{n_A} \sum_{j=1}^{n_A} l_i^{(j)}$; $\bar{l}_i^B = \frac{1}{n_B} \sum_{j=n^*}^m l_i^{(j)}$; $n_A = 22,000$; $n_B =$

110,000; $n^* = 110,001$; and with $\hat{S}_i^A(0)$ and $\hat{S}_i^B(0)$; and the respective estimates of spectral density in zero frequency were obtained through SPECTRA procedure of SAS (Statistical Analysis System, version 9.2), for the first n_A and the last n_B cycles of the MCMC chain of length m . Extreme absolute values of the Z_i score for a two-tailed test indicate rejection of the convergence test.

The following criteria were used to verify the best fit model: Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002); Deviance based on Conditional Predictive Ordinate (CPO) as described by Gelfand (1996) and Deviance based on Bayes Factors (BF), described as the deviance based on the Monte Carlo estimator proposed by Newton and Raftery (1994). These deviations represent the degree of separation of the evaluated model in relation to a hypothetically perfectly adjusted model, and lower values indicate better adjustment.

Results and Discussion

The mean and standard deviation observed for W550 was 316±68 kg. Convergence was obtained through Geweke's test at 5% ($P > 0.05$) for all variance component parameters of all models within an interval from 55,000 to 220,000 cycles. Cardoso et al. (2011) used Geweke's test and found medium convergence for the standard animal model ($Z = 1.08$; $P = 0.2788$); for RNHM₂₅Hm ($Z = 2.15$; $P = 0.0310$); for RNHM₁₅Hm ($Z = -1.68$; $P = 0.0913$); for RNHM₂₅He ($Z = -2.25$; $P = 0.0238$); and for RNHM₁₅He ($Z = -0.92$; $P = 0.3545$).

The proposed model choice criteria agreed to point out that RN models provided better adjustment to the data when compared with AM (Table 1). However, there was some divergence among the criteria to indicate the best model within the RN specifications. Overall, it seems that the RNHM₁₅Hm offered superior adjustment, being the best model for BF and obtaining second classification for the other two criteria (DIC and CPO). Moreover, among RNHM the assumption of residual variance homogeneity tends to provide a better fit than heterogeneity.

For model RNHM₁₅Hm, the environmental gradient solutions varied from -135 to 153 kg, characterizing

Table 1 - Deviance criterion based on Bayes factors (BF), deviance information criterion (DIC) and deviance based on condition predictive ordinate (CPO) in the animal standard model (AM) and of the hierarchical reaction norm models: homoscedastic two-step (RNHM_{2S}Hm), one-step (RNHM_{1S}Hm) and heteroscedastic two-step (RNHM_{1S}He) and one step (RNHM_{1S}He)

Model	DIC	CPO	BF
AM	85664.73(5th)	86026.83(5th)	84401.13(5th)
RNHM _{2S} Hm	84674.64(3rd)	85600.42(1st)	82631.65(3rd)
RNHM _{1S} Hm	83243.20(2nd)	85667.42(2nd)	82175.05(1st)
RNHM _{2S} He	85109.88(4th)	85696.22(3rd)	83573.59(4th)
RNHM _{1S} He	83084.69(1st)	85773.87(4th)	82454.08(2nd)

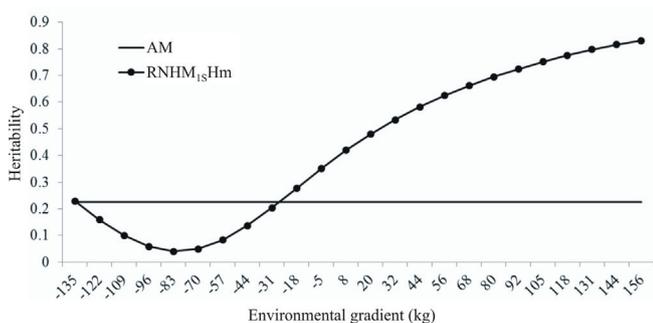
1st, 2nd, 3rd, 4th and 5th indicate best adjustment rank.

the lowest and highest environmental levels. The environmentally constant estimate of heritability under the AM was 0.22 ± 0.03 (Figure 2). When comparing results via the animal model in the present study with those obtained by Souza, et al. (2011) for W550 of Polled Nellore in Brazil, lower values are observed for inheritability (0.09 ± 0.02).

This value is the same as the RNHM_{1S}Hm estimate in lowest environmental level, and it is higher than that found by Cardoso et al. (2004), Corrêa et al. (2009), and Cardoso et al. (2011) for standardized post-weaning gain for 345 days (0.19 ± 0.02 , 0.13 ± 0.017 , and 0.10 ± 0.001 , respectively). Differently from the present work, which was carried out with Brazilian Northeast Zebu data, these studies used European animals bred in the South of Brazil.

