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SUMMARY

The tropics have considerable potential in animal production but their production systems are characterized by low animal performance which is partly due to an unfavourable environment and poor breeding methods for the indigenous animals. The phenotypic plasticity is the property of the organisms of a genotype to develop systematically different phenotypes in different environments. The aim is to develop robust animals that do not show plasticity over different environments. A variation in plasticity exists when the difference in phenotypic value between animals among different environments is not constant. This variation in phenotypic plasticity results in the genotype by environment interaction (GxE). This present study intends to analyze the GxE interaction in tropical conditions on growth traits for Creole beef cattle during fattening. The experiment was carried out with 516 animals separated after weaning in two different fattening environments. The first group received an intensive feeding regime, consisting of cropped grass and concentrates. The other group was conducted at pasture. During the fattening period, animals were weighted every fifteen days. Two statistical analyses have been chosen in the study; a multivariate analysis and the Random Regression Model (RRM) over the entire fattening period. The growth rate at pasture was 413 g/day versus 678 g/day in intensive feeding regime. Heritability for the weight of the animals raised at pasture was 60% smaller than in intensive feeding regime. This proved a better expression of the genetic potential in intensive feeding regime and therefore the residual variance was reduced in favor of the genetic variance; the genetic variance at pasture represented 12% of the genetic variance in intensive feeding regime. Genetic correlations tended to decrease with the age and consequently it indicated an increase of the GxE interaction (from 0.97 at 300 days to 0.59 at 540 days). The relationship between the breeding values for the weights at fifteen and eighteen months in intensive feeding regime and at pasture was supported by a low R^2 (equal to 0.597). Only one third of the 10% best animals in one fattening group were also the best in the other. These observations were the clear evidence of the GxE interaction. Moreover, these results pointed out the consequence of the GxE interaction on the re-ranking of the animals. It was observed that 19.6% of the animals contributing to the genetic improvement of one trait made the genetic gain of the other trait decreased. This study also showed the great advantages of the RR model which allowed an appreciation of the genetic parameters along the entire fattening period.

Key words: genotype by environment interaction, Creole beef cattle, fattening, intensive feeding regime, pasture, Random Regression Model.

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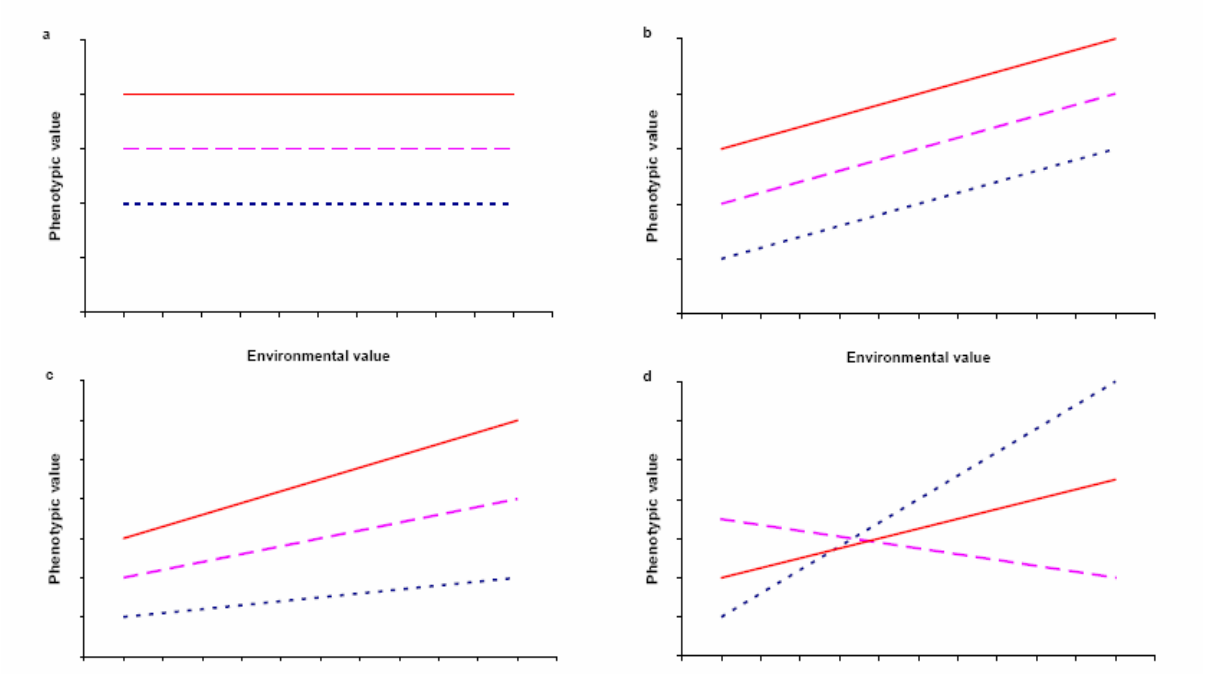
1. INTRODUCTION

The human population continues to grow and consequently the demand for food, particularly of animal origin, increases as well. Developing methods and procedures in order to improve livestock production is therefore necessary. The tropics, i.e. the region lying between the tropics of Cancer and Capricorn, have considerable potential to meet the escalating world demand for animal production. However, the tropical production systems are characterized by low animal performance which is partly due to an unfavorable environment, poor breeding methods and poor recording systems for the indigenous animals. The aim is consequently to develop adapted breeding programs able to increase the productive potential of the local animals according to the environment (Jarvis, 1991). Importation of specialized breeds with high production levels from temperate countries and their introduction to tropical regions were tried as a solution to solve the problem of low production levels in the tropics. In most of the cases, the experience has been disappointing and sometimes almost disastrous. Diseases, high mortality rates and low fertility have been frequent problems among the imported animals and their progenies, which have failed to reach the expected production levels (Syrstad, 1989, Ayalew and al., 2003). This method considered that the genotype was the only determinant factor of the animal production and did not take into account the animals' adaptation capacity. However, the environment is also an important factor and creates the conditions to identify the better and more adapted animals to variable environments (Beilharz, 1998). The property of the organisms of a genotype to develop systematically different phenotypes in different environments is called phenotypic plasticity (de Jong and Bijma, 2002).



(Strandberg, 2006)

Figure 1. Description of the reaction norms for three genotypes. a) No plasticity but genetic variation in level. b) Plasticity but no variation in plasticity. c) Variation in plasticity but no re-ranking of genotypes. d) Variation in plasticity and re-ranking of genotypes.

Phenotypic plasticity is often quantified by the “norm of reaction” which describes the phenotypic expression as a function of a genotype and the environment. Genotypes that show no variability in phenotypes across environments are called “robust” (Figure 1a). Genotypes that show variable phenotypes across environments are called “plastic” (Figure 1b, 1c and 1d). Variation in plasticity between different genotypes exists when the difference in phenotypic value between animals among different environments is not constant (Figure 1c and 1d). When genotypes react in the same way to environmental change, there is no variation in plasticity (Figure 1b). The variation in plasticity may lead to a re-ranking of genotypes, i.e. the best genotype is not the same in the different environments (Figure 1d) (Strandberg, 2006). This variation in phenotypic plasticity between genotypes results in the genotype by environment interaction (GxE). When the GxE interaction exists, the different genotypes have different reaction norms. One of the breeding target in order to improve the production in the tropics is to have animals presenting high performance and well adapted to heterogeneous environmental conditions found in these regions, therefore inclusion of plasticity in breeding models is crucial to breed for increased robustness of animals or to optimize breeding programs that develop stock for multiple environments. Consequently the GxE interaction should be well understood.

