Genotype by feed interaction for feed efficiency and growth performance traits in pigs¹

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ABSTRACT: A major objective of pork producers is to reduce production cost. Feeding may account for over 75% of pork production costs. Thus, selecting pigs for feed efficiency (FE) traits is a priority in pig breeding programs. While in the Americas, pigs are typically fed high-input diets, based on corn and soybean meal (CS); in Western Europe, pigs are commonly fed diets based on wheat and barley with high amounts of added protein-rich coproducts (WB), e.g., from milling and seed-oil industries. These two feeding scenarios provided a realistic setting for investigating a specific type of genotype by environment interaction; thus, we investigated the genotype by feed interaction (GxF). In the presence of a GxF, different feed compositions should be considered when selecting for FE. This study aimed to 1) verify the presence of a GxF for FE and growth performance traits in different growth phases (starter, grower, and finisher) of 3-way crossbred growing-finishing pigs fed either a CS (547 boars and 558 gilts) or WB (567 boars and 558 gilts) diet; and 2) to assess and compare the expected responses to direct selection under the 2 diets and the expected correlated responses for one diet to indirect selection under the other diet.

We found that GxF did not interfere in the ranking of genotypes under both diets for growth, protein deposition, feed intake, energy intake, or feed conversion rate. Therefore, for these traits, we recommend changing the diet of growing-finishing pigs from high-input feed (i.e., CS) to feed with less valuable ingredients, as WB, to reduce production costs and the environmental impact, regardless of which diet is used in selection. We found that GxF interfered in the ranking of genotypes and caused heterogeneity of genetic variance under both diets for lipid deposition (LD), residual energy intake (REI), and residual feed intake (RFI). Thus, selecting pigs under a diet different from the diet used for growing-finishing performance could compromise the LD in all growth phases, compromise the REI and RFI during the starter phase, and severely compromise the REI during the grower phase. In particular, when pigs are required to consume a WB diet for growing-finishing performance, pigs should be selected for FE under the same diet. Breeding pigs for FE under lower-input diets should be considered, because FE traits will become more important and lower-input diets will become more widespread in the near future.

Key words: breeding program, correlated response, feed efficiency, genetic gain, genotype by feed interaction

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INTRODUCTION

A major objective of pork producers is to reduce production costs. Feeding may account for over 75% of pork production costs (Ali et al., 2017). Thus, selecting pigs based on feed efficiency (FE) traits is a priority in pig breeding programs. Average daily feed intake (ADFI) and residual feed intake (RFI), were shown to be more environmentally sensitive than the average daily gain (ADG) and back-fat thickness (BF) in growing-finishing pigs (Knap and Wang, 2012). Indeed, in addition to differences in climate (Bloemhof et al., 2012; Sevillano et al., 2016) and typical differences in health status and farm management (Mathur et al., 2014; Herrero-Medrano et al., 2015), feed content can be a major source of environmental variation. Differences in feed content can give rise to a specific type of genotype by environment interaction (GxE), the interaction between genotype and feed (GxF). While in the Americas, pigs are typically fed high-input diets based on corn and soybean meal (corn/soy); in Western Europe, pigs are commonly fed diets based on wheat and barley, with high amounts of added protein-rich coproducts, like rapeseed and sunflower seed meals (wheat/barley/coproducts). Thus, in the presence of GxF, selecting pigs for FE should take into account the different feed compositions.

It is widely known that the nutritional requirements of pigs change during the growing-finishing period, and thus, different diets are designed to meet the requirements of pigs in each growth phase. However, there is a lack of information about the genetic characteristics of FE during different growth phases (Shirali et al., 2014). In addition, because pigs are fed different diets in the different growth phases, the level of GxF can be expected to change in the different phases. Therefore, the current study aimed to 1) verify the presence of GxF for FE and growth performance traits in different growth phases (starter, grower, and finisher) of 3-way crossbred pigs fed diets of corn/soy or wheat/barley/coproducts; and 2) to assess and compare the expected responses to direct selection under the 2 diets, and the expected correlated response in one diet to indirect selection under the other diet.

MATERIAL AND METHODS

Ethic Statement

Data for this study were collected at the Schothorst Feed Research B.V. farm during

data recordings routinely performed in a commercial breeding program. All farm operations strictly adhered to Dutch legal regulations regarding the protection of animals (Gezondheids- en welzijnswetvoordieren).

Data

We retrieved phenotypic records for 2,230 3-way crossbred pigs offspring of F1 sows (product of a Large White line crossed with 1 of 2 Landrace lines) sired by a synthetic sire line. The experiments were conducted in Schothorst Feed Research facilities (Lelystad, the Netherlands), under near commercial production conditions. We tested 29 successive batches of pigs. Each batch comprised a single contemporary group entrance on test and was allocated entirely in 1 of 7 compartments on the farm available for the experiment. Each compartment had 8 pens and, a minimum of 7 and maximum of 10 pigs were allocated per pen. Pigs were put on test at around 22 kg, and were taken off test and slaughtered at around 122 kg (Table 1). The test period lasted around 106 days. The experimental design was a split-plot 2×2 factorial arrangement. The factors were diet (corn/soy and wheat/barley/coproducts) and sex (boars and gilts). Littermates were evenly distributed between the diets to ensure no difference in the genetic background of pigs fed either diet. In total, 547 boars and 558 gilts were fed corn/soy, and 567 boars and 558 gilts were fed wheat/barley/coproducts. Pedigree records were available for all animals, up to a maximum of 9 generations. A total of 3,991 animals were included in the pedigree file, with 608 different sires and 1,065 different dams.