Increasing differences among the genetic values of animals were observed in better-management environments characterized with a GEI scale effect on W550 (Figure 2).

Complex GEI was also observed with changes in the animal genetic values classification in the low, medium and high environmental levels. Animals with higher overall genetic values responded better to environmental improvement, being the genotypes with highest plasticity and response.



AM - animal model; RNHM_{1S}Hm - one-step hierarchical reaction norms model.

Figure 2 - Heritability of weight adjusted to 550 days of age in the models proposed by the environmental gradient.

The slopes of the animals reaction norms varied from 0.88 to 0.74 degrees, which demonstrates the occurrence of sires with plastic genotypes; however, there was a higher incidence of robust and intermediate genotypes corresponding to 81.04% of the animals (6,852 animals) which had slopes between -0.20 and 0.20 degrees. Plastic genotypes (-0.88 to -0.21 degrees and 0.21 to 0.74 degrees) were observed in 18.96% of the animals (1,603 animals). It was also observed that the genetic differences among animals increased in better environmental conditions, probably due to the fact that the animals had an environment that allowed the expression of their genetic potential (Figure 3).

Spearman's correlations among the genetic values of sires obtained by the different models according to the environmental level varied from 0 to 0.93, when only the top 5% of sires for higher genetic values were chosen (above the diagonal) and from 0 to 0.98, when the top 10% sires (below the diagonal) were used, respectively (Table 2). Most correlations were from low to high, confirming the presence of GEI. As expected, an increased difference was observed when 5% of the best sires were considered in relation to 10% of the best sires (Table 2).

The greatest ranking differences were obtained between the AM and the low level of RNHM (Spearman correlation 0%) for 5% and 10% of breeding sires with higher genetic value. No correlations were observed between the low level of RNHM and the medium and high levels of RNHM, which demonstrates that the selection of breeding sires for a low-level production environment will not result in genetic gain in a medium- and high-level environment. When comparing the correlations between the AM for the 5% and 10% of breeding sires, and the medium and high levels of RNHM, the correlations were low and medium (0.28% and 0.30%; 0.71% and 0.72%, respectively). This indicates that by applying higher selection intensity (5% of breeding sires) the changes in the classification of the AM

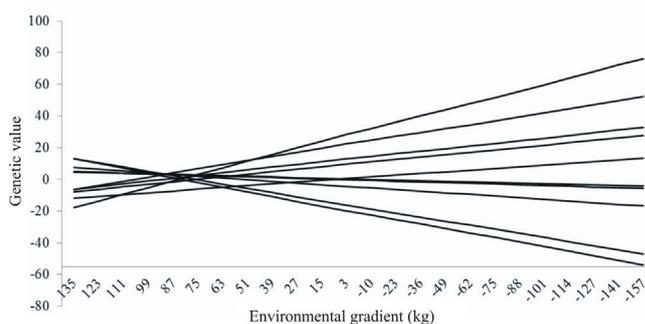


Figure 3 - Reaction norm along the environmental gradient for weight adjusted to 550 days of age obtained for the 10 sires with the highest number of progeny.

compared with RNHM will be greater and therefore some bulls will not lead to gains in certain environments.

Comparing the medium level with the high level of RNHM, were no changes in classification (0.93% and 0.98% to 5% and 10% of breeding sires, respectively). These results confirm that the selection in the medium environment leads to gains in environments of better management and vice versa, showing low genotype-environment interaction (GEI) in this situation.

The fact that classification changes are greater when 5% of the best sires are considered in relation to 10% is a matter of concern to the Brazilian livestock sector, because a very small number of sires is often selected and intensively used. This has been evidenced in various genetic structure population studies involving a number of breeds in Brazil (Marcondes et al., 2007; Oliveira et al., 2011) and indicates the need to consider GEI in genetic evaluations, to select animals to be used in herds under different production systems.

Corrêa et al (2010) obtained estimates of Spearman's correlations higher than those in the present study, with values of 0.12 to 0.98 for 5% of the best sires and higher for 10% of the sires, with values of 0.75 to 0.99 for post-weaning gain standardized at 365 days. According to these authors, moderate-to-high change was observed in the classification

of Devon breed sires. Kolmodin et al. (2002) observed change in the classification of dairy sires, demonstrating that for low-performance records, the selection would have benefits if carried out in a specific environment.