Two statistical models exist to study the GxE interaction; the character state model (CSM) and the reaction norm model (RNM). The CSM is used when the environment is a discrete variable, classified in categories. The expressions in two or more environments are considered as different traits. In the RNM the environment can be described as a continuous variable. It offers a function that represents the evolution of the genetic variability of a character in all environmental trajectories (Menendez Buxadera et al., 2006; Strandberg, 2006). The CSM gives the phenotypic expression of a genotype in each environment whereas the RNM gives the total expression of the same genotype in the entire environmental gradient. In other terms, the CSM aims to find the best animals for a certain environment whereas the RNM aims to find the best animals in all environments i.e. the animals with the best adaptation capacities to different environmental adaptations (Menendez Buxadera, 2004). Many studies have proven the importance of the GxE interaction. Generally, the studies analyzed the interaction through the genetic correlation of the same trait evaluated in different environments such as different countries (Falconer, 1990; Meyer, 1995), different management conditions (Naves et al., 2006) or different temperatures (Hayes et al., 2003; Zwald et al., 2003). When the genetic correlation (rg) is significantly different from 1, it means that the performance of the genotype is not the same in different environments and therefore this is an indication of the GxE interaction (Falconer, 1952 cited by de Jong and Bijma, 2002). In the context of dairy cattle, several publications had analyzed the relationship among the breeding values of Holstein sires estimated in developed countries using generally intensive feeding system and in tropical countries using pasture. The results clearly showed the existence of sire-environment interactions (Menendez Buxadera and Mandonnet, 2006). Bertrand et al. (1987) worked on the Limousin animals’ production over nine regions of the USA and concluded on the existence of the GxE interaction with values of genetic correlation from 0.73 to 0.81. It also showed important changes in the ranking of the sires. A study aimed to verify the importance of the GxE interaction in the tropical beef cattle Nelore bulls for the 550-day adjusted weight on fifteen environmental groups obtained by the average herd-year weights. The genetic correlation ranged from

values near unity, between environments with similar averages and to values near zero, between extreme environmental groups (Pegolo et al., 2006). This showed that the magnitude of the GxE interaction increases when the difference in environmental conditions becomes larger. Menendez Buxadera and Mandonnet (2006) and Ceron-Munoz et al. (2004) concluded on the higher importance of the GxE interaction in the tropics mainly due to large variation in climate and consequently in feeding proprieties of fodder and in disease and parasite pressure. The performance of the Creole cattle breed was studied in Guadeloupe where the animals after weaning were separated within two management systems, either in intensive feeding regime or at pasture. The traits analyzed included weights at different ages and post weaning growth rates and were analyzed using the CSM. Very low correlations between growth traits obtained in both management systems were observed (rg equals to 0.203) indicating the importance of the GxE interaction (Naves et al., 2006).

This present study intends to analyze the GxE interaction in tropical conditions on growth traits for Creole beef cattle in two different fattening systems, either in intensive feeding regime or at pasture. Different statistical models exist to analyze growth traits. The simplest aims to describe one or several weights studied in a multivariate analysis. More recently, longitudinal analysis have been developed through Random Regression Model (RRM) in order to describe the genetic parameters of weight over the entire growth curve. Both applications have been chosen for the present study, using a CSM approach in order to give the phenotypic expression of a genotype in each environment. These methods will be used to get more knowledge on the GxE interaction that will help to improve the breeding strategies in tropical countries in order to obtain robust animals against the heterogeneity of the tropical environment.

2. MATERIALS AND METHODS

2.1 Herd management and data collection

The animals belonged to INRA Domaine de Gardel experimental farm, located in Guadeloupe, in the French West Indies (Lat. 16°CN, Long 61°W). The experimental herds were composed exclusively of cattle belonging to the Creole breed. They were composed of 90 cows and a total of about 200 animals including calves and sires. All Creole calves born in the years 1998 to 2005 were included in the study.

2.1.1 Origin of the calves

In total, 516 animals from 27 sires were recorded. Matting was performed either by artificial insemination (15% of the calves) or natural stud (85%). The number of offspring per sire depended on the mating strategy (artificial insemination or natural stud) and the duration of the stay of the sires in the farm. Concerning the breeding strategy of the herd, the selection of the replacement females was based on the weaning weight and the weight at eighteen months of age. About two third of the sires used in this experiment (nineteen sires) were originated from the herd and were chosen on the weaning weight and the growth between six and eighteen months of age in order to be representative of the herd's variation. The other sires (eight sires) came from private herds and were chosen based on their conformation and also to be representative of the Creole beef cattle population. Parentage testing was performed by DNA microsatellite analysis on calves. The pedigree of all animals present in the study was recorded from the creation of the herd in 1970 and contained in total 815 animals.

2.1.2 Suckling period

The suckling herds were managed entirely at pasture, on either natural savannahs or implanted pastures, with or without irrigation, resulting in four different meadow managements. The type of grass in natural savannahs was mainly *Dichanthium aristatum* and *Digitaria decumbens* in implanted pastures. The herd was divided into seven different suckling groups (B4, D1, D2, E1, MP, PC, PF). During the two first years, the calving occurred in two seasons but later, calving was concentrated within three months at the end of the dry season. Weaning occurred at an average of 210 days, in half-herd at a time depending on the different times of calving. The weight and date of birth were known. During suckling, weighing of the animals occurred every month. The date and weight at weaning (WW) was also recorded and the daily growth rate was calculated (ADGs).

2.1.3 Fattening period

Calves were dewormed just after weaning. After a short period of transition (from fifteen days to one month), calves were separated in four different management groups according to sex, balanced for sire origin and weaning weight and age at weaning. Half of both sexes were maintained in a feed lot and received an intensive feeding regime, consisting of cropped grass ad lib and concentrates representing 60% of the theoretical ingestion capacity (between 2.5 and 4.5 kg/d according to the live

weight). Concentrates were composed of corn (675 g in one Kg of concentrates), middling (220 g in one Kg of concentrates), soybean meal (80 g in one Kg of concentrates), limestone (10 g in one Kg of concentrates), urea (10 g in one Kg of concentrates), minerals and vitamins (5 g in one Kg of concentrates). The other calves were conducted at pasture, on artificial grasslands, with irrigation and fertilizers. The stocking rate was between 1500 and 2500 Kg/ha. This group was only fed with grass and no concentrate was provided. Acaricide treatments were applied to all the animals in outside herds every two weeks to prevent ticks infestation, in suckling herds as well as after weaning. The growing period lasted until the age of thirteen to eighteen months in intensive feeding regime, and until the age of sixteen to 22 months at pasture. After that period, from one to three males and fifteen to twenty females were kept for breeding per year. The rest of the males was slaughtered and the rest of the females was sold. The Herd-Year-Sex (HYSf) group depending on the fattening environment, the weaning period and the sex was recorded for all animals. Animals were first weighted (initial weight) between 25 and 65 days after weaning (initial age) and their last weighing (final weight) occurred between 180 and 445 days after weaning (final age) depending on the fattening environment and the future of the animals. Animals were weighted every two weeks and the average daily gain was calculated (ADGf). Weights at fixed ages were calculated at monthly interval after the seventh month of age on each animal, from the measured weights, by interpolation according to the procedure used in the French performance testing scheme (Institut de l'Elevage and INRA, 2005).

2.2 Statistical analysis

2.2.1 Generalized linear models

The generalized linear model used to describe the average daily gain during fattening (ADGf) was:

$$y = \text{sire} + \text{dam} + \text{HYSf} + \text{weaning weight} + \text{weaning age} + \text{sire*fattening environment} + \text{fattening duration} + \varepsilon$$

where **y** was the average daily gain.
HYSf was the Herd-Year-Sex group during fattening depending on the fattening environment, the weaning period and the sex.
ε was the error.

