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Exploring underlying drivers of genotype by environment interactions in feed efficiency traits for dairy cattle with a mechanistic model involving energy acquisition and allocation

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ABSTRACT

Feed efficiency (FE) is a complex phenotype made up of multiple traits for which there is potential for substantial genotype by environment interaction (G × E). The objective of this study is to evaluate the extent of G × E for FE traits with a simulation approach. We used a mechanistic model of the dairy cow that simulates trajectories of phenotypes throughout lifetime, depending on trajectories of resource acquisition and allocation, driven by 4 genetic scaling parameters, and depending on the nutritional environment (quantity and quality of feed resources). The cow model, calibrated for a grass-based farming system and seasonal calving, was combined with a genetic module. This simulated genetic variation in the 4 genetic scaling parameters related to resource acquisition and allocation, based on a simple balanced pedigree structure (200 paternal half-sib groups each of 100 daughters). The population of 20,000 cows generated was simulated in 4 nutritional environment scenarios, representing a gradient of feeding constraints. In each scenario, 6 traits derived from the model outputs were analyzed to obtain population genetic parameters. Genetic correlations between second-lactation production and FE were positive and high in all scenarios and increased as the nutritional environment became more constraining. A measure of lifetime FE was positively correlated with second-lactation production under a less constrained environment, but these correlations decreased as the environment became more constraining. The genetic correlation between body reserves at second calving, and lifetime FE was positive and low in the least constraining scenario and increased as the environment became more constraining. In addition to genetic parameters, we looked at the distributions of acquisition and allocation parameters among the best performing cows for lactation and life FE, in the 2 most contrasted scenarios. The 4 subpopulations of best cows had acquisition and allocation strategies different from the whole population. In conclusion, this simulation study identifies the potential underlying biological basis for important G × E in FE traits. This highlights the importance of having a balanced breeding goal when undertaking selection that should also be based on phenotypes relevant to the target performance environment.

Key words: lifetime efficiency, biological trade-off, body reserves, multitrait selection

INTRODUCTION

Feed efficiency (**FE**) in dairy cows is traditionally measured as a ratio between energy captured as milk product divided by the gross energy consumed by the cow (Tempelman and Lu, 2020). Alternative definitions to this conversion ratio exist (for instance, residual feed intake) and are subject to debate regarding their applications and benefits (Hurley et al., 2016). These debates highlight that FE is an increasingly important trait for the dairy sector: primarily motivated by saving feed costs to improve farm profitability, this trait is also contributing to a more sustainable way of producing animal products. Efficient cows make best use of resources, which limits competition with land dedicated to crops for human food, and produce less waste such as greenhouse gases or nitrogen losses. To implement successful breeding programs for improved FE, 2 challenges need to be addressed. First, it is important to ensure that improvement in short-term FE (e.g., at lactation scale) avoids detrimental correlated responses in cow functionality and resilience. Second, it is important to ensure that animals with high merit for FE are able to accommodate changes in environmental conditions. The first challenge pertains to the complexity of FE, which is a composite trait; it results from various underlying component traits, or subtraits, which are

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dynamic in the way they interact (Fischer et al., 2018). As these subtraits are generally very costly to measure (e.g., feed intake), new selection strategies are based on using multitrait genetic evaluations for FE. However, different combinations of the underlying component traits may achieve the same gain in FE. These different combinations will likely target different aspects of animal physiology that may incur unwanted consequences arising from the selection for FE (e.g., decreased fertility or decreased propensity to withstand environmental challenges). The second challenge pertains to genotype by environment interactions (G × E): benefits from selecting animals with high FE genetic merit should ideally hold up across a wide range of farm systems and environments (Richardson and Herd, 2004; Berry and Crowley, 2013), both in the current conditions but also in the future. The relative importance of the underlying component traits will vary both through time and according to the environment, making it difficult to ascribe them a weight in the multitrait evaluation.

Using mechanistic models or any theoretical framework to relate observed animal traits and genetic variation in their underlying mechanistic drivers is a promising avenue to better explain the observed variation in FE and also to better describe correlations among FE subtraits, which can facilitate the development of a more informed and rational approach to multiple-trait prediction of FE. Existing models have been developed for a single function (growth: Doeschl-Wilson et al., 2007; body reserves mobilization: Friggens et al., 2004; reproduction: Dennis et al., 2018). At the whole-animal level, a mechanistic model of the dairy cow (Puillet et al., 2016) that simulates lifetime dynamics of energy utilization has been developed. The core concept of this model is that energy utilization is made of 2 processes: feed intake (acquisition) and energy partitioning among biological functions (allocation). These processes can be manipulated by changing values of input parameters, which allows the exploration of the functions underlying FE. This model has shown that the same value of a trait (such as FE) can be obtained with various combinations of resource allocation and acquisition. It has also shown that combinations of acquisition and allocation mechanisms that maximize short-term (single lactation) and long-term (lifetime) FE are not the same.

Based on this mechanistic model, the overall aim of this study was to evaluate the existence of genotype by environment interactions for FE traits with a simulation approach. The specific aims were to: (1) estimate genetic parameters of efficiency traits in contrasted environments; (2) estimate genetic correlations of efficiency, production, and functional traits; and (3) quantify the level of G × E on efficiency traits.

MATERIALS AND METHODS

Dairy Cow Lifetime Model

A model of the dairy cow lifetime trajectory was developed (Puillet et al., 2016). On the basis of acquisition and allocation trajectories, which are driven by 4 genetic scaling parameters, and the nutritional environment (DM availability and energy density), the model simulates trajectories of phenotypes: DMI, body mass components (body reserves, nonlabile mass, and uterus), milk production, and quantities of energy used by biological functions (maintenance, lactation, gestation, body reserves mobilization, and repletion). Using conception and survival probabilities, which are driven by phenotypes and by management rules (reproduction and culling), the model also simulates timings of reproductive events throughout the lifespan of an individual cow. The virtual cow can die naturally or can be culled for reproductive reasons. Natural death occurs when the simulated cow has no body reserves left and therefore is not able to cover maintenance requirements. Longevity is therefore an output of the simulation. All the simulated phenotypes result from the acquisition and allocation trajectories, reflecting the innate characteristics of the cow, and the expression of these trajectories permitted by a given environment (resource availability and quality, management rules).