Diets

Pigs were fed ad libitum according to a 3-phase feeding program that mirrored the 3 growth phases: starter from day 0 to day 25, grower from day 26 to day 67, and finisher from day 68 to slaughter, when pigs achieved around 120 kg. For details on the feeding program and the diet formulations, see [Supplementary Appendix 1](#). In brief, pigs were assigned to 1 of 2 target diets (TD). One diet was based on corn/soy, and the other diet was based on wheat/barley/coproducts. Both diets were formulated to supply sufficient digestible amino acids in each growth phase to meet or exceed the nutrient requirements of growing-finishing pigs, according to CVB ([Centraal Veevoederbureau, 2011](#)). To ensure a fair comparison between the two feeding scenarios, the 2 diets were formulated with

Table 1. Mean, standard deviation, minimum and maximum for pigs' age, permanence on test, body weight, and back fat thickness

Traits	CS				WB			
	μ	SD	Min	Max	μ	SD	Min	Max
Age_ontest, days	62	2.1	54	69	62	2.1	54	68
Age_midtest, days	117	2.4	109	124	117	2.4	109	123
Age_offtest, days	169	8.3	141	188	168	8.3	141	187
Test_length, days	107	8.3	81	125	106	8.5	81	125
BW_starter, kg	22	3.2	12	39	23	3.3	14	34
BW_grower ¹ , kg	45	4.8	30	62	46	4.8	31	63
BW_midtest, kg	70	7.6	44	93	71	7.6	45	98
BW_finisher ¹ , kg	84	7.9	59	114	85	8.1	50	115
BW_slaughter, kg	122	8.2	91	155	122	8.6	64	147
BF_offtest, mm	12	2.1	7	20	11	1.8	6	18

BF = back fat thickness; CS = diet based on corn and soybean meal; WB = diet based on wheat and barley with high addition of coproducts.

¹BW adjusted for the age animal had when feeding program changed.

a similar net energy (NE)/digestible lysine ratio and similar NE and crude protein contents. The corn/soy diet had a higher starch content than the wheat/barley/coproducts diet. Conversely, compared to the corn/soy diet, the wheat/barley/coproducts diet had a higher nonstarch polysaccharide content, due to the high amount of coproducts, and a higher crude fat content, due to the lipids added to increase the final NE content.

Traits

BW (kg) was recorded in individuals at the start (day 0), in the middle (day 54), and at the end (around day 107) of the test period. At the end of the test period, BF was measured in all animals with the CGM (Capteur Gras Maigre, Sydel, France) at slaughter (Table 1). Individual daily feed intake was recorded with IVOG®-stations (Insentec, Marknesse, the Netherlands). The test period was divided into 3 periods, according to the feeding program, which followed the growth phases, i.e., starter, grower, and finisher phases. Pigs' BW were adjusted to the pig's age at the time the feeding phase changed (Table 1). Traits were calculated for each feeding phase and for the overall test period (Table 2).

We analyzed traits related to the FE, including the feed conversion rate (FCR), residual energy intake (REI), and RFI. In addition, we analyzed other growing-finishing traits, including the average daily gain on test (ADG), ADFI, average daily energy intake (ADEI), lipid deposition (LD), and protein deposition (PD). The latter traits were included to assess whether GxF was detectable in traits that were potentially less environmentally sensitive. The ADG (g/d) was defined as the change in the live BW from the beginning to the end of the

phase, divided by the length of the phase. ADFI (g/d) was defined as the cumulative feed intake during the phase, divided by the length of the phase. The ADEI (MJ/d) was defined as the cumulative metabolizable energy (ME) intake during the phase, divided by the length of the phase. LD (g/d) and PD (g/d) were estimated as the increments in lipid and protein masses, respectively, during the phase, based on the BW and BF measurements (de Greef et al., 1994), as follows:

$$\%fat_{end} = \frac{BF, mm - 1.87}{53.3},$$

$$\%fat_{start} = \%fat_{end} \times \frac{-0.000005(BW_{start})^2 + 0.0019(BW_{start}) + 0.0665}{-0.000005(BW_{end})^2 + 0.0019(BW_{end}) + 0.0665},$$

$$Protein\ water\ ratio = 5.39(BW \times 0.14)^{-0.145},$$

$$Ash = 0.03 \times BW,$$

$$Lipid\ mass(LM) = \%fat \times 0.95 \times BW,$$

$$Protein\ mass(PM) = \frac{0.95 \times BW - LM - Ash}{Protein\ water\ ratio + 1},$$

$$LD = \frac{(LM_{end} - LM_{start}) \times 1000}{Test\ length, d},$$

$$PD = \frac{(PM_{end} - PM_{start}) \times 1000}{Test\ length, d},$$

Table 2. Mean, standard deviation, minimum and maximum for the traits¹ by feeding phase