The generalized linear model used to describe the weights at nine, twelve, fifteen and eighteen months was:

$$y = \text{sire} + \text{dam} + \text{HYSf} + \text{weaning weight} + \text{weaning age} + \text{sire*fattening environment} + \varepsilon$$

where **y** was the weight at fixed ages of respectively nine, twelve, fifteen and eighteen months.
HYSf was the Herd-Year-Sex group during fattening depending on the fattening environment, the weaning period and the sex.
ε was the error.

General data analysis and the variance analysis using the generalized linear models were done by SAS. The following statistical analyses (multivariate, bivariate and random regression analysis) were performed by ASReml.

2.2.2 Multivariate analysis: comparison within fattening environments

Weights at fixed ages were analysed first separately in each environments, the following multivariate animal model was used to the sub-sample between intensive feeding regime and pasture.

$$\begin{bmatrix} y_9 \\ y_{12} \\ y_{15} \end{bmatrix} = \begin{bmatrix} X_9 & 0 & 0 \\ 0 & X_{12} & 0 \\ 0 & 0 & X_{15} \end{bmatrix} \begin{bmatrix} b_9 \\ b_{12} \\ b_{15} \end{bmatrix} + \begin{bmatrix} Z_9 & 0 & 0 \\ 0 & Z_{12} & 0 \\ 0 & 0 & Z_{15} \end{bmatrix} \begin{bmatrix} a_9 \\ a_{12} \\ a_{15} \end{bmatrix} + \begin{bmatrix} \varepsilon_9 \\ \varepsilon_{12} \\ \varepsilon_{15} \end{bmatrix}$$

where:

$\mathbf{y_i}$ represented the vector of each three traits analysed (live weight at nine months, twelve months and at fifteen months) on the i^{th} animal within each environment.
$\mathbf{b_i}$ was a vector of fixed effects, including the sex (two levels) and the contemporary group within sex and feeding system (eighteen groups in each fattening environment); the weaning weight (WW) and weaning age (WA) as linear covariables.
$\mathbf{X_i}$ was the incidence matrix connecting the **y** variables with the fixed effects.
$\mathbf{a_i}$ was a vector of additive genetic effects of dimension **n** = number of animal in the respective fattening environment.
$\mathbf{Z_i}$ was the incidence matrix of order **n** of the additive genetic effects.
$\mathbf{e_i}$ was a vector of residual random effects common to all the observations in each environment.

2.2.3 Bivariate analysis: comparison between fattening environments

Combinations of weights at fixed age measured in each environment (H: intensive feeding regime, L: pasture management) were studied similarly with the following bivariate animal model:

$$\begin{bmatrix} y_H \\ y_L \end{bmatrix} = \begin{bmatrix} X_H & 0 \\ 0 & X_L \end{bmatrix} \begin{bmatrix} b_H \\ b_L \end{bmatrix} + \begin{bmatrix} Z_H & 0 \\ 0 & Z_L \end{bmatrix} \begin{bmatrix} a_H \\ a_L \end{bmatrix} + \begin{bmatrix} \varepsilon_H \\ \varepsilon_L \end{bmatrix}$$

where:

y was a vector of one weight calculated on animal i^{th} in H or L.
$\mathbf{b_i}$ was a vector of fixed effects, including the sex (two levels) and the contemporary group within sex and fattening environment (eighteen groups in each feeding system); the weaning weight (WW) and weaning age (WA) as linear covariables.
$\mathbf{X_i}$ was the incidence matrix connecting the **y** variables with the fixed effects.
$\mathbf{a_i}$ was a vector of additive genetic effects of dimension **n** = number of animal in the respective fattening environment.
$\mathbf{Z_i}$ was the incidence matrix of order **n** of the additive genetic effects.
$\mathbf{e_i}$ was a vector of residual random effects common to the observations, within each fattening environment.

In the previous model **a** and **b** were obtained after solving the mixed model equation:

$$\begin{bmatrix} X'X & X'Z \\ Z'Z & ZZ' + A^{-1} \otimes G^{-1} \end{bmatrix} \begin{bmatrix} b \\ a \end{bmatrix} = \begin{bmatrix} Xy \\ Zy \end{bmatrix}$$

where:

$\mathbf{G} = \mathbf{G}^{-1} \otimes \mathbf{A}^{-1}$

$\mathbf{G}$ was the additive var-covariance respectively between the j^{th} traits.

A was the numerator relationship matrix.

$\otimes$ was the direct product operator.

2.2.4 Random regression: comparison between fattening environments along the fattening period

The live weights of each animal maintained in both fattening environments were recorded regularly and these data were studied with the following bivariate random regression model. (H: intensive feeding regime, L: pasture management)

$$\begin{bmatrix} y_H \\ y_L \end{bmatrix} = \begin{bmatrix} X_H & 0 \\ 0 & X_L \end{bmatrix} \begin{bmatrix} b_H \\ b_L \end{bmatrix} + \begin{bmatrix} Z_H & 0 \\ 0 & Z_L \end{bmatrix} \begin{bmatrix} a_H \\ a_L \end{bmatrix} + \sum_{p_H=0}^{k-1} Z_3 \lambda_{p_H} + \sum_{q_L=0}^{k-1} Z_4 \lambda_{q_L} + \in_{ij}$$

where:

y was a vector of the live weight of the i^{th} animal at the age j in H or L.

b was a vector of fixed effects linked to the combination of date at weighing, fattening environment and sex. A general regression equation on age of order three was included into the model as well as another one intra calving number of the dam.

$\mathbf{X_i}$ was the incidence matrix connecting the **y** variables with the fixed effects.

$\mathbf{a_H}$ and $\mathbf{a_L}$ were vectors (of dimension **n** = number of calves) of k random regression coefficients of order **m** for the additive genetic effects ($\mathbf{a_i}$) in the H and L respectively.

$\boldsymbol{\lambda_p}$ and $\boldsymbol{\lambda_q}$ were vectors of dimension $\mathbf{l_{nH}}$ and $\mathbf{l_{nL}}$ (**nH** and **nL** = number of calves in both fattening environments) of the individual permanent environment random effects ($\boldsymbol{\lambda_p}$ and $\boldsymbol{\lambda_q}$) due to the repetition of the dependant variable on each animal in H and L respectively. The order of adjustment of the ***k*** random regression coefficients was k_p and k_q.

$\mathbf{Z_H}, \mathbf{Z_L}, \mathbf{Z_3}$ **and** $\mathbf{Z_4}$ were the incidence matrixes of dimension ***n*** x k_m for $\mathbf{Z_H}$ and ZL, and dimension **n x** k_{pH} and **n x** k_{pL} for $\mathbf{Z_3}$ and $\mathbf{Z_4}$. These matrices included the elements $\mathbf{Z_H} = \sum_{H=0}^{k-1} \phi_H(t_{ij}^*)$ and $\mathbf{Z_L} = \sum_{L=0}^{k-1} \phi_L(t_{ij}^*)$ for the additive genetic effects. For the individual permanent environment random effects these matrices were $\mathbf{Z_3} = \phi_{p_H}(t_{ij}^*)$ and $\mathbf{Z_4} = \phi_{q_L}(t_{ij}^*)$. For both random effects the elements $\phi_{x_i}(t_{ij}^*) = \Phi_i$ corresponded to the coefficient of Legendre polynomial.

t_{ij}^* was the age transformed in standardized form between –1 and +1, which was necessary for the use of orthogonal polynomials ($\boldsymbol{\Phi_i}$) of order k_i.

$\sum$ meant that the total effects were estimated as the sum of the corresponding terms $\boldsymbol{\Phi_i}$.

$\in_{ij}$ was a vector of residual random effects common to all the observations.