The model was calibrated to simulate a reference dairy cow within farming systems with grass-based diets and seasonal calving, typical of New Zealand, and to obtain the values for the 4 input parameters of acquisition and allocation. We assumed that mating season starts on October 10 each year and lasts for 10 wk. At the end of the mating season, if the cow is not pregnant, she is culled at the next drying-off (or immediately for heifers). Drying-off occurs 90 d before calving but never after mid-May (end of milking for the whole herd).

Scenarios of Nutritional Environment

The dairy cow model is connected to the nutritional environment through 2 variables: ME content (**MEC**) of feed resource (MJ/kg of DM) and DM offer (**DMO**, kg of DM/cow per day). Regarding feed resource quality, MEC was set according to data from Roche et al., 2009 to account for seasonal changes consistent with the New Zealand context. It varied between 10.85 MJ/kg of DM in February to 12.45 MJ/kg of DM in August with a yearly average of 11.7 MJ/kg of DM. Regarding feed resource availability, the seasonal changes in DMO over a year were based on Doole et al. (2013). This baseline was then modified to generate 4 scenarios of nutritional environment, with a gradient of constraints on feed availability. The first scenario, namely high and stable (**HS**), is the most favorable and represents a nonlimiting environment where DMO is high and stable between years. The second scenario, namely moderate and stable (**MS**), represents a seasonal and moderately constraining nutritional environment where DMO can be limiting for high acquisition cows. The average yearly offer was 12.2 kg of DM/cow per day, with a minimum of 10 kg of DM/cow per day in June and July and maximum of 16.8 kg of DM/cow per day in December. The third scenario, namely moderate and perturbed (**MP**), represents the same environment as MS, but every 3 years DMO decreased in late winter and spring, representing a slowdown in grass growth due to cold and wet weather, and decreased in summer, representing a drought. The average yearly offer during a bad year was 11.1 kg of DM/cow per day with a minimum of 8 kg of DM/cow per day and a maximum of 15 kg of DM/cow per day. Finally, the fourth scenario, namely low and stable (**LS**), is the less favorable and represents a very limiting environment, stable between years. The average yearly offer was 9.8 kg of DM/cow per day with a minimum of 8 kg of DM/cow per day and a maximum of 13.4 kg of DM/cow per day. The 3 scenarios with limited feed resources, MS, MP, and LS, are illustrated in Figure 1.

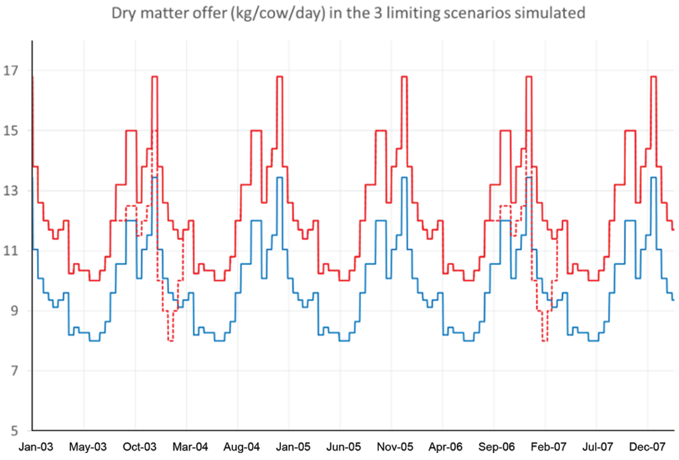

Figure 1. Example of the DM offer dynamics in the 3 simulated scenarios with limiting resource (plain red: moderate and stable; dotted red: moderate and perturbed; plain blue: low and stable).

Genetic Module

The original version of the model described the characteristics of one virtual cow (Puillet et al., 2016). To allow study of G × E, a genetic module was added to simulate genetic variation in the 4 genetic scaling parameters related to acquisition (basal acquisition and lactation acquisition, kg of DM/d) and allocation of energy resource (growth allocation and lactation allocation, dimensionless). With this new module, it is possible to generate phenotypic trait values of the parameters for a set of cows with a simple balanced pedigree structure. This pedigree structure is important for simulating the underlying genetic variation among cows so as to facilitate efficient computation of genetic parameters for aggregate genetic traits obtained as model outputted cow phenotypes. Unrelated sires and dams were simulated to generate a single generation of cows with traits in 200 paternal half-sib groups each of 100 animals. The sire and dam genetic contributions along with a Mendelian sampling term were combined to generate a true breeding value ($TBV_{i,j}$) for the ith parameter of the jth animal as follows:

$$TBV_{i,j} = \left(\frac{1}{2}\lambda_j^s + \frac{1}{2}\lambda_j^d + \sqrt{\frac{1}{2}}\lambda_j^{ms}\right)\sigma_{G_i} \quad \text{with}$$

$$\sigma_{G_i} = \sqrt{h_i^2\sigma_{P_i}^2},$$

where λ_j^s, λ_j^d, λ_j^{ms} are independent random standard deviates $N(0,1)$, corresponding to sire, dam, and Mendelian sampling components of the additive genetic variance for jth animal, h_i^2 is the heritability and $\sigma_{P_i}^2$ is the phenotypic variance of the ith parameter being simulated.

Then, the phenotypic value of the ith parameter for the jth animal ($\alpha_{i,j}$) is calculated as:

$$\alpha_{i,j} = \mu_{\mathrm{i}} + TBV_{i,j} + \sqrt{(1-h_i^{\,2})\cdot\sigma_{P_i}^2}\cdot\lambda_j^e,$$

where μ_{i} is the mean of the trait, and λ_j^e is a random standard deviate representing environmental variance.