Traits	CS				WB			
	μ	SD	Min	Max	μ	SD	Min	Max
Starter phase								
ADG, g/d	887 ^a	98	515	1,225	895 ^a	98	450	1,353
ADFI, g/d	1,354 ^a	237	604	2,169	1,401 ^b	216	716	1,981
ADEI, MJ/d	17.9 ^a	3.1	8	29	18.9 ^b	2.9	9.7	27
LD, g/d	128 ^b	36	44	297	122 ^a	33	40	310
PD, g/d	146 ^b	16	88	196	149 ^a	16	77	212
FCR	1.53 ^a	0.2	0.8	2.2	1.57 ^b	0.2	1.0	2.9
REI, g/d	-185 ^a	193	-815	539	-102 ^b	176	-717	476
RFI, g/d	-16 ^a	175	-655	640	15 ^b	159	-451	545
Grower phase								
ADG, g/d	915 ^a	94	577	1,259	917 ^a	96	379	1,346
ADFI, g/d	2,160 ^a	312	1,169	3,332	2,248 ^b	312	1,208	3,420
ADEI, MJ/d	29 ^a	4.2	16	45	30 ^b	4.1	16	45
LD, g/d	185 ^b	52	74	448	173 ^a	46	36	430
PD, g/d	150 ^b	15	100	212	154 ^a	16	68	204
FCR	2.36 ^a	0.3	1.7	4.0	2.45 ^a	0.3	1.7	4.8
REI, g/d	138 ^a	227	-513	1,244	204 ^b	202	-410	965
RFI, g/d	-38 ^a	195	-647	695	38 ^b	182	-554	715
Finisher phase								
ADG, g/d	977 ^a	122	562	1,437	975 ^a	123	286	1,478
ADFI, g/d	2,911 ^a	450	1,593	4,759	3,130 ^b	424	1,269	4,605
ADEI, MJ/d	40 ^a	6.1	22	65	40 ^a	5.4	16	58
LD, g/d	236 ^b	66	90	610	219 ^a	57	32	512
PD, g/d	160 ^b	20	99	244	164 ^a	21	52	243
FCR	2.98 ^a	0.3	2.0	4.7	3.22 ^b	0.3	2.1	5.2
REI, g/d	377 ^a	277	-669	1,785	457 ^b	248	-478	2,073
RFI, g/d	-125 ^a	263	-1,110	1,324	123 ^b	240	-891	1,681
Overall Period								
ADG, g/d	938 ^a	98	593	1,300	941 ^a	100	396	1,388
ADFI, g/d	2,256 ^a	252	1,510	3,071	2,379 ^b	249	1,335	3,254
ADEI, MJ/d	31 ^a	3.4	20	42	31 ^a	3.3	17	42
LD, g/d	191 ^b	52	80	449	179 ^a	45	36	419
PD, g/d	154 ^b	16	103	219	158 ^a	16	70	213
FCR	2.41 ^a	0.2	1.9	3.2	2.54 ^b	0.2	2.0	4.0
REI, g/d	147 ^a	159	-477	943	217 ^b	155	-383	1,105
RFI, g/d	-66 ^a	145	-673	479	65 ^b	145	-439	910

CS = diet based on corn and soybean meal; WB = diet based on wheat and barley with high addition of coproducts.

¹ADG = average daily gain; ADFI = average daily feed intake; ADEI = average daily energy intake; FCR = feed conversion rate; LD = lipid deposition; PD = protein deposition; REI = residual energy intake; RFI = residual feed intake.

Means followed by different letters differ according to *T*-test ($P < 0.05$).

The FCR was calculated as the ADFI divided by the ADG. The REI (g/d), which represents the efficiency of energy metabolism, was calculated as a linear function of energy intake, energy required for maintenance of live BW, and energy required for lipid and protein accretion (Bergsma et al., 2013), as follows:

$$REI = \frac{ADFI \times ME_{diet} - ME_m - (LD + PD) \times 53}{ME_{diet}},$$

where, the ME_{diet} is the ME provided by the diet, calculated as $(NE_{diet}, MJ/kg / 74) \times 100$, and the

ME_m is the average ME intake required for maintenance of live BW calculated based on the metabolic BW (de Haer et al., 1993) using a ME intake value for maintenance of 420 kJ ME per kg^{0.75}, as follows:

$$ME_m = \frac{(BW_{end}^{1.75} - BW_{start}^{1.75}) \times 420}{(BW_{end} - BW_{start}) \times 1.75}.$$

RFI (g/d) was defined as the difference between the observed and predicted ADFI (Cai et al., 2008), calculated as follows:

$$ADFI = \mu + b_1 BW_{start} + b_2 BW_{end} + b_3 BF + b_4 ADG + b_5 Age_{ontest} + e,$$

where Age_{ontest} is the age at which the animal was put on test, b_1 , b_2 , b_3 , b_4 , and b_5 are the linear coefficients of the regression on covariates, and e is the RFI.

Genetic Parameter Estimation and GxF Analyses

For the GxF analyses, each trait was considered a different trait when observed in pigs fed corn/soy and when observed in pigs fed wheat/barley/coproduets. Univariate analyses were performed to estimate the variance components and heritabilities of all traits. Differences observed in these estimates when traits were measured under different diet conditions indicated the presence of heterogeneity of genetic variance, due to the presence of GxF. Genetic correlations (r_g) were estimated with bivariate analyses. Values of r_g below 1 indicated the presence of GxF (Falconer and Mackay, 1996).