The equation of the mixed model equation for the random effects included in the model would be:

$$\begin{bmatrix} X'X & X'Z_H & X'Z_L & X'Z_3 & X'Z_4 \\ Z_H'X & Z_H'Z_H + A^{-1} \otimes K_{HH}^{-1} & Z_H'Z_L + A^{-1} \otimes K_{HL}^{-1} & Z_H'Z_3 & Z_2'Z_4 \\ Z_L'X & Z_L'Z_L + A^{-1} \otimes K_{LH}^{-1} & Z_L'Z_L + A^{-1} \otimes K_{LL}^{-1} & Z_L'Z_3 & Z_2'Z_4 \\ Z_3'X & Z_3'Z_H & Z_3'Z_L & Z_3'Z_3 + I_{pH} \otimes K_{pH}^{-1} & Z_2'Z_4 \\ Z_4'X & Z_4'Z_H & Z_4'Z_L & Z_4'Z_3 & Z_4'Z_4 + I_{qL} \otimes K_{qL}^{-1} \end{bmatrix} \begin{bmatrix} b_i \\ a_H \\ a_L \\ p_H \\ q_L \end{bmatrix} = \begin{bmatrix} X'y \\ Z_H'y \\ Z_L'y \\ Z_3'y \\ Z_4'y \end{bmatrix}$$

where:

A was the matrix of the numerator of the relationship.

$\otimes$ was the symbol of the product of Kronecker.

$\mathbf{K_i}$ was the (co)variance matrix of the random regression coefficients applied to each effect indicated by the sub-indices.

Various runs were done for the selection of the best model, according to the recommendations of Foulley and Robert-Granie (2000). The random effects due to the animal and the permanent environment were compared using polynomial of order two or three.

From these elements, it was achieved a complex (co)variance structure between intercept (0) and the random regression coefficients, for both genetic effects ($\mathbf{a_H}$ and $\mathbf{a_L}$) and permanent environment effects (***pH*** and ***qL***). The global (co)variance structure of the random effects of this model, for a simple case of linear adjustment (order one) was:

$$\mathbf{V}\begin{bmatrix} a_{H_0} \\ a_{H_1} \\ a_{L_0} \\ a_{L_1} \\ p_0 \\ p_1 \\ q_0 \\ q_1 \\ r \end{bmatrix} = \begin{bmatrix} A\sigma^2_{aH_{00}} & A\sigma_{aH_{10}} & A\sigma_{aH_0L_0} & A\sigma_{aH_0L_1} & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{aH_{01}} & A\sigma^2_{aH_{11}} & A\sigma_{H_1L_0} & A\sigma_{aH_1L_1} & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{aH_0L_0} & A\sigma_{aH_1L_0} & A\sigma^2_{aL_{00}} & A\sigma_{aL_{01}} & 0 & 0 & 0 & 0 & 0 \\ A\sigma_{aH_0L_1} & A\sigma_{aH_1L_1} & A\sigma_{aL_{10}} & A\sigma^2_{aL_{11}} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_p\sigma^2_{p_{00}} & I_p\sigma_{p_{10}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_p\sigma_{p_{01}} & I_p\sigma^2_{p_{11}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I_q\sigma^2_{q_{00}} & I_q\sigma_{q_{10}} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I_q\sigma_{q_{01}} & I_q\sigma^2_{q_{11}} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \epsilon_{ij} \end{bmatrix}$$

It was noticed that this model gave matrixes of random regression coefficients for each feeding systems and across systems as well. According to Jamrozik and Schaeffer (1997), the estimation of the heritability (h^2), the genetic correlations (rg) and the genetic variances for the life weight at the age of j days in the two fattening environments were expressed as:

$$\sigma^2_{g_j} = \Phi_j \, K_{HH} \Phi'_j$$

$$\sigma^2_{g_j} = \Phi_j \, K_{LL} \Phi'_j$$

Similarly, the components for the individual permanent environment effects in the both fattening environments were obtained.

The covariance for the live weight at the same age in both systems was:

$$\sigma_{g_{HL}} = \Phi_j K_{HL} \Phi'_j$$

From these components, heritability and genetic correlations were estimated with the classic method, using the residual variance.

From these RRM procedures, the solution for each animal for the m random regression coefficients was also obtained, from which was calculated the Breeding Value (**BV**) for each animal at whatever age between 210 and 540 days, in both fattening environments:

$$BV^{i}_{j_H} = \sum_{m=0}^{k-1} \Phi_j a'_H$$

$$BV^{i}_{j_L} = \sum_{m=0}^{k-1} \Phi_j a'_L$$

where: $\mathbf{a_i} = [m_0 , m_1 , m_2]$ represented the solution for the animal i[th] in each environments, obtained from a polynomial of order k_m.
m_0, m_1, m_2 corresponded to the intercept, the lineal coefficient and the quadratic coefficient of the genetic model used.

3. RESULTS

3.1 Description of the data

3.1.1 Origin of the animals

In total, 27 sires were used in different frequency over the herd. Nine sires had less than ten offspring and ten sires had between eleven and twenty offspring. Only three sires gave between 21 and 30 calves and five sires gave more than 30 calves (Table 1). Only sixteen calves were born from unknown sire.

Nb. of offspring	from 1 to 10	from 11 to 20	from 21 to 30	> 30	**Total**
Nb. of sires	9	10	3	5	**27**

Table 1. Repartition of the sires.

In the experiment, 267 females and 249 males for a total of 516 animals were used. The distribution of the animals was rather equal between the four different suckling meadow managements and between the sexes. Indeed, between the suckling meadow managements, the repartition of the animals varied from 113 to 141 and from 53 to 72 for the sexes within each suckling meadow management (Table 2).

Suckling meadow management	Female	Male	**Total**
Implanted pasture with irrigation	72	69	**141**
Implanted pasture without irrigation	55	58	**113**
Savannahs with irrigation	70	69	**139**
Savannahs without irrigation	70	53	**123**
Total	**267**	**249**	**516**

Table 2. Repartition of the males and females over the different meadow managements during the suckling period.

The number of animals born over the different calving periods varied from twenty to 76. The distribution of the animals over the different suckling meadow managements within the years was homogeneous except for 2005. That year, no animal was raised in non-irrigated implanted pasture whereas 30 and 27 animals were raised in irrigated implanted pasture and savannah and only seventeen in non-irrigated savannah (Table 3). Before 2000, two calving seasons were applied, and the number of calves from each system was less than 10 calves.

Suckling meadow management	Implanted pasture with irrigation	Implanted pasture without irrigation	Savannahs with irrigation	Savannahs without irrigation	**Total**
Suckling group	MP, PC, B4, PF *	PC	D2, E1 *	D1	
1998-1	5	5	6	4	**20**
1998-2	7	8	8	7	**30**
1999-1	7	6	8	8	**29**
1999-2	6	10	8	8	**32**
2000	14	18	16	15	**63**
2001	16	14	15	14	**59**
2002	18	15	15	13	**61**
2003	20	18	16	18	**72**
2004	18	19	20	19	**76**
2005	30	0	27	17	**74**
Total	**141**	**113**	**139**	**123**	**516**

Table 3. Repartition of the animals over the different meadow managements, herd groups and years during the suckling period.
* In the meadow management implanted pasture with irrigation, 127 animals belonged to the herd group MP, nine to PC, three to B4 and two to PF. In savannahs with irrigation, 130 belonged to D2 and nine to E1.

In total, 284 animals were fattened with an intensive feeding regime; 135 females and 149 males. Fattening at pasture concerned 232 animals; 132 females and 100 males. Over the calving periods, the number of animals in each fattening group varied from eight to 42 for the intensive feeding regime and from seven to 36 at pasture (Table 4).