For each trait, the mean value μ_{i} was equal to the value of the corresponding genetic scaling parameter of the reference cow. We assumed a heritability of 0.35 for the 4 traits and a phenotypic variance corresponding to a coefficient variation of 10%. This assumption was made based on the reported values for genetic variation in milk volume and liveweight in the New Zealand context. Indeed, the parameters related to acquisition and allocation are theoretical and reflect underlying processes. As they cannot be experimentally measured, information on related phenotypes were used. All genetic correlations among these underlying traits were assumed to be zero. This allowed easier interpretation of the genetic correlations that emerged from the genetic analysis of the simulated phenotypes. The variability generated by the genetic module for acquisition and allocation input parameters around the mean values corresponding to a reference cow is illustrated in Figure 2.

Simulation Study

A population of 20,000 cows generated by the genetic module was simulated in the 4 nutritional environment scenarios, generating 80,000 simulated lifetime trajectories. For each individual trajectory, simulated daily phenotypes (for instance DMI, energy allocated to milk production) were used to compute 6 aggregated traits: milk production in second lactation (kg), efficiency in second lactation (%, energy invested in milk over energy acquired from the environment throughout second lactation), life efficiency (%, energy invested in milk over energy acquired from the environment throughout lifetime), body weight (BW) at second calving (kg), level of body reserves at second calving (%) and delay from the start of the mating season until the second conception (days). For simulated cows that failed to conceive during the second mating season, a penalty phenotype value of 84 d was attributed for the conception delay trait. For milk production in second lactation and efficiency metrics, only cows that achieved at least 220 d of the second lactation were considered. The workflow of the study is illustrated in Figure 3.

To estimate the genetic parameters of the 6 aggregated traits, 3 types of models were tested. The first type of model is a single-trait animal model, implemented for each of the 6 traits in each of the 4 scenarios (24 single-trait models):

$$y_i = \mu + a_i + e_i,$$

where y_i is the value of the trait for cow i in the nutritional environment scenario, μ is the fixed effect of the scenario (average value of the trait), a_i is the random genetic effect of cow i and e_i is the residual effect.

The second type of model is a multiple-trait animal model, implemented for each scenario (4 models with 6 traits each):

$$\mathbf{y} = \mathbf{b} + \mathbf{Za} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of values for the 6 traits in a nutritional environment scenario, $\mathbf{b}$ is the vector of fixed effects of the scenario (average value of the trait), $\mathbf{a}$ is the vector of random additive genetic effects, $\mathbf{Z}$ is an incidence matrix, and $\mathbf{e}$ is the vector of random residuals.

The third type of model is a multiple-trait animal model implemented for each FE metric across the 4 scenarios (2 models with 4 traits each):

$$\mathbf{y} = \mathbf{b} + \mathbf{Za} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of values of the efficiency metric in the 4 nutritional environment scenarios, $\mathbf{b}$ is the vector of fixed effects, $\mathbf{a}$ is the vector of random additive genetic effects, $\mathbf{Z}$ is an incidence matrix, and $\mathbf{e}$ is the vector of random residuals. We assumed that correlations of random residuals were zeros, as scenarios were independent. All analyses were carried out using the WOMBAT software (Meyer, 2007).

As a complementary approach to genetic parameters evaluation, simulations were also analyzed to find out the best performing genotypes, i.e., the best combinations of genetic scaling parameters for acquisition and allocation. In the 2 most contrasted scenarios (HS; LS), the 5% best simulated cows for second lactation and lifetime efficiency were selected. The distributions of acquisition and allocation parameters of these cows were compared with the rest of the population to assess if efficiency in a given environment results from a particular combination of acquisition and allocation strategies.

RESULTS

Phenotypic Traits Simulated

The mean (±SD) values for the simulated traits in the 4 nutritional environment scenarios are presented in Table 1. The number of cows that reached at least 220 d of their second lactation decreased along the gradient of environments from 17,945 cows in HS (90% of total cows simulated) to 13,640 cows in LS (68% of total cows simulated). The average level of constraint imposed by the nutritional environment scenario on simulated cows (DMI compared with total potential acquisition) was 0% in HS, −5.5% in MS, −8.2% in MP and −14.7% in LS. Milk production in second lactation decreased from 4,866 to 3,543 kg between HS and LS, as the environment became more constraining. Efficiency in second lactation was very similar across scenarios with only a slight decrease as the environment became more constraining. The proportion of energy invested in lactation, and therefore second-lactation efficiency, is driven by the parameter for lactation allocation, which is independent from the environment. This explains why the decrease in resource availability along the gradient of environments only slightly affected the efficiency in second lactation. Life efficiency decreased