A linear mixed model, implemented in ASReml (Gilmour et al., 2009), was used to the univariate and bivariate analyses, as follows:

$$y = Xb + Za + Wl + Vg + e, \quad (1)$$

where y is the vector of observations; X , Z , W , and V are known incidence matrices; b is a vector of fixed effects (Table 3); a is a vector of random additive genetic effects (breeding values), $a \sim N(0, A \otimes \sum_a)$; l is a vector of random nongenetic effects common to individuals born in the same litter, $l \sim N(0, I_l \otimes \sum_l)$; g is a vector of random contemporary group effects (contemporary pen-mates nested within batch-mates), $g \sim N(0, I_g \otimes \sum_g)$; and e is a vector of residuals,

Table 3. Fixed effects included in the vector b of equation [1] for the traits¹

Model	Dependent trait(s) ¹
	Fixed effects ²
A	ADG; LD; PD; FCR
	$\mu + SEX_j + CROSS_k + COMP(PEN)_l + b_1 \times BW_{birth}$
B	ADFI; ADEI; REI; RFI
	$\mu + SEX_j + CROSS_k + COMP(PEN)_l + b_1 \times BW_{start}$

¹ADG = average daily gain; FCR = feed conversion rate; ADFI = average daily feed intake; ADEI = average daily energy intake; LD = lipid deposition; PD = protein deposition; REI = residual energy intake; RFI = residual feed intake. ² μ is the mean of the trait; SEX = the sex of the animal; CROSS = according to the line of the dam lines used to generate the cross; COMP(PEN) = pen nested within compartment; BW_{birth} = body weight at birth; BW_{start} = body weight at the start of the growing-finishing period.

$e \sim N(0, I_e \otimes \sum_e)$. A is a matrix of additive genetic relationships among all individuals; I_l , I_g , and I_e are identity matrices of the appropriate dimensions; and $\sum_a$, $\sum_l$, $\sum_g$, and $\sum_e$ are covariance matrices related to each effect. In the case of univariate analyses, the covariance matrix, $\sum_i$, is a scalar, with the variance component, σ_i , associated with the respective effect.

Responses to Selection

To assess the genetic progress a breeding program can obtain with data collected in the 2 feeding scenarios herein studied, we use the breeders' equation to calculate the response to selection, i.e., the expected change of the population mean for the trait that will be observed in the next generation after selection. As a trait was considered 2 different traits when measured under either diet, we calculated and compared 2 different responses to selection: 1) the response (R_{TD}) of the trait to be improved (target trait) to direct selection, i.e., when selection is conducted under the diet pigs will be required to perform, the TD; and 2) the correlated response (CR_{TD}) of the target trait for the TD to indirect selection, i.e., when selection for the target trait takes place under the non-TD. The CR_{TD} expresses the expected change of the population mean for the TD that will be observed in the next generation after selection, when selection was carried out under the non-TD.

The R_{TD} and the CR_{TD} were calculated as follows (Falconer and Mackay, 1996):

$$R_{TD} = i_{TD} \times h_{TD} \times \sigma_{A_{TD}},$$

where R_{TD} is the response of a trait to direct selection under the TD; i_{TD} is the intensity of selection under the TD (assumed to be 1 in this study); h_{TD} is the accuracy of selection under the TD; and $\sigma_{A_{TD}}$ is the genetic standard deviation under the TD;

$$CR_{TD} = i_{non-TD} \times h_{non-TD} \times r_g \times \sigma_{A_{TD}},$$

where i_{non-TD} is the intensity of selection under the non-TD (assumed to be 1 in this study); and, h_{non-TD} is the accuracy of selection under the non-TD.

RESULTS

Variance Components

Estimates of genetic variance (σ_A^2) and heritability (h^2) are presented in Table 4. The contribution

Table 4. Estimates of genetic variance and heritability (SE) for the traits¹ by feeding phase

	CS	WB	CS	WB
Traits	σ_A^2		h^2	
Starter phase				
ADG	2,476	1,551	0.27 (0.11)	0.18 (0.10)
ADFI	12,483	6,592	0.29 (0.10)	0.21 (0.11)
ADEI	2,189	1,199	0.29 (0.10)	0.21 (0.11)
LD	249	181	0.21 (0.11)	0.19 (0.10)
PD	78	32	0.33 (0.11)	0.14 (0.09)
FCR	1.11E-02	1.29E-02	0.27 (0.09)	0.35 (0.10)
REI	9,171	8,847	0.26 (0.10)	0.31 (0.10)
RFI	7,978	7,227	0.27 (0.09)	0.32 (0.11)
Grower phase				
ADG	2,864	1,837	0.34 (0.11)	0.21 (0.11)
ADFI	19,164	15,922	0.26 (0.11)	0.23 (0.11)
ADEI	3,493	2,764	0.26 (0.11)	0.23 (0.11)
LD	607	346	0.24 (0.11)	0.18 (0.10)
PD	78	51	0.37 (0.11)	0.23 (0.11)
FCR	5.00E-03	1.16E-02	0.08 (0.08)	0.18 (0.09)
REI	3,892	4,070	0.08 (0.06)	0.11 (0.07)
RFI	3,184	5,418	0.09 (0.07)	0.18 (0.10)
Finisher phase				
ADG	4,358	2,722	0.31 (0.11)	0.19 (0.10)
ADFI	62,966	28,852	0.33 (0.10)	0.18 (0.10)
ADEI	11,707	4,636	0.33 (0.10)	0.18 (0.10)
LD	1,030	499	0.24 (0.11)	0.16 (0.09)
PD	121	91	0.33 (0.10)	0.23 (0.10)
FCR	1.31E-02	1.39E-02	0.17 (0.07)	0.20 (0.10)
REI	11,388	10,299	0.14 (0.05)	0.18 (0.09)
RFI	9,597	8,374	0.14 (0.05)	0.16 (0.09)
Overall period				
ADG	3,089	2,036	0.34 (0.11)	0.22 (0.11)
ADFI	21,779	9,374	0.42 (0.12)	0.20 (0.11)
ADEI	3,978	1,642	0.42 (0.12)	0.20 (0.11)
LD	597	311	0.23 (0.11)	0.16 (0.09)
PD	88	57	0.38 (0.11)	0.24 (0.11)
FCR	5.37E-03	1.09E-02	0.19 (0.08)	0.34 (0.10)
REI	2,071	5,322	0.09 (0.06)	0.25 (0.09)
RFI	3,397	5,110	0.18 (0.08)	0.29 (0.11)

CS = diet based on corn and soybean meal; WB = diet based on wheat and barley with high addition of coproducts; σ_A^2 = additive genetic variance, h^2 = heritability estimate.