Fattening environment	Intensive feeding regime			Pasture			
Sex	Female	Male	Total	Female	Male	Total	**Total**
1998-1	0	9	9	11	0	11	**20**
1998-2	0	8	8	14	8	22	**30**
1999-1	11	11	22	7	0	7	**29**
1999-2	9	9	18	6	8	14	**32**
2000	15	23	38	14	11	25	**63**
2001	14	17	31	13	15	28	**59**
2002	21	14	35	14	12	26	**61**
2003	21	21	42	16	14	30	**72**
2004	23	17	40	18	18	36	**76**
2005	21	20	41	19	14	33	**74**
Total	**135**	**149**	**284**	**132**	**100**	**232**	**516**

Table 4. Repartition of the animals over the fattening environments, sexes and years during the fattening period.

Table 5 shows that the distributions of the animals weaned from each meadow managements were rather equal within the fattening environments. In other terms, the composition of the fattening groups was balanced according to the meadow managements.

	Fattening environment		
Suckling meadow management	Intensive feeding regime	Pasture	**Total**
Implanted pasture with irrigation	78	63	**141**
Implanted pasture without irrigation	61	52	**113**
Savannahs with irrigation	74	65	**139**
Savannahs without irrigation	71	52	**123**
Total	**284**	**232**	**516**

Table 5. Repartition of the animals within the different meadow managements during the suckling period and the fattening environments.

The distribution of the calves according to the calving number of their dam is given in Table 6. The Creole cows showed an exceptional longevity with 126 calves having their dams from parity order seven and higher.

Parity order	1	2	3	4	5	6	7	8	9	10	11	12	≥13	**Total**
Number of calves	79	71	74	65	57	44	36	25	19	11	11	10	14	**516**

Table 6. Distribution of the calves according to the parity order of their dam.

3.1.2 Means and frequencies of the variables

Table 7 represents basic information of the variables of interest in the study such as the number of animals, the observed mean, the standard deviation, the minimum and the maximum. The means of the weaning weight and suckling ADG were calculated on 515 animals only because the weaning weight has not been recorded for one animal in the data set. The means of the weights at fifteen and eighteen months were calculated with the animals not slaughtered yet at that moment.

Variable	N	Mean	Std Dev	Minimum	Maximum
Birth weight	516	27	4.38	12	45
Weaning weight	515	157	28.46	82	236
Weaning age	516	212	17.43	164	273
Suckling ADG	515	615	131.31	246	981
Weight at 9 months	514	174	32.41	90	255
Weight at 12 months	516	220	47.72	88	358
Weight at 15 months	488	273	58.44	109	428
Weight at 18 months	355	310	63.82	147	509
Fattening duration	516	283	66.96	112	421
Fattening ADG	516	559	205.83	4	1141
Num. of weighings	516	18	6.01	4	30

Table 7. Basic statistics on the growth variables.
AGD: average daily gain. Weights are in Kg, age and duration are in days and ADG are in g/day.

Growth traits until weaning were similar between the two fattening environments. The birth weight was equal in groups (27 Kg), the weaning weight and the suckling average daily gain reached 155 Kg and 606 g/day in intensive feeding regime against 159 Kg and 626 g/day at pasture (Table 8). After weaning, all weights reached lower levels at pasture. The growth rate at pasture was about 40% smaller than the growth rate in intensive feeding regime (678 g/day versus 413 g/day).

	Intensive feeding regime		Pasture	
Variable	Mean	StDev	Mean	StDev
Birth weight	27	4.41	27	4.34
Weaning weight	155	29.79	159	26.64
Weaning age	212	17.17	212	17.78
Suckling ADG	606	139.22	626	120.39
Weight at 9 months	176	35.59	172	27.93
Weight at 12 months	237	48.81	201	37.87
Weight at 15 months	297	54.58	246	50.29
Weight at 18 months	342	59.26	287	56.83
Fattening duration	245	51.10	329	53.97
Fattening ADG	678	161.91	413	153.63
Num. of weighings	17	4.86	20	6.74

Table 8. Basic statistics on the growth variables in the two different fattening environments.
AGD: average daily gain. Weights are in Kg, age and duration are in days and ADG are in g/day.

3.1.3 Analysis of variance: generalized linear models

The average daily gain during fattening, the weights at nine, twelve, fifteen and eighteen months were studied in separate generalized linear model analyses. All models fitted the data with an R^2 varying between 86.9% and 93.4%. The Herd/Year/Sex group during fattening and the weaning weight were highly significant for all five variables. The interaction between the fattening environment and the sire was a significant covariable for the weight at eighteen months and showed a tendency for the weight at twelve months (Table 9).

Variable	N	R^2	√MSE	sire	dam	HYSf	WW	WA	FE*sire	FD
ADGf	500	86.9	100.1	NS	NS	***	**	NS	NS	**
W9	498	91.9	12.3	NS	NS	***	***	***	NS	
W12	500	91.2	19.0	T	NS	***	***	***	T	
W15	474	90.4	25.0	T	NS	***	***	***	NS	
W18	347	93.4	25.9	**	***	***	***	***	**	

Table 9. Analysis of variance for the average daily gain during fattening, the weights at nine, twelve, fifteen and eighteen months.
***: p<0.001, **: p<0.01, *: p<0.05, T (tendency): p<0.1, NS: Not significant.
ADGf: fattening average daily gain, W9: weight at nine months, W12: weight at twelve months, W15: weight at fifteen months, W18: weight at eighteen months, HYSf: herd/year/sex group during fattening, WW: weaning weight, WA: weaning age, FE: fattening environment, FD: fattening duration.

3.2 Multivariate analysis

3.2.1 Multivariate analysis: comparison within fattening environments

The analysis included the weights at nine, twelve and fifteen months as dependent variables when the animals were either fattened with an intensive feeding regime or raised at pasture.

The heritability in intensive feeding regime was higher than at pasture for all three weights. In both fattening environments, the trait with the smallest heritability was the weight at nine months (0.23 +/- 0.15 in intensive feeding regime and 0.09 +/- 0.11 at pasture) (Table 10). Table 11a shows high genetic correlations between the different weights in intensive feeding regime (between 0.85 +/- 0.09 and 0.98 +/- 0.08). The same observation was given at pasture (genetic correlation between 0.97 +/- 0.24 and 1.14 +/- 0.27) although the precision was lower (Table 11b). In both fattening environments, the genetic variance increased with the age of the animals.

	Heritability	
	Intensive feeding regime	Pasture
W9	0.23 +/- 0.15	0.09 +/- 0.11
W12	0.50 +/- 0.17	0.15 +/- 0.13
W15	0.44 +/- 0.17	0.19 +/- 0.15

Table 10. Heritability for the weights at nine, twelve and fifteen months in intensive feeding regime and at pasture.
W9: weight at nine months, W12: weight at twelve months and W15: weight at fifteen months.

	W9	W12	W15
W9	66.0	0.98 +/- 0.08	0.90 +/- 0.13
W12	143.2	323.6	0.85 +/- 0.09
W15	148.6	310.9	415.8

Table 11a. Genetic variances, covariances and correlations for the weights at nine, twelve and fifteen months in intensive feeding regime.

	W9	W12	W15
W9	7.7	0.97 +/- 0.24	1.14 +/- 0.27
W12	73.7	32.7	1.03 +/- 0.11
W15	99.9	244.9	84.1

Table 11b. Genetic variances, covariances and correlations for the weights at nine, twelve and fifteen months at pasture.

Table 11a and 11b. The diagonals of the tables present the genetic variances (Kg^2). Above the diagonal stand the genetic correlations with their precisions and below stand the genetic covariances (Kg^2). W9: weight at nine months, W12: weight at twelve months and W15: weight at fifteen months.

3.2.2 Bivariate analysis: comparison between fattening environments

The bivariate analysis included as dependent variables simultaneously two weights measured in the two different fattening environments, in different combinations of the weight at fixed ages of nine, twelve and fifteen months in both environments, and of eighteen month at pasture.