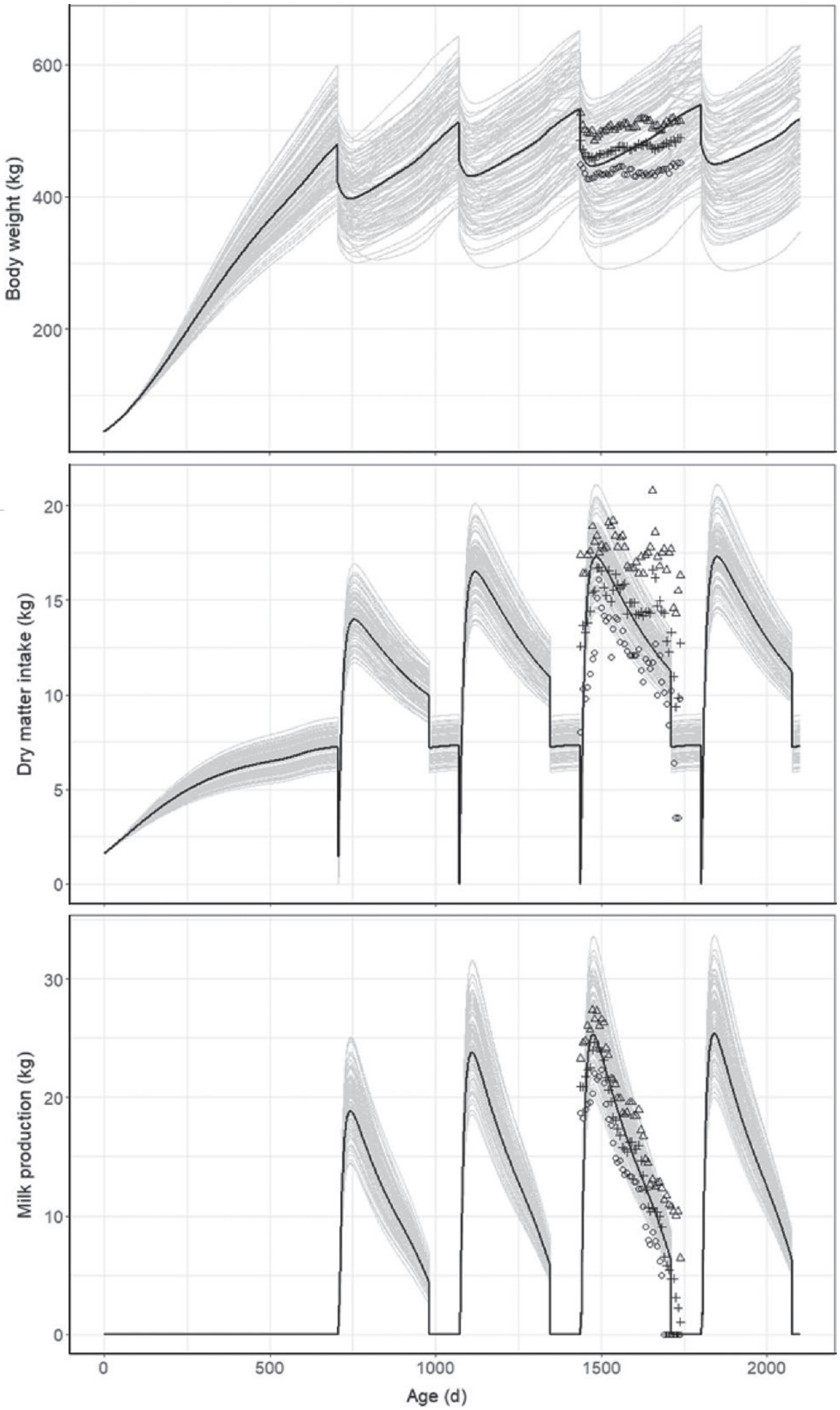

Figure 2. Illustration of the variability in lifetime trajectories for BW, DMI, and milk production from birth to fourth lactation, generated by the genetic module around the mean value of acquisition and allocation parameters corresponding to a reference cow, representative of a typical seasonal grass-based system. The solid line corresponds to the reference cow. The gray lines correspond to 100 cows randomly chosen. The points correspond to experimental data from Roche et al. (2009), used to determine the reference cow (triangle = maximum value; cross = average value; circle = minimum value).