Genetic correlations between genetic values and the environmental gradient (Figure 4) displayed high amplitude for $RNHM_{15}Hm$ (-0.85 to 1.00). For the two-step model - the second best model - the correlations also displayed greater variation (-0.79 to 1.00), which denotes GEI. The results obtained herein indicate that the genetic material necessary for production in various environmental levels must be different, even if partially, and differ only in magnitude from those presented by Corrêa et al. (2009), who observed the negative genetic correlations among environmental gradient levels for standardized post-weaning gain at 365 days. Mattar et al. (2011) observed higher values than those in the present study (0.24 to 1.00). In both studies it was characterized that the animals were more sensitive to the different environmental gradient levels. The application of reaction norm models in GEI studies of Polled Nellore cattle from northeastern Brazil is new and allowed identifying GEI in this population. Scale effect was observed, with different responses of genotypes to environmental gradient and change in the classification of animals. Differences were greater in superior production conditions, that is, as

Table 2 - Spearman's correlations among the classifications of Polled Nellore sires in Northeast Brazil with higher genetic values (5% above the diagonal and 10% below the diagonal), obtained by the animal model and by the one-step hierarchical reaction norms model ($RNHM_{15}Hm$) for different environmental levels

Models	Animal model	$RNHM_{15}Hm$ (Low)	$RNHM_{15}Hm$ (Medium)	$RNHM_{15}Hm$ (High)
Animal model		0 (0.0)	0.28 (0.3440)	0.30 (0.3156)
$RNHM_{15}Hm$ (Low)	0 (0.0)		0 (0.0)	0 (0.0)
$RNHM_{15}Hm$ (Medium)	0.71 (0.0001)	0 (0.0)		0.93 (0.0001)
$RNHM_{15}Hm$ (High)	0.72 (0.0001)	0 (0.0)	0.98 (0.0001)	

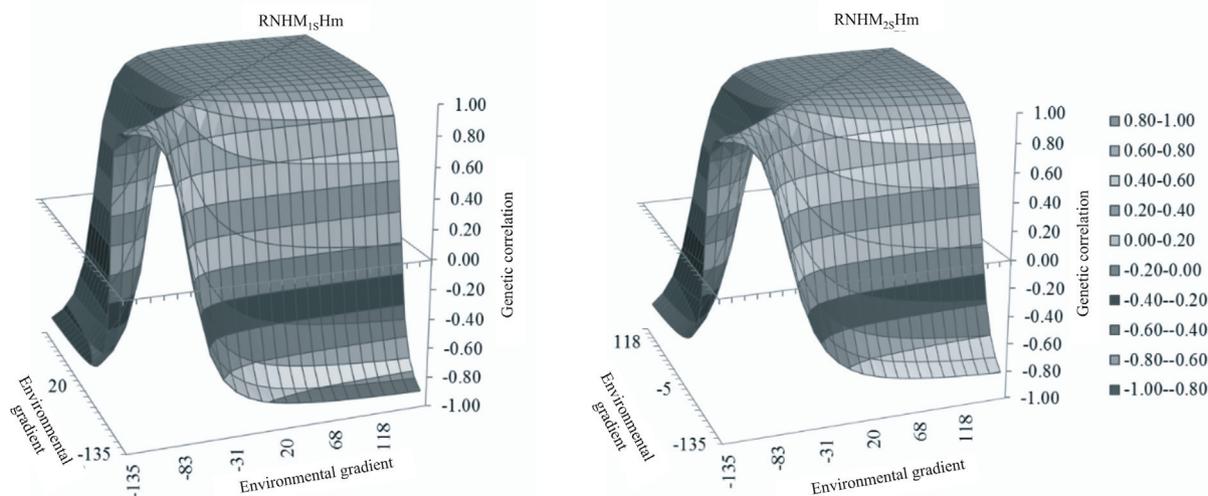


Figure 4 - Response surface graph of correlations between genetic values and the environmental gradient.

the environment became more favorable, the variance of genetic values increased, since the individuals have full opportunity to express their genetic potential.

There is an increase in the number of studies that indicate the need to have specific genetic value predictions for each environment (Bryant et al., 2006; Hammami et al., 2008; Corrêa et al., 2010; Pegolo et al., 2011; Cardoso et al., 2012). Thus, it is possible that GEI studies change the modeling traditionally used in the usual genetic evaluations. Higher genetic gains can be provided, since the genes would act in a more effective way, regulating physiological systems for lower management expenses and higher production in specific environments. This would be especially important in countries and/or regions with extreme climate diversity, as is the case of Brazil and its Northeast Region.

Conclusions

The existence of genetic-environment interaction in the population of Polled Nelore cattle in Northeast Brazil is confirmed. Scale effect in genetic-environment interaction and inversion in the classification of environment gradient levels is observed, confirmed by the magnitude of Spearman's correlations among sires with higher genetic values, evidencing a change in sire classification from moderate to high magnitude.

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