The heritability of the different weights measured in intensive feeding regime was higher than at pasture (Table 12). The heritability of the weights at nine and twelve months at pasture was almost null. It increased to 0.18 +/- 0.15 and 0.28 +/- 0.18 for the weights at fifteen and eighteen months. The genetic variance was notably higher in intensive feeding regime than at pasture and increased with the age of the animals. Indeed the genetic variance for the weight at nine months was equal to 80 in the intensive feeding regime and four at pasture. The genetic variance for the weight at fifteen months was equal to 401 in the intensive feeding regime and 82 at pasture. All genetic correlations showed very poor precision (Table 13).

	Heritability		Genetic variance		Genetic covariance
	Intensive feeding regime	Pasture	Intensive feeding regime	Pasture	
W9	0.28 +/- 0.16	0.05 +/- 0.1	80	4	8
W12	0.53 +/- 0.17	0.08 +/- 0.12	343	18	17
W15	0.42 +/- 0.18	0.18 +/- 0.15	401	82	-20
W18		0.28 +/- 0.18		223	

Table 12. Heritability, genetic variance and genetic covariance for the weights at nine, twelve, fifteen and eighteen months in intensive feeding regime and at pasture.
W9: weight at nine months, W12: weight at twelve months, W15: weight at fifteen months and W18: weight at eighteen months.
Genetic variance and genetic covariance in Kg^2.

	W9 pasture	W12 pasture	W15 pasture	W18 pasture
W9 intensive feeding regime	0.50 +/- 0.97	0.26 +/- 0.71	-0.56 +/- 0.47	-0.15 +/- 0.48
W12 intensive feeding regime	0.87 +/- 1.3	0.22 +/- 0.58	-0.38 +/- 0.37	-0.33 +/- 0.33
W15 intensive feeding regime	1.67 +/- 1.28	0.52 +/- 0.75	-0.11 +/- 0.46	-0.19 +/- 0.38

Table 13. Genetic correlation for different weights in intensive feeding regime and at pasture.
W9: weight at nine months, W12: weight at twelve months, W15: weight at fifteen months and W18: weight at eighteen months.

3.3 Random regression: comparison between fattening environments along the fattening period

The heritability for weights during the whole fattening period was higher in intensive feeding regime than at pasture. At pasture, heritability was rather constant varying from 0.18 to 0.23 whereas in intensive feeding regime, the heritability first showed a small increase from 0.40 at 210 days of age to 0.45 at 270 days of age and then decreased to 0.23 at 540 days. The genetic correlation presented an increase from 0.70 to 0.97 between 210 and 300 days of age followed by a decrease until 0.59 at 540 days (Figure 2 and Annex 1).

Genetic correlation for weights within each fattening environment presented high values between closed ages. The genetic correlations decreased comparing weights at more distant ages. This tendency was more visible at pasture where the values dropped from 1 to 0.46 instead of 1 to 0.73 in intensive feeding regime (Figure 3, Annex 2 and 3).

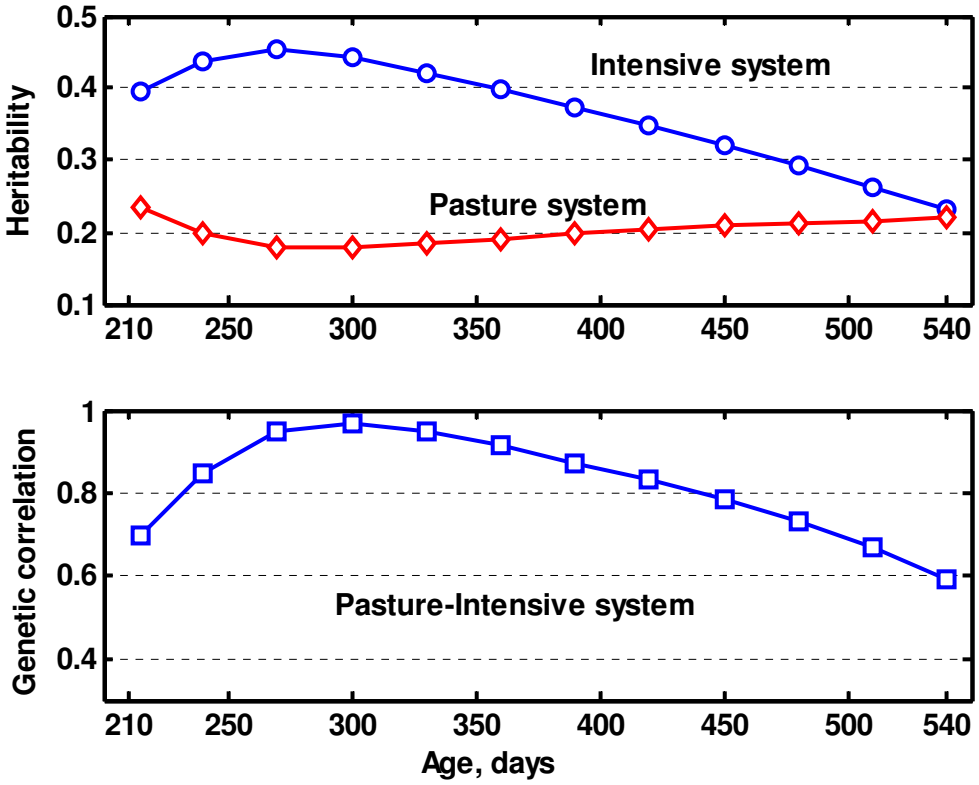


Figure 2. Heritability and genetic correlation between live weight at different ages and between the two fattening environments.

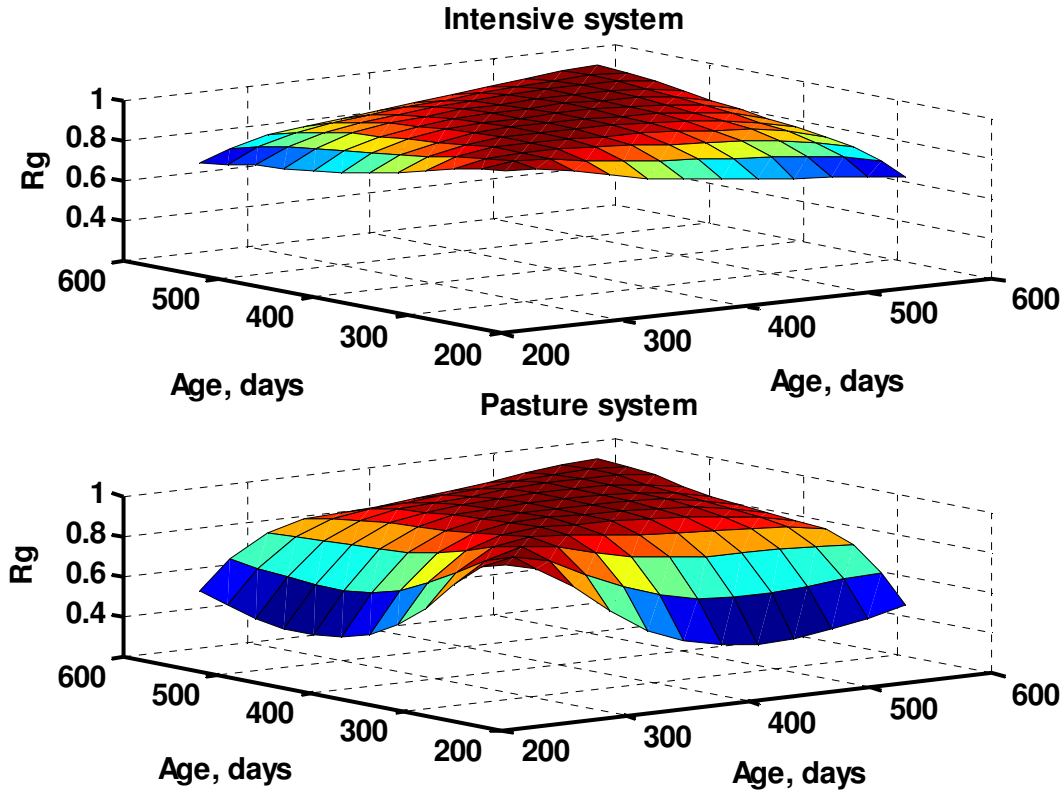


Figure 3. Genetic correlation between live weights at different ages in intensive feeding regime and at pasture.