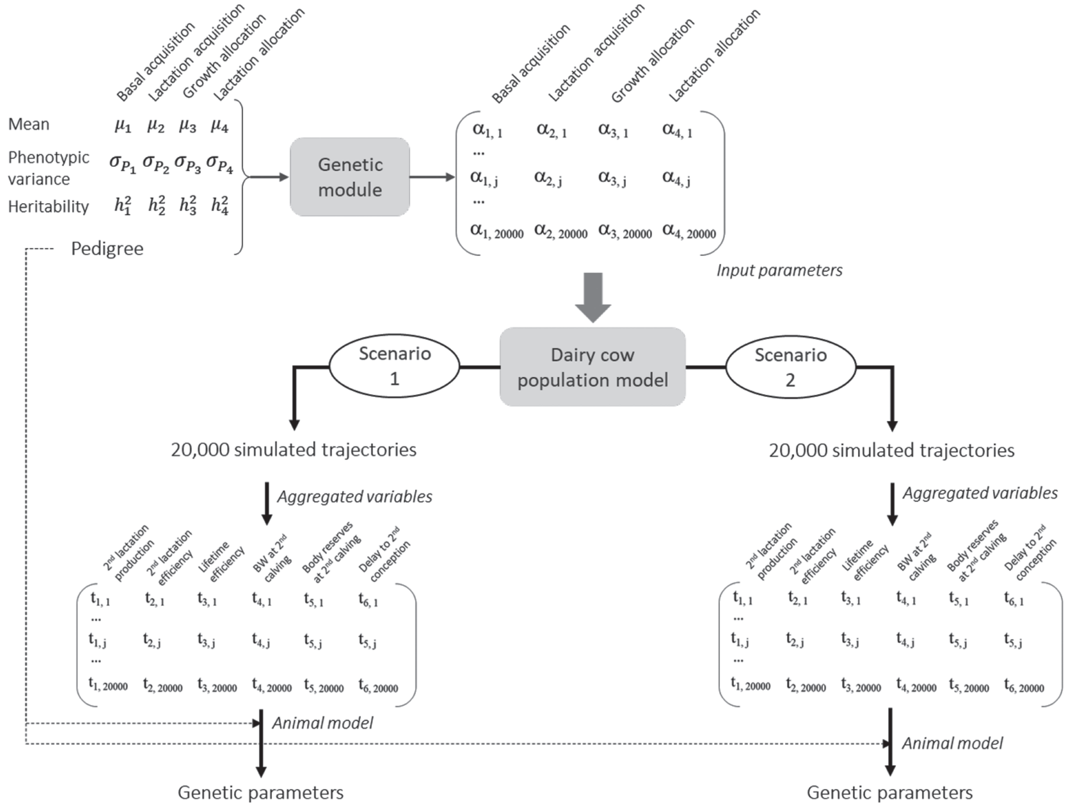

Figure 3. Description of the workflow used in the simulation study (illustrated here with 2 nutritional environment scenarios) with: (1) the genetic module used to create a virtual population of 200 sires with breeding values for the 4 input parameters (α_1, α_2, α_3, α_4) of the dairy cow lifetime model and generate 100 half-sib group of daughters; (2) the simulation of the lifetime trajectories of 20,000 cows corresponding to the acquisition and allocation parameter combination ($\alpha_{i,j}$), in each nutritional environment scenario, and (3) the calculation of 6 aggregated phenotypes ($t_{i,j}$) and estimation of their genetic parameters to study genotype by environment interactions. The 6 aggregated phenotypes correspond to: milk production in second lactation (kg), efficiency in second lactation (%, energy invested in milk over energy acquired from the environment throughout second lactation), life efficiency (%, energy invested in milk over energy acquired from the environment throughout lifetime), BW at second calving (kg), level of body reserves at second calving (%) and delay from the start of the mating season until the second conception (days).

from 38.9 to 32.15% between HS and LS environments. This is mainly explained by a decrease in longevity and total number of days in lactation. At lifetime scale, productive time is playing a major role and allows the dilution of the fixed costs associated with unproductive days (i.e., time before first calving and during the dry period). A decrease in total number of productive days leads to a decrease in life efficiency. The cow BW and the proportion of body reserves at second calving decreased when the environment became more constraining. When resource availability is limited, body reserves are used to compensate for the low offer of DM. As the probability of conception is depending on BCS and energy balance, limiting environments induce a decrease in conception and an increase in risk of being culled for infertility, leading to less lactations. The delay to second conception was slightly affected by the environment with an increase of 2 d between HS and LS.

Genetic Parameters of Simulated Traits

The estimates of heritability for each trait and each nutritional environment are given in Table 2. Heritability estimates for milk production and efficiency in second lactation decreased between the most favorable environment HS and the less favorable environment LS. An opposite trend was found for life efficiency, for which the heritability estimate tended to increase from the most favorable environment HS to the less favorable environment LS. Estimates for BW at second calving were roughly constant across environments. For body reserves at second calving, a decrease of heritability was observed in the less favorable environment LS. Finally, estimates of heritability for delay to second conception were low across all environments.

The estimates of heritability and genetic correlations with a multiple-trait model in each environment

Table 1. Phenotypic description of traits simulated (mean ± SD) in the 4 nutritional environment scenarios

	Nutritional environment scenario[1]			
Trait	HS	MS	MP	LS
n	17,945	17,518	15,643	13,640
Second-lactation milk production (kg)	4,866.3 ±569.5	4,357.6 ±414.7	3,842.2 ±368.1	3,543.1 ±322.2
Second-lactation efficiency[2] (%)	54.4 ±4.2	54.2 ±4.3	53.7 ±4.0	53.4 ±4.0
Life efficiency[3] (%)	38.9 ±4.5	36.6 ±4.2	35.6 ±4.2	32.1 ±3.8
n	18,171	18,059	17,967	17,019
BW at second calving (kg)	529.9 ±59.4	524.4 ±55.3	524.3 ±55.1	486.9 ±39.8
Body reserves at second calving (%)	21.8 ±5.8	21.5 ±5.6	21.5 ±5.6	18.1 ±5.3
Delay to second conception[4] (d)	18.7 ±20.0	18.9 ±20.2	18.9 ±20.0	20.4 ±21.0

[1] n = number of simulated cows that reached at least d 220 of their second lactation; HS = high and stable, nonlimiting environment where DM offer is high and stable between years; MS = moderate and stable, seasonal and moderately constraining nutritional environment where DM offer can be limiting for high-acquisition cows; MP = moderate and perturbed, same environment as MS, but every 3 years DM offer decreased in late winter and spring, representing a slowdown in grass growth due to cold and wet weather, and decreased in summer, representing a drought; LS = low and stable, very limiting environment, stable between years.

[2] Second-lactation efficiency is calculated as the percentage of energy invested in milk over energy acquired from the environment throughout the second lactation.

[3] Life efficiency is calculated as the percentage of energy invested in milk over energy acquired from the environment throughout the lifetime.

[4] Delay to conception is calculated as the number of days from the start of mating season until the second conception.

are presented in Table 3. Heritability estimates from multiple-trait models were consistent with estimates from univariate models, except for delay to second conception in MP scenario. However, multiple-trait models tended to lead to slightly higher estimates of heritability than univariate models (Table 2).

Genetic correlations between milk production and efficiency in second lactation were positive and high in all scenarios and increased as the nutritional environment became more constraining. Lifetime efficiency was positively correlated with milk production and efficiency in second lactation but these correlations decreased and became substantially less than one as the environment became more constraining. BW at second calving was negatively correlated with milk production and efficiency traits, except for milk production in the HS scenario. These genetic correlations became more negative as the environment became more constraining. Regarding level of body reserves at second calving, the genetic correlation with milk production and efficiency in second lactation was low across all environments. The genetic correlation for body reserves at second calving with life efficiency was positive and low in HS scenario and increased as the environment became more constraining. Finally, the genetic correlation with BW at second calving was moderate and similar across environment, except for the most constraining environment LS. The genetic correlation estimates between the delay to second conception and the other traits were generally moderate. Sampling errors for genetic correlation estimates were large for this trait, reflecting the low heritability. The results of genetic parameters for the 2 efficiency metrics are presented in Table 4.