¹ADG = average daily gain; ADFI = average daily feed intake; ADEI = average daily energy intake; FCR = feed conversion rate; LD = lipid deposition; PD = protein deposition; REI = residual energy intake; RFI = residual feed intake.

of all random effects to the estimation of the traits, expressed as percentage of the phenotypic variance is given in [Supplementary Appendix 2](#). Although the standard errors of these estimates for all traits in all growth phases were high, their absolute values differed according to the diet in which the trait was measured. Heterogeneity of genetic variance indicated that GxF was present. We found lower σ_A^2 and h^2 estimates under the wheat/barley/coproducts diet compared to the corn/soy diet for all growth performance traits (ADG, ADFI, ADEI, LD, and PD) in all growth phases. The estimates of σ_A^2 and h^2 for the

FE traits (FCR, REI, and RFI) were slightly lower under the wheat/barley/coproducts diet compared to the corn/soy diet during the starter and finisher phases, but they rose to 2.4 and 2.8 times the values estimated under the corn/soy diet during the grower phase and for the overall period, respectively.

Genetic Correlations

The values of genetic correlation estimates (r_g) between the performances of pigs under each diet are presented in [Table 5](#). All r_g values of 0.99

Table 5. Genetic correlations (SE) between the performances of pigs fed a diet based on corn and soybean meal and pigs fed a diet based on wheat and barley with high addition of coproducts

Traits	Starter phase	Grower phase	Finisher phase	Overall period
ADG	0.99 (0.23)	1.00 (0.20)	0.99 (0.25)	1.00 (0.19)
ADFI	0.91 (0.16)	0.99 (0.17)	1.00 (0.23)	1.00 (0.22)
ADEI	0.91 (0.16)	1.00 (0.17)	1.00 (0.24)	1.00 (0.21)
LD	0.72 (0.21)	0.65 (0.22)	0.63 (0.23)	0.62 (0.23)
PD	1.00 (0.19)	1.00 (0.12)	0.99 (0.13)	0.99 (0.15)
FCR	1.00 (0.17)	1.00 (0.28)	1.00 (0.21)	1.00 (0.14)
REI	0.81 (0.17)	0.41 (0.36)	1.00 (0.27)	0.76 (0.23)
RFI	0.86 (0.13)	0.74 (0.29)	0.99 (0.30)	0.89 (0.16)

ADG = average daily gain; ADFI = average daily feed intake; ADEI = average daily energy intake; FCR = feed conversion rate; LD = lipid deposition; PD = protein deposition; REI = residual energy intake; RFI = residual feed intake.

and above were interpreted as unity, which indicated the absence of GxF according to this criterion. Values of r_g between 0.80 and 0.91 were interpreted as high, which indicated the presence of low-magnitude GxF. Values of r_g between 0.41 and 0.76 were interpreted as moderate, which indicated the presence of moderate-magnitude GxF. ADG, FCR, and PD presented r_g estimates of unity in all phases; therefore, showing that these traits presented no GxF. ADFI and ADEI presented r_g estimates of unity during the grower and finisher phase, and during the overall period; therefore, showing no GxF during these phases. However, during the starter phase, both ADFI and ADEI presented an r_g estimate of 0.91, which indicated the presence of GxF during this phase. LD presented r_g estimates of 0.72, 0.65, 0.63, and 0.62 during the starter, grower and finisher phases and overall period, respectively, which indicated the presence of a moderate-magnitude GxF in all phases. In fact, LD was the only trait presenting GxF during the finisher phase. REI presented r_g estimates of 0.81, 0.41, 1.00, and 0.76 during the starter, grower and finisher phases, and overall period, respectively. These values indicated a low-magnitude GxF during the starter phase, a moderate-magnitude GxF during the grower phase, the absence of GxF during the finisher phase, and a moderate GxF for the overall period. RFI presented r_g estimates of 0.86, 0.74, 0.99, and 0.89 during the starter, grower and finisher phases, and overall period, respectively, which indicated a low-magnitude GxF during the starter phase, a moderate GxF during the grower phase, no GxF during the finisher phase, and a low GxF for the overall period.

Responses to Selection Under a Diet

We calculated the trait responses to selection under the corn/soy (R_{CS}) and the wheat/barley/coproducts (R_{WB}) diets (Table 6). The FCR responses to selection under the 2 diets were similar during the starter and finisher phases, but the R_{WB} was at least 2-fold higher than the R_{CS} during the grower phase and for the overall period. The REI and RFI responses to selection were similar between the two diet groups during the starter and finisher phases, but the R_{WB} was 1.2- to 2.7-fold higher than the R_{CS} during the grower phase and for the overall period. For the growth performance traits (ADG, ADFI, ADEI, LD, and PD), the R_{WB} values were always lower than the R_{CS} by 0.2- to 0.6-fold (starter phase), 0.1- to 0.4-fold (grower phase), 0.3- to 0.5-fold (finisher phase), and 0.3- to 0.6-fold (overall).