3.4 Breeding value estimations

Estimated breeding value obtained as solutions of the Random Regression analysis of the weight at fifteen and eighteen months in intensive feeding regime and at pasture respectively are presented in Figure 4.

The 76 best animals (10% out of the total animals for whom breeding values were calculated) for each trait were represented. When both subgroups of elite animals were merged, 38 animals were present in both top ranking groups. In other words, this meant that one third of the elite animals shared both 10% top groups. Over the all 762 animals, these animals present in the top ranking for both fattening groups corresponded to 5% of the population. The coefficient of determination obtained by the regression line linking the breeding value for the weight at eighteen months at pasture and the weight at fifteen months in intensive feeding regime was not highly significant (0.597). Fifty-two animals with a positive breeding value for the weight at eighteen months at pasture had a negative breeding value for the weight at fifteen months in intensive feeding regime. Vice-versa, 97 animals with a positive breeding value for the weight at fifteen months in intensive feeding regime had a negative breeding value for the weight at eighteen months at pasture. In total, 149 animals (19.6%) presented a positive breeding value for one trait and a negative breeding value for the other trait.

Table 14 shows that 43.9% of the animals shared the same rank for the breeding values in both fattening environments. For the 427 animals left, they had different breeding value ranks according to the fattening environments.

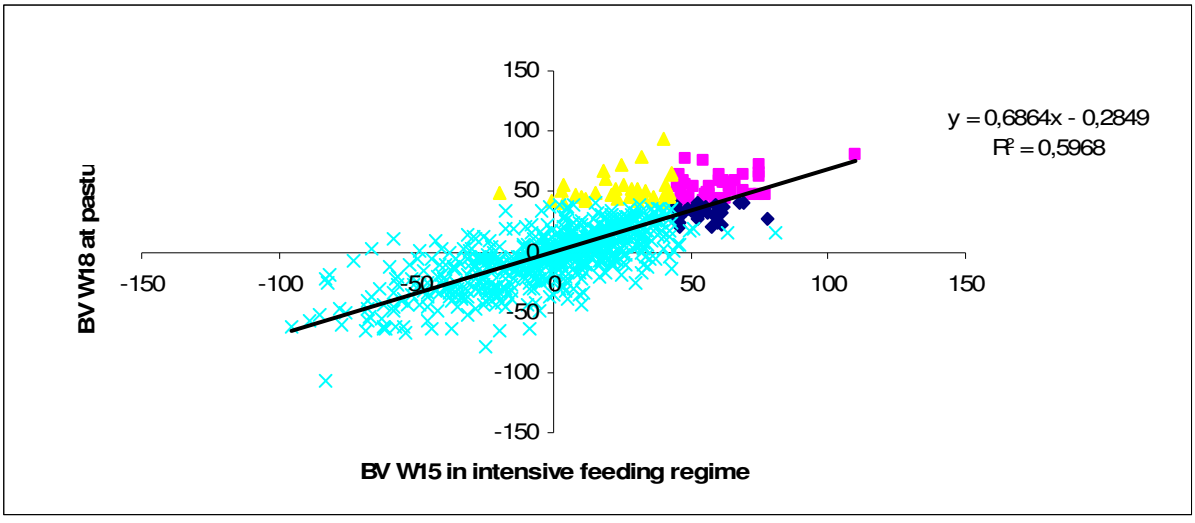


Figure 4. Representation of estimated breeding values for the weights at fifteen and eighteen months, in intensive feeding regime and at pasture.
W15: weight at fifteen months, W18: weight at eighteen months, BV: Breeding value in Kg.

▲ 10% best animals for the BV of W15 in intensive feeding regime (76 animals).
♦ 10% best animals for the BV of W18 at pasture (76 animals).
■ animals present in both previous groups (BV of W15 in intensive feeding regime and BV of W18 at pasture) (38 animals).
X All the other animals

		Rank BV W18 at pasture						
		1	2	3	4	5	6	**Total**
Rank BV W15 intensive feeding regime	1	38 (5.0%)	31 (4.1%)	6 (0.8%)	1 (0.1%)	0	0	**76 (10%)**
	2	22 (2.9%)	42 (5.5%)	36 (4.7%)	10 (1.3%)	4 (0.5%)	0	**114 (15%)**
	3	11 (1.4%)	33 (4.3%)	84 (11.0%)	47 (6.2%)	12 (1.6%)	4 (0.5%)	**191 (25%)**
	4	4 (0.5%)	7 (0.9%)	50 (6.6%)	91 (11.9%)	33 (4.3%)	6 (0.8%)	**191 (25%)**
	5	1 (0.1%)	1 (0.1%)	11 (1.4%)	33 (4.3%)	41 (5.4%)	27 (3.5%)	**114 (15%)**
	6	0	0	4 (0.5%)	9 (1.2%)	24 (3.1%)	39 (5.1%)	**76 (10%)**
	Total	**76 (10%)**	**114 (15%)**	**191 (25%)**	**191 (25%)**	**114 (15%)**	**76 (10%)**	**762 (100%)**

Table 14. Repartition of the animals according to their breeding values for the weights at fifteen and eighteen months in both fattening environments.
Ranks of breeding value:

1: 10% of the animals having the best breeding values
2: 15% of the animals having breeding values belonging to the second best rank for breeding value
3: 25% of the animals having breeding values belonging to the third best rank for breeding value
4: 25% of the animals having breeding values belonging to the fourth best rank for breeding value
5: 15% of the animals having breeding values belonging to the fifth best rank for breeding value
6: 10% of the animals having breeding values belonging to the sixth best rank for breeding value

The table presents the number of animals in each class and in brackets the corresponding percentage.
W15: weight at fifteen months, W18: weight at eighteen months, BV: breeding value.

4. Discussion

The initial results have shown a better growth potential for animals fattened in intensive feeding regime rather than at pasture (Table 8). The analysis of variance with generalized linear model indicated the influence of the Herd/Year/Sex (variable depending on the fattening environment, the weaning period and the sex) as well as the weaning weight on the growths traits of the heifers and bulls during fattening (Table 9). The results also gave a first tendency for the presence of the GxE interaction's influence on growth traits by the means of the interaction between the variables sire and fattening environment.

In the analyses of (co)variance components, the genetic variance of the weights increased with the age of the animals (Table 11a, 11b and 12). These results were in accordance with Plasse et al. (2002) who observed a genetic variance for the weights of beef cattle raised at pasture in tropical condition varying from 4.86 to 98.76 Kg^2 between birth and eighteen months. This was due to an increase of the weight and of the environmental impact with the age.

The estimates of heritability obtained were consistent with the literature on these parameters obtained in tropical cattle (Lobo et al., 2000 and Plasse et al., 2002). According to all analysis, the lowest heritability for the weight was associated to the animals raised at pasture and the highest heritability for the weight was associated to the animals fattened in intensive feeding regime (Table 10, 12 and Figure 2). This proved the better expression of the genetic potential in intensive feeding regime. In intensive feeding regime, animals were raised in more homogenous and controlled conditions than at pasture and therefore the residual variance due to the environment was reduced in favour of the genetic variance. This statement was confirmed by the fact that genetic variances observed were higher in intensive feeding regime than at pasture (Table 11a, 11b and 12). The lower heritability at pasture could also reflect the incidence of adaptation traits, such as adaptation to direct effect of tropical climate or to internal or external parasites. Indeed, such traits were generally described as poorly heritable (Burrows and Prayaga, 2004). Other physiological traits could also play a role in this observation, such as individual variability for forage digestion (Boval et al., 1996).