Table 2. Heritability of traits within each nutritional environment scenario (single-trait analysis)

Trait	High and stable	Moderate and stable	Moderate and perturbed	Low and stable	SE
Second-lactation production	0.302	0.241	0.194	0.179	0.023–0.032
Second-lactation efficiency	0.343	0.315	0.314	0.291	0.032–0.035
Lifetime efficiency	0.124	0.143	0.146	0.179	0.016–0.023
BW at second calving	0.395	0.419	0.405	0.390	0.039–0.041
Body reserves at second calving	0.307	0.291	0.302	0.262	0.029–0.032
Delay to second conception	0.007	0.017	0.003	0.008	0.005–0.006

Table 3. Genetic parameters (diagonal: heritability; lower diagonal: genetic correlations) of the 6 simulated traits estimated with a multitrait model for each nutritional environment scenario[1]

Parameter	Second-lactation production	Second-lactation efficiency	Lifetime efficiency	BW at second calving	Body reserves at second calving	Delay to second conception
High and stable						
n	17,945	17,945	17,945	18,171	18,171	18,171
Second-lactation production	0.301					
Second-lactation efficiency	0.697	0.348				
Lifetime efficiency	0.708	0.854	0.123			
BW at second calving	0.265	−0.425	−0.394	0.396		
Body reserves at second calving	0.136	−0.225	0.184	0.366	0.307	
Delay to second conception	0.126	0.432	0.080	−0.251	−0.473	0.008
Moderate and stable						
n	17,518	17,518	17,518	18,059	18,059	18,059
Second-lactation production	0.243					
Second-lactation efficiency	0.929	0.325				
Lifetime efficiency	0.631	0.656	0.143			
BW at second calving	−0.188	−0.449	−0.636	0.419		
Body reserves at second calving	−0.053	−0.279	0.333	0.326	0.291	
Delay to second conception	−0.071	0.114	−0.478	0.112	−0.609	0.017
Moderate and perturbed						
n	15,463	15,463	15,463	17,967	17,967	17,967
Second-lactation production	0.182					
Second-lactation efficiency	0.977	0.332				
Lifetime efficiency	0.592	0.609	0.149			
BW at second calving	−0.292	−0.458	−0.679	0.405		
Body reserves at second calving	−0.032	−0.198	0.366	0.322	0.302	
Delay to second conception	0.450	0.527	−0.274	−0.119	−0.784	0.007
Low and stable						
n	13,640	13,640	13,640	17,019	17,019	17,019
Second-lactation production	0.185					
Second-lactation efficiency	0.983	0.311				
Lifetime efficiency	0.526	0.477	0.211			
BW at second calving	−0.528	−0.598	−0.768	0.390		
Body reserves at second calving	0.011	−0.139	0.616	0.015	0.263	
Delay to second conception	0.241	0.402	−0.314	−0.285	−0.862	0.011

[1] Sampling errors ranged from 0.006 to 0.041 for heritability estimates and from 0.012 to 0.30 for genetic correlations.

The estimation process based on restricted maximum likelihood led to a reduce rank matrix. The estimates of heritability for second-lactation efficiency and life efficiency were consistent with estimates from previous models (Table 2 and Table 3). For second-lactation efficiency, all genetic correlations were equal to 1 showing no G × E for this short-term metric of efficiency. Regarding life efficiency, the genetic correlations were

Table 4. Genetic parameters (diagonal: heritability; lower diagonal: genetic correlations) of the 2 efficiency metrics (second-lactation efficiency and lifetime efficiency) estimated with a multitrait model across nutritional environment scenarios[1]

Parameter	High and stable	Moderate and stable	Moderate and perturbed	Low and stable
n	17,945	17,518	15,463	13,640
Second-lactation efficiency				
High and stable	0.331			
Moderate and stable	1.000	0.309		
Moderate and perturbed	1.000	1.000	0.312	
Low and stable	1.000	1.000	1.000	0.292
Lifetime efficiency				
High and stable	0.124			
Moderate and stable	0.907	0.147		
Moderate and perturbed	0.862	0.995	0.154	
Low and stable	0.760	0.963	0.985	0.186

[1] Sampling errors ranged from 0.033 to 0.87 for heritability estimates and from 0.016 to 0.058 for genetic correlations.

close to 1 between constrained environments (MS, MP, and LS). However, the genetic correlations with HS scenario decreased from 0.907 to 0.760, showing a G × E interaction for this long-term metric of efficiency.

Best Performing Cows in High and Low Nutritional Environment Scenarios

As a complementary approach to genetic parameters evaluation, simulations were also used to look at the best performing genotypes, i.e., combinations of genetic scaling parameters for acquisition and allocation, in the different nutritional environments. In the 2 most contrasted scenarios, HS and LS, the 5% best cows for lactation efficiency and the 5% best cows for life efficiency were selected, thus forming 4 subpopulations of cows. The distribution of allocation and acquisition parameters in these 4 subpopulations were compared with the distribution of parameters in the whole population of simulated cows. The results are given in Figure 4. This allowed us to evaluate which acquisition and allocation strategies lead to the highest efficiency in the short and in the long term and depending on the nutritional environment.

In the HS scenario, the best cows for second-lactation efficiency had values of acquisition parameters close to the rest of the simulated population. Regarding allocation parameters, on average they had lower allocation to growth and higher allocation to lactation. The best cows for life efficiency in the HS scenario had higher values for acquisition in lactation than the rest of the population. They had lower values for allocation to growth and higher values for allocation to lactation.

In the LS scenario, the best cows for second-lactation efficiency had distributions of parameters similar to those of the best cows for second-lactation efficiency in the HS scenario, except that they allocate less to growth and less to lactation. Finally, the best cows for life efficiency in the LS scenario, in contrast with the best ones for life efficiency in the HS scenario, had the same lactation acquisition as the rest of the population but they had a lower basal acquisition than the rest of the population and the other subpopulations of best cows.