Correlated Responses to Selection Under the Other Diet

The calculated correlated responses of traits for the corn/soy diet to indirect selection under the wheat/barley/coproducts diet (CR_{CS}), and for the wheat/barley/coproducts diet to indirect selection under the corn/soy diet (CR_{WB}), and the ratios between the correlated response and the response to direct selection (i.e., CR_{CS}/R_{CS} and CR_{WB}/R_{WB}) are presented in Table 6. In all growth phases, the growth performance traits, ADG, ADFI, ADEI, and PD, presented 0.1- to 0.3-fold lower CR_{CS} values than R_{CS} values, and 0.1- to 0.5-fold higher CR_{WB} values than R_{WB} values. LD was the only trait that CR_{TD} was lower than R_{TD} in both diets and in all growth phases. For this trait, the CR_{CS} was 0.3- to 0.5-fold lower than the R_{CS} , and the CR_{WB} was 0.2- to 0.3-fold higher than R_{WB} , depending on the growth phase. For FCR, the CR_{TD} and R_{TD} were similar under both diets during the starter and finisher phases, but during the grower phase and for the overall period, the CR_{CS} was 0.3- to 0.5-fold higher than the R_{CS} , and the CR_{WB} was 0.3-fold lower than the R_{WB} . For REI, the CR_{CS} was 0.1- and 0.5-fold lower than the R_{CS} during the starter and grower phases, respectively, but the CR_{CS} was 0.1- and 0.3-fold higher than the R_{CS} during the finisher phase and for the overall period, respectively. For this trait, the CR_{WB} was 0.1- to 0.7-fold lower than the R_{WB} , depending on the growth phase. For RFI, the CR_{CS} and R_{CS} were similar in all phases, but the CR_{WB} was 0.1- to 0.4-fold lower than the R_{WB} , depending on the growth phase.

Table 6. Response to direct selection and correlated response to indirect selection for the traits¹ by feeding phase

Traits	R _{CS}	R _{WB}	$\frac{R_{WB}}{R_{CS}}$	CR _{CS}	CR _{WB}	$\frac{CR_{CS}}{R_{CS}}$	$\frac{CR_{WB}}{R_{WB}}$
Starter phase							
ADG, g/d	26	17	0.6	21	20	0.8	1.2
ADFI, g/d	25	16	0.6	20	17	0.8	1.1
ADEI, MJ/d	60	37	0.6	47	40	0.8	1.1
LD, g/d	7.2	5.9	0.8	5.0	4.4	0.7	0.8
PD, g/d	5.1	2.1	0.4	3.3	3.3	0.7	1.5
FCR	0.05	0.07	1.2	0.06	0.06	1.1	0.9
REI, g/d	49	52	1.1	43	39	0.9	0.7
RFI, g/d	46	48	1.0	43	38	0.9	0.8
Grower phase							
ADG, g/d	31	20	0.6	25	25	0.8	1.3
ADFI, g/d	30	25	0.8	28	27	0.9	1.1
ADEI, MJ/d	71	61	0.9	66	64	0.9	1.1
LD, g/d	12	7.9	0.7	6.8	5.9	0.6	0.8
PD, g/d	5.4	3.4	0.6	4.2	4.3	0.8	1.3
FCR	0.02	0.05	2.3	0.03	0.03	1.5	0.7
REI, g/d	18	21	1.2	8	7	0.5	0.3
RFI, g/d	17	31	1.8	18	16	1	0.5
Finisher phase							
ADG, g/d	37	23	0.6	28	29	0.8	1.3
ADFI, g/d	62	29	0.5	46	39	0.7	1.4
ADEI, MJ/d	144	72	0.5	106	98	0.7	1.4
LD, g/d	16	8.9	0.6	8.1	6.9	0.5	0.8
PD, g/d	6.3	4.6	0.7	5.3	5.5	0.8	1.2
FCR	0.05	0.05	1.0	0.05	0.05	1.0	1.0
REI, g/d	40	43	1.1	45	38	1.1	0.9
RFI, g/d	37	37	1.0	39	34	1.1	0.9
Overall period							
ADG, g/d	32	21	0.7	26	26	0.8	1.2
ADFI, g/d	41	18	0.4	27	25	0.7	1.4
ADEI, MJ/d	96	42	0.4	64	63	0.7	1.5
LD, g/d	12	7.1	0.6	6.1	5.2	0.5	0.7
PD, g/d	5.7	3.7	0.7	4.5	4.6	0.8	1.2
FCR	0.03	0.06	2.0	0.04	0.05	1.3	0.7
REI, g/d	14	36	2.7	17	17	1.3	0.5
RFI, g/d	25	38	1.6	28	27	1.1	0.7

CS = diet based on corn and soybean meal; CR_{CS} = correlated response for CS to indirect selection under the WB; CR_{WB} = correlated response for WB to indirect selection under CS; R_{CS} = response to direct selection under the CS; R_{WB} = response to direct selection under the WB; WB = diet based on wheat and barley with high addition of coproducts.

¹ADG = average daily gain; ADFI = average daily feed intake; ADEI = average daily energy intake; FCR = feed conversion rate; LD = lipid deposition; PD = protein deposition; REI = residual energy intake; RFI = residual feed intake.