The random regression among the fattening period showed a decrease in the heritability for the weight in intensive feeding regime (Figure 2) which could be explained by a higher effect of the environment on the phenotypic variance with the age. However, this tendency was not observed at pasture and this would mean that the proportion between genetic variance and phenotypic variance stayed equal during the whole fattening period at pasture. It resulted in an optimal selection at the beginning of the fattening period (between 210 and 350 days) for intensive feeding regime. At pasture, no real moment during the fattening period could optimize the selection although the heritability was slightly increased at the end of the fattening period (after 450 days). The reasons for this difference in heritability evolution between intensive feeding regime and pasture are still unclear and more research would be needed to give some clues.

In multivariate analysis, genetics correlations calculated between weights at nine, twelve and fifteen months within the same fattening environment were closed to one with satisfactory precisions (Table 11a and 11b). The random regression along the age also presented high correlation between different

weights within the same fattening environment but these correlations decreased when the weights comparisons were made at distant ages (Figure 3). This seemed logical as more variance due to the environment was involved between weights measured at distant ages. This decrease was more obvious at pasture than in intensive feeding regime meaning that weights at distant ages were less linked at pasture that in intensive feeding regime. This showed that the influence of the environment on the weight was higher at pasture than in intensive feeding regime. In bivariate analysis, genetic correlations between same weights obtained in each fattening environment were very low and even below zero (Table 13). Negative genetic correlations between pasture and intensive feeding regime indicated that the animals with a high growth potential in one system would have poor performances in the other system. This observation could have been a strong evidence of the existence of genotype by environment interaction, however the results varied between comparisons and the precisions were too low. Therefore results with satisfactory precision were needed to confirm this observation.

The random regression allowed observing the evolution of the genetic correlation for weight between the two fattening environments along the fattening period. Genetic correlations tended to decrease with the age so it indicated a higher divergence in animals' performances when the animals have been for a long time in different environments and therefore an increase in the GxE interaction. The increase of the genetic correlations from 210 to 300 days of age was certainly not due to a diminution of the GxE interaction but more probably caused by a lack in the statistical model. Indeed, it did not take into account different parameters such as the genetic variance due to the dam or the variance due to the mothering environment and this could have biased the genetic correlation estimations. The decrease in genetic correlation between fattening environments along the time was not found in the literature, however other articles observed a decrease in the genetic correlation when the distance between herd production levels increased (Menendez and Mandonnet, 2006; Hayes et al., 2003 and Pegolo et al. 2006). This indicated that the GxE interaction could only be appreciated when the difference in environmental conditions was enough contrasting.

The analysis of the breeding values for the weights at fifteen months in intensive feeding regime and at eighteen months at pasture illustrated that the relationship between the breeding values was supported by a low level of significance (R^2=0.597). These two traits were chosen as they were closer to the end point of the fattening period in the two systems, and they could represent a good selection objective in each management condition. Only one third of the 10% best animals in one fattening group were also the best in the other (Figure 4). These observations demonstrated the presence of GxE interaction. Moreover, these results pointed out the consequence of the GxE interaction on the re-ranking of the animals. It was observed that 19.6% of the animals contributing to the genetic improvement of one trait made the genetic gain of the other trait decreased. These observations pointed out the importance to take into account the environmental condition when the purpose is to make genetic improvement. The efficiency of breeding programs may consequently depend on the adequation between the environment during the performance testing and in commercial farms (e.g.: climate, sanitary conditions, nutrition or housing). The introduction of the GxE interaction will guarantee a more precise genetic evaluation of animals present in different environmental conditions. The objective would be either to select the best animals in a specific environment that is common to

commercial farms or to select the most “robust” animals, i.e. the animals presenting good performances among different environments. This last option seems really promising under the tropics, where environmental conditions are heterogeneous. These animals that met the requirement to belong to the 10% best animals for both traits represented 5% out of a population of 762.
This study also compared two kinds of statistical analysis used to appreciate the GxE interaction and showed the great advantages of the RR model for the genetic evaluation of the animals. This statistical procedure allowed an appreciation of the genetic parameters such as the heritability, the genetic variance and the genetic correlation, along the entire age trajectory. The random regression analysis was also expected to give more precise estimates for the genetic correlations between the fattening groups, as it took into account the repetition of the trait within animal (Menendez Buxadera, 2004).

Using two different statistical approaches, this study has confirmed the existence of the GxE interaction during the fattening period for beef cattle raised in tropical conditions. Such results are important to consider for selection of beef cattle for post weaning growth depending on the fattening environment. The results also illustrated the change in individual performances with the environmental conditions, called re-ranking. The random regression model is an important tool in the GxE interaction investigation and should be used to carry out studies on other important traits such as nutrition, carcass measurements, fertility, health or behavior. These studies could help to elucidate the reasons of this interaction and lead to raise the interest for local breeds, well adapted to their local environments.

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ANNEXES

Annex 1

	Heritability		Genetic correlation
Age	Intensive feeding regime	pasture	Intensive feeding regime/pasture
210	0.40	0.23	0.70
240	0.44	0.20	0.85
270	0.45	0.18	0.95
300	0.44	0.18	0.97
330	0.42	0.18	0.95
360	0.40	0.19	0.91
390	0.37	0.20	0.87
420	0.35	0.20	0.83
450	0.32	0.21	0.79
480	0.29	0.21	0.73
510	0.26	0.21	0.67
540	0.23	0.22	0.59

Heritability for the weight at different ages. Genetic correlations between live weight at different ages and between the two fattening environments.
Age in days. Genetic correlation in Kg^2

Annex 2

	210	240	270	300	330	360	390	420	450	480	510	540
210	1											
240	0.97	1										
270	0.85	0.96	1									
300	0.71	0.87	0.97	1								
330	0.59	0.78	0.93	0.99	1							
360	0.52	0.72	0.89	0.97	1.00	1						
390	0.48	0.68	0.86	0.95	0.99	1.00	1					
420	0.46	0.67	0.85	0.94	0.98	0.99	1.00	1				
450	0.47	0.67	0.84	0.93	0.97	0.98	0.99	1.00	1			
480	0.49	0.68	0.84	0.92	0.95	0.97	0.98	0.99	1.00	1		
510	0.53	0.70	0.83	0.90	0.92	0.94	0.95	0.97	0.98	0.99	1	
540	0.57	0.71	0.82	0.87	0.88	0.89	0.91	0.93	0.95	0.97	0.99	1

Genetic correlations between live weights at different ages at pasture.
Age in days.

Annex 3

	210	240	270	300	330	360	390	420	450	480	510	540
210	1											
240	0.99	1										
270	0.95	0.99	1									
300	0.91	0.97	0.99	1								
330	0.88	0.94	0.98	1.00	1							
360	0.85	0.92	0.97	0.99	1.00	1						
390	0.83	0.90	0.96	0.98	0.99	1.00	1					
420	0.81	0.89	0.94	0.97	0.99	0.99	1.00	1				
450	0.79	0.87	0.93	0.96	0.97	0.99	0.99	1.00	1			
480	0.78	0.85	0.91	0.94	0.96	0.97	0.98	0.99	1.00	1		
510	0.76	0.83	0.88	0.91	0.93	0.94	0.96	0.97	0.98	1.00	1	
540	0.73	0.79	0.84	0.86	0.88	0.90	0.92	0.93	0.95	0.98	0.99	1

Genetic correlations between live weights at different ages in intensive feeding regime.
Age in days.