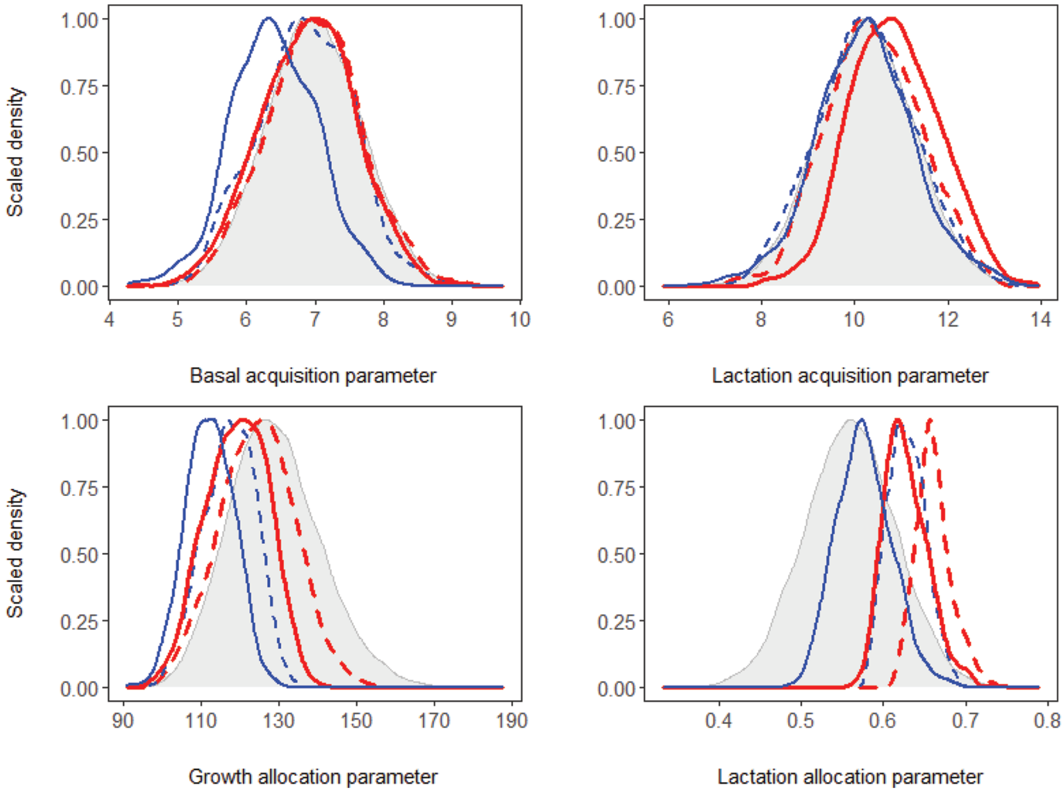

Figure 4. Distributions of genetic scaling parameters of the 5% best simulated cows for second-lactation and life efficiency in high and low nutritional environment scenarios (red dotted = best for second-lactation efficiency in high and stable scenario; blue dotted = best for second-lactation efficiency in low and stable scenario; red plain = best for life efficiency in high and stable scenario; blue plain = best for life efficiency in low and stable scenario; gray area = all cows distribution)

DISCUSSION

This study aimed at assessing the extent of genotype by environment interactions for FE traits with a simulation approach, using a mechanistic model of the dairy cow. The strategy consisted of generating a simple additive genetic determinism among underlying drivers of FE, that is to say resource acquisition and allocation. This then allowed us to estimate the genetic parameters of phenotypic traits expressed in contrasted nutritional environments within a seasonal calving system.

The HS scenario can be considered as the environment that allows full expression of the cow's acquisition and allocation strategy (i.e., the intake of the animal is not constrained by the nutritional environment but is instead determined by the genetic value of resource acquisition). It was assumed to be the scenario that best reflects the nutritional environment used in herds focused on producing elite breeding stock within the New Zealand context. The heritabilities found for this scenario were consistent with the national genetic evaluation (0.36 for milk volume, 0.35 for BW, and 0.25 for body condition score, Dairy NZ, 2020). Heritability for lifetime efficiency was low (0.12 in HS) which is consistent with the fact that in general, longevity is a low heritability trait (0.06, Dairy NZ, 2020). Heritability for delay to second conception was very low (0.007 in HS) compared with values found in real data studies (Berry et al., 2014). This suggests that the model is missing some variation in fertility that is not driven by nutritional stress.

The heritability estimates in the 4 simulated scenarios showed that the contribution of genetic variation to milk production in second lactation decreased (from 0.30 to 0.19) as the nutritional environment increasingly constrained feed availability. Milk production in second lactation is a trait resulting from both acquisition (determining the amount of energy acquired that can be transformed) and allocation parameters (determining the proportion of energy allocated to lactation). When the environment is nonlimiting, genetic variations in these parameters are fully expressed. When feed availability decreases, the expressed variation in acquisition is constrained and the energy transformed is based on what is available in the environment, whatever the value of the acquisition parameter. Accordingly, the genetic variation for acquisition contributes less to variation in milk, which becomes more based on variation in allocation parameters. The heritability estimates for efficiency in second lactation were stable in the 4 scenarios (around 0.32) and close to the heritability assigned to the underlying parameters in the genetic module (0.35). The genetic correlations for second-lactation efficiency across environments were equal to 1. These results are mainly due to the strong role that allocation plays in determining efficiency at the level of a single lactation cycle (Puillet et al., 2016). The parameter for lactation allocation determines the time-profile of allocation and therefore the cumulated proportion of energy transformed into milk. As efficiency is calculated as the ratio between energy invested into milk over energy acquired throughout lactation, this trait is closely linked to the lactation allocation parameter. Further, as lactation efficiency is evaluated in second parity in our case, that is to say at an early stage of productive life, the effect of previous reproductive cycles is low and the trait is reflecting more directly the expression of the underlying acquisition and allocation parameters.