DISCUSSION

Genetic Correlations

According to Falconer and Mackay (1996), r_g values below 1 reveal the presence of a G×E. However, quantifying the G×E remains challenging. Clearly, for a given trait, the lower the r_g value, the higher the sensitivity to the environment. However, defining boundaries to create grades of r_g values may

be confusing and imprecise. Furthermore, making decisions and inferences based solely on a defined r_g scale, without combining it with other parameters, might be misleading. Nevertheless, we defined a scale for the magnitude of r_g to provide inferences and comparisons between the G×F detected for the different traits in the different phases of pig growth studied herein.

We found, r_g of unity between diets for ADG, FCR, and PD in all phases, for ADFI and ADEI

during the grower and finisher phases and for the overall period, and for REI and RFI during the finisher phase. These results showed that, according to this criterion, these traits behaved as the same trait, regardless of whether pigs were fed corn/soy or wheat/barley/coproducts. Therefore, the genetic progress obtained for these traits would be fully expressed under either diet, and the expected response to selection would depend solely on the σ_A^2 and h^2 estimates under each diet. In contrast, we found low-magnitude GxF for ADFI, ADEI, REI, and RFI, during the starter phase, and for RFI for the overall period. Based on these results, we expected that, for these traits, the genetic progress observed during selection under one diet would not be fully carried over to the other diet during these phases. We observed a moderate GxF found for LD in all phases, for REI during the grower phase and for the overall period, and for RFI during the grower phase. These results suggested that, for these traits, genetic progress would be compromised after changing diets, due to a reranking of the genotypes.

In this study, the diets were formulated to be isoenergetic to facilitate a fair comparison. In addition, pig diets were designed to meet the requirements of net energy and essential amino acids in each growth phase, to prevent limitations on PD, and thus growth. This design might explain why the r_g of PD was unity in all phases. Because both diets met the minimal requirements for crude protein, net energy, and amino acids during the entire growing-finishing periods, we hypothesized that pigs were not challenged by the environment, and hence, PD was not compromised.

On the other hand, LD presented moderate GxF in all phases. When replacing corn and soybean meal by wheat and barley, starch and simple carbohydrates (highly available in the corn) and crude protein (highly available on the soybean meal) decrease. Wheat and barley are weaker in these nutrients when compared to corn and soybean meal. The addition of the protein-rich coproducts offset the lack of crude protein in cereals (wheat and barley), but it increased the level of nonstarch polysaccharides (fiber). To compensate for the lack of simple carbohydrates in the wheat/barley/coproducts diet, animal, palm, and soybean oils were added to increase the net energy of the diet. Thus, the wheat/barley/coproducts diet was richer in crude fat than the corn/soy diet. Consequently, although the 2 diets were isoenergetic and balanced in amino acids and crude protein, they differed in nutrient content, due to the different sources of energy. The corn/soy diet was richer in starch and

poorer in fat and fiber, compared to the wheat/barley/coproducts diet. Thus, based on our results, we hypothesized that the LD, REI, and RFI traits in pigs were sensitive to changes in the source of energy nutrients in the diets.

In addition, the REI and RFI traits can capture sources of variation other than those related to production (ADG, LD, and PD). For example, they reflect factors related to the animal's immunity, gut function, energy required for live weight maintenance, physical activity, heat production, metabolic pathways, and others (Patience, 2012). Indeed, REI and RFI could reflect different digestion pathways that might be responsible for interactions between the genotypes and the different diets. Based on the large differences in the quantity and types of fiber in the 2 diets, differences in the intestinal region and the gut microbiota involved in dietary fiber digestion might give rise to variations in the capacity for nutrient utilization in pigs on different diets. In addition, the higher fiber content in the wheat/barley/coproducts diet increased its volume compared to the volume of the corn/soy diet. This difference might also explain why we found a low GxF effect on ADFI, and thus the ADEI, during the starter phase. At this young age, the pig's digestive system would not be fully developed, and high-volume feed might represent an environmental challenge that could compromise the feed intake capacity.

Direct Versus Indirect Selection

The heterogeneity of genetic variance observed in this study (Table 4) is important for breeding programs, because it is likely to impact the responses to selection (Table 6) that can be achieved by selecting under these diets. Our results suggested that the R_{TD} levels that can be achieved in FE traits during most growth phases are likely to be higher under the wheat/barley/coproducts than under the corn/soy diet. Conversely, growth performance traits are likely to display higher R_{TD} levels under a corn/soy than under a wheat/barley/coproducts diet.

The CR_{TD} depended on the σ_A^2 of the TD, the r_g between pig's performances under the 2 diets, and the intensity and accuracy of selection under the non-TD. Therefore, both sources of GxF: the heterogeneity of genetic variance and the reranking of genotypes, could impact the CR_{TD} . The benefit of indirect selection on the non-TD over direct selection on the TD was assessed with the ratio, CR_{TD}/R_{TD} (Table 6). Assuming equal intensity of selection with both diets, this ratio can also be assessed with the formula: $h_{\text{non-TD}} \times r_g / h_{TD}$, where h

is the accuracy of selection (Falconer and Mackay, 1996). Thus, when the r_g equals unity, the benefit of direct selection under the TD over indirect selection under the non-TD depends solely on whether the h_{TD} is higher than the h_{non-TD} . However, when the r_g is less than unity, the benefit of indirect over direct selection depends on whether the $h_{non-TD} \times r_g$ is higher than the h_{TD} . Thus, when the h_{TD} is higher than the h_{non-TD} , and when the r_g is less than unity, the benefit of direct selection increases.