The heritability estimates for lifetime efficiency in the 4 different scenarios show that the genetic variation relative to the phenotypic variance increased as the environment became more constraining (0.12 to 0.21). Achieving high lifetime efficiency does not only imply a good production level (dilution of maintenance costs) but also a better ability to have many lactation cycles (dilution of nonproductive days). This time dimension is of great importance for lifetime efficiency and therefore reproductive success is a key component, as it triggers the next lactation and increases total production time. When the environment becomes more constraining, body reserves are more mobilized and the probability of conception decreases. There is less opportunity for random success of some acquisition and allocation strategies: only the ones that lead to enough body reserves at breeding can achieve a good lifetime efficiency. This increase in selection pressure as resource availability decreases may explain the increase in heritability for lifetime efficiency.

Comparing correlations estimated in different environments is a way to estimate G × E interactions. In this study, we found that genetic correlations between milk production and efficiency in second lactation were positive and increased as the environment became more constraining (from 0.69 to 0.98). Indeed, as resource availability decreases, variation in intake is squeezed. Thus, differences in second-lactation production and efficiency become more strongly correlated with differences in allocation to milk. Lifetime efficiency was positively correlated to both milk production and efficiency in second lactation but, in contrast, this correlation decreased when the environment became more constraining. This means that if selecting on second-lactation traits improves lifetime efficiency in a favorable environment, this is not the case in less favorable environments. In addition, the genetic correlations between life efficiency in the most favorable environment and life efficiency in the 3 constrained environments decreased. This suggests that there is a significant G ×

E effect and thus it seems likely that animals selected in highly favorable environments could have reduced fitness when they are in a poor environment. This has to some extent been observed in studies that compared New Zealand and North American Holstein cows under Irish grazing conditions (Horan et al., 2005, 2006).

Correlations among BW at second calving and productive traits (milk production and efficiencies) were mainly negative and increased when feed availability decreased. This effect is due to the trade-off between growth and survival in the dairy cow model. A high BW is mainly achieved by having a high structural mass, which is the nonlabile component of the total mass and which directly competes with the resources available for survival, principally body reserves.

Beyond the effect of the level of resource availability on genetic correlations, the results of MS and MP scenarios show that dynamics of resource availability is also a factor to consider when evaluating G × E interactions. The genetic correlation between second-lactation production and delay to conception goes from zero in the MS scenario to 0.45 in the MP scenario (i.e., the trade-offs between production and reproduction are only revealed in the perturbed environment). The genetic correlation between lifetime efficiency and delay to conception is also strongly affected by the perturbations in the MP scenario (from −0.478 to −0.274). Even if the number of perturbations is relatively small (1 perturbed year every 3 yr), the MP scenario further erodes the genetic correlation between second-lactation and lifetime efficiency (from 0.656 to 0.609). This suggests that both the level and the variability in time of the nutritional resources should be considered. Such effects of the environment have already been shown in ecology or evolutionary biology studies (e.g., Muller and Nisbet, 2000; Fischer et al., 2009; Lee et al., 2016). Exploring how the characteristics of perturbations in the nutritional environment (e.g., number, intensity, and timing) interact and shape G × E interactions is an interesting perspective for future simulation studies.

As a complementary approach to genetic correlations among traits in different scenarios, simulations were also used to determine the best performing genotypes, in the sense of the best strategies of acquisition and allocation, in the 2 most contrasted environments, HS and LS, and for 2 metrics of efficiency (second-lactation and life efficiencies). The best strategy in the short term (lactation level) and in a favorable environment is to allocate more to lactation. In an adverse environment, the previous strategy has to be adapted by slightly reducing allocation to lactation and to growth, so as to preserve body reserves. The best strategy in the long term (lifetime level) and in a favorable environment is to acquire more resource in lactation (thus saving body reserves), allocate more to lactation and less to growth. In an adverse environment, the best strategy is to have a lower acquisition and to reduce both allocation to lactation and to growth so as to ensure that functional lifespan is preserved. These results highlight the interest of using theoretical biological frameworks that integrate underlying mechanisms to better understand how phenotypes are elaborated depending on the environmental conditions. The need to combine both an adequate specification of animal's genotype and an interaction between genetic and environmental components is essential for evaluating G × E (Bryant et al., 2005).

Results from this simulation study highlight the importance of having a balanced breeding goal when undertaking selection. Based on our knowledge of underlying nutritional principles, we hypothesize that selection criteria that target short-term efficiency through dilution of maintenance might not directly correspond with lifetime efficiency, and that this misalignment could be environment dependent. In practice, selection is typically applied simultaneously across a broad range of traits, which should help circumvent problems, for example antagonistic genetic relationships between FE and fertility and survival. Selection for short-term FE is not straightforward to apply in practice. Our results indicate that the value of short-term FE as a selection criterion within a breeding objective targeting a broad cross section of traits, might be more adequate when genetic improvement is targeting dairy systems with a reasonably benign environment. When the target is for dairy production in lower input pastoral environments, with large year-to-year variability in feed availability, the value of short-term FE as a selection criterion may be quite modest, especially after consideration of the additional recording cost. Further, it will be critically important to make sure that selection candidates are accurately predicted for functional traits reflecting genetic variation in fertility and survival. The wholesale switch to selection of young industry sires based on genomic predictions of merit and will further build on predictions for fertility and survival traits are not that well validated. In this context, there may be considerable risks of unintended deterioration in cow functionality. Our results indicate that these risks will be greatest for dairy farm systems where nutritional management is subject to unpredictable seasonal and annual variation in pasture availability. Biologically-grounded simulation models, such as this one, are a cost-effective tool for exploring different future genetic selection strategies ahead of more costly implementation and evaluation with field data.

CONCLUSIONS

From this simulation study, we found that G × E interactions exist between efficiency, productive, and functional traits. The interactions with functional traits imply that selection strategies based on short-term efficiency will probably not improve lifetime efficiency. Preserving body reserves and survival while investing in productive functions is a complex balance, requiring a well-tuned resource allocation strategy and largely affected by how the environment limits resource acquisition. Further research is required to understand the role of resource fluctuations in G × E and better adapt genetic improvement to farming system context with less control on the feed resource environment.

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