We found estimates of r_g equivalent to unity for the traits ADG, ADFI, ADEI, PD, and FCR in all growth phases. This finding suggested that no reranking of genotypes occurred, and that all genetic progress gained in these traits under one diet would be carried over, when the pigs will be fed the other diet. However, independent of which diet the pigs are required to consume, the R_{TD} and the CR_{TD} values indicated that selection under the corn/soy diet would always lead to greater genetic progress in ADG, ADFI, ADEI, and PD, and selection under the wheat/barley/coproductions diet would always lead to higher genetic progress in the FCR.

We detected a GxF for LD. This effect caused reranking among the genotypes and heterogeneity of genetic variance. The moderate r_g values estimated for LD in all growth phases caused the CR_{TD} to be lower than the R_{TD} under both diets, in all growth phases. Thus, selecting pigs under a diet different from the diet pigs consume for growing-finishing performance will always compromise the genetic progress of the LD trait. Selection for LD should always be conducted under the diet pigs will be required to perform.

We detected GxF for REI and RFI. This effect caused reranking among genotypes and heterogeneity of genetic variance. Given the higher h^2 estimates under the wheat/barley/coproductions diet compared to the corn/soy diet, the CR_{CS} was consistently higher than the R_{CS} in all phases for both traits, except for REI during the grower phase (in the latter case, $CR_{CS}/R_{CS} = 0.5$). However, the CR_{WB} declined to 0.7-fold lower than the R_{WB} , which suggested that, selecting pigs under a corn/soy diet would severely compromise genetic progress in the REI and RFI, for the wheat/barley/coproductions diet. In addition, we observed CR_{TD}/R_{TD} ratio values below unity with both diets during the starter phase for both REI and RFI, and a particularly low value for REI during the grower phase. These results indicated that these 2 traits should not be considered the same trait, when growing-finishing pigs are raised under a different diet. Selecting pigs under a diet different from the one pigs will be required

to perform will always compromise genetic progress in REI and RFI. For these traits, selection should always be conducted under the same diet used in the growing-finishing period.

Breeding for Improved FE Under Lower-input Diets

Pig producers in many countries have historically benefited from access to corn and soybean grains. However, the continuous growth of the human population and increasing demand for grains from the biofuel industry have pressured animal production systems into using diet inputs in a more effective way (Neeteson-van Nieuwenhoven et al., 2013). Therefore, less use of high-input diets and inclusion of coproducts is a promising alternative for reducing the pork production footprint. In addition to reducing the environmental impact of pork production, the inclusion of coproducts in pig diets is a good strategy for improving economic results by reducing the price of diet inputs (Ali et al., 2017). There is a need for efficient pork production under different local circumstances; thus, breeding for efficiency should take into account differences in diets, when GxF is present.

We found that, when pigs were raised under the different diets, reranking of genotypes did not occur for ADG, PD, or FCR, during any growth phase, or for ADFI and ADEI during the grower and finisher phases and for the overall period. Therefore, although selection under a corn/soy diet could accelerate genetic progress in these traits, the ranking of genotypes will remain the same when pigs will be required to perform under the different diets. Thus, for these traits, changing from high-input diets (i.e., corn and soybean meal) to less valuable ingredients (wheat, barley, and coproducts) would not require a change in the genetic selection process. Consequently, changing the diet from corn/soy to wheat/barley/coproductions in growing-finishing pigs is advisable to reduce production costs and the environmental impact, independent of the diet used for trait selection.

We found that GxF interfered in the ranking of genotypes and caused heterogeneity of genetic variance under both diets for LD, REI, and RFI. Thus, selecting pigs under a diet different from the diet used for growing-finishing performance could compromise the LD in all growth phases, compromise the REI and RFI during the starter phase, and severely compromise the REI during the grower phase. Moreover, for all 3 FE traits, the CR_{WB} was 0.2- to 0.7-fold lower than the R_{WB} . Consequently, when pigs selected under corn/soy, will be required to perform under wheat/barley/coproductions, their

efficiency will be declined. Therefore, we recommend that, when pigs are required to perform under wheat/barley/coproducts, selection for FE should be conducted under the same diet. In future, FE traits are expected to become more important as the pressure placed on animal production systems increases and as diet inputs become more expensive. Diets like the wheat/barley/coproducts diet studied herein are a good alternative. Breeding for FE under lower-input diets should be considered as FE traits become more important and lower-input diets become more widespread in the near future.

CONCLUSIONS

We found that GxF did not interfere in the ranking of genotypes under either a corn/soy or a wheat/barley/coproducts diet for ADG, PD, and FCR during all growth phases, and for ADFI and ADEI during the grower and finisher phases and for the overall period. Therefore, for these traits, we recommend changing the diet of growing-finishing pigs from high-input feed (i.e., corn/soy) to feed with less valuable ingredients, as wheat/barley/coproducts, to reduce production costs and the environmental impact, regardless of which diet is used in selection.

We found that GxF interfered in the ranking of genotypes and caused heterogeneity of genetic variance under both diets for LD, REI, and RFI. Thus, selecting pigs under a diet different from the diet used for growing-finishing performance could compromise the LD in all growth phases, compromise the REI and RFI during the starter phase, and severely compromise the REI during the grower phase. In particular, when pigs are required to consume a wheat/barley/coproducts diet for growing-finishing performance, pigs should be selected for FE under the same diet. Breeding pigs for FE under lower-input diets should be considered, because FE traits will become more important and lower-input diets will become more widespread in the near future.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

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