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Digestive efficiency traits in growing pigs are genetically correlated with sow litter traits in the Large White breed

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ABSTRACT

Digestive efficiency traits are promising selection criteria to improve feed efficiency in pigs. However, the genetic relationships between digestive efficiency and sow reproductive traits are mostly unknown and need to be estimated. In this study, reproductive traits were available for 61 601 litters recorded on 21 719 Large White purebred sows. The traits were comprised of the number of born alive (**NBA**) and the number of weaned piglets (**NWP**), the number of stillbirths (**NSB**) and piglet mortality during suckling (**PM**). For a subset of 32 518 litters, the mean (**MBW**) and CV of piglet birth weights (**CVBW**) were deduced from individual piglet weights as well as the proportion of piglets weighing less than 1 kg (**PPL1K**). Growth and feed efficiency traits were available for 4 643 Large White male pigs related to sows with reproductive performances. They comprised average daily gain (**ADG**), daily feed intake (**DFI**) and feed conversion ratio (**FCR**). A subset of 1 391 pigs had predictions for digestibility coefficients (**DC**) of energy, organic matter and nitrogen obtained by analysing faecal samples with near-infrared spectrometry. Estimated heritabilities were low for NBA, NSB, NWP and PM (0.08 ± 0.01 to 0.11 ± 0.01) and low to moderate for litter weight characteristics (0.14 ± 0.02 to 0.38 ± 0.01). Heritability estimates were moderate to high for ADG, DFI and FCR (0.37 ± 0.04 to 0.54 ± 0.05) and moderate for DC traits (0.26 ± 0.06 to 0.38 ± 0.07). Genetic correlations were low between ADG, or alternatively FCR, and reproductive traits. They were significantly different from zero with MBW (0.19 ± 0.06 with ADG and −0.15 ± 0.06 with FCR) and PPL1K (−0.19 ± 0.07 with ADG and 0.18 ± 0.07 with FCR). All genetic correlations between DFI and reproductive traits were low and not significantly different from zero. Genetic correlations between DC traits and NBA were significantly different from zero for DC of organic matter and energy (<−0.25 ± 0.11). DC traits were moderately correlated with MBW (>0.30 ± 0.11), CVBW (<−0.36 ± 0.11) and PPL1K (<−0.37 ± 0.11) at the genetic level. Genetic correlations between DC traits and PM were significantly negative and hence favourable (<−0.38 ± 0.12). Finally, genetic correlations between DC traits and NWP were close to zero. These results suggested that sows closely related to growing pigs with the best digestive efficiency would produce heavier and more homogeneous piglets, with slightly smaller litter sizes at birth but better survival. Hence, there is usable genetic variation in DC that could be exploited to define new selection strategies in maternal lines aiming at improving not only feed efficiency but also piglet survival.

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Implications

Reducing piglet mortality is a major goal in pig breeding programmes for both economic and ethical considerations. However, breeding for increased piglet survival is difficult due to low heri-

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tability and the absence of measures on candidates at the time of selection. Findings in the present study revealed that digestive efficiency traits in growing pigs are genetically related to piglet weight characteristics and survival modelled as traits of the sows. This suggested that there is genetic variation to be used for defining novel breeding strategies to improve both digestive efficiency and sow productivity at weaning through reduced piglet mortality.

Introduction

Digestive efficiency traits are promising new selection criteria to improve feed efficiency in pigs. Recently, Déru et al. (2021) reported genetic parameters for digestibility coefficients (**DC**) of energy, nitrogen and organic matter for pigs fed a cereal-based conventional diet and pigs fed an alternative diet with increased fibre content. In this study, DC traits were predicted by analysing faecal samples obtained from spot collection with NIRS in 65 kg BW pigs. Moderate to high heritabilities were estimated for DC traits with both diets. Furthermore, favourable genetic correlations were estimated with daily feed intake (**DFI**) and feed conversion ratio (**FCR**), although antagonistic genetic correlations were also evidenced with growth rate and carcass yield (Déru et al., 2021). Improving by selecting the ability to digest feed, *i.e.* extracting more nutrients from feed at the gut level, may have consequences not only on production traits but also on other traits such as reproductive traits. To our knowledge, genetic and phenotypic correlations between digestive efficiency and reproduction traits are unknown in pigs. In a selection experiment on litter size at weaning in rabbit lines, differences in digestive efficiency were observed in lactating does: does selected for higher litter size at weaning had larger DC for DM, organic matter and gross energy than does selected for higher reproductive longevity (Pascual et al., 2010).

Low genetic correlations are usually reported between feed efficiency traits measured in growing pigs and sow reproduction traits (Rotschild and Ruvinsky, 2011). However, if the genetic variability of digestive efficiency estimated during the growing phase is at least partly maintained for adult sows, we may postulate that sows with higher digestive efficiency will have more nutrients available for the growth of foetuses during gestation at a given feed intake. This could lead to heavier piglets at birth and reduced mortality during the suckling period, since the birth weight is an important factor influencing piglet survival (Feldpausch et al., 2019). In order to test this hypothesis, genetic correlations between digestive efficiency traits and reproductive traits, including weight characteristics of litters, were estimated in connected French Large White commercial lines.

Material and methods

Reproductive traits

Reproductive performances of Large White purebred sows were extracted from the national database for litters born between January 2014 and October 2020 in nucleus herds of the breeding companies AXIOM (Azay-sur-Indre, France) and NUCLEUS (Le Rheu, France). Sow reproduction traits comprised the number of piglets born alive (**NBA**), the number of stillborn piglets (**NSB**), the number of weaned piglets (**NWP**) and the piglet mortality during the suckling period expressed in percentage (**PM** = 100 * (NBA − NWP)/NBA). Stillborn piglets were identified by farm operators either as delivered dead during the farrowing process or found dead within the membranes behind the sow after farrowing is complete. In purebred litters only, all live-born piglets were individually weighed on the day of birth (66%) or on the following day (34%). These individual birth weights were used to estimate litter traits: the mean birth weight (**MBW**), the CV of piglet birth weights (**CVBW**), the litter weight at birth (**LWB**), and the proportion of live-born piglets lighter than 1 kg (**PPL1K**). The LWB and PPL1K performances were discarded for litters in which the number of weighed piglets at birth was not equal to the number of born alive piglets (13% of the litters). Because the absence of a birth weight for a single piglet impacts very little MBW and CVBW of litters with more than 10 piglets, MBW and CVBW performances were kept for litters with more than 10 piglets in which only one birth weight was missing. This led to removing 6% of MBW and CVBW performances from the initial dataset. All performances that were three SDs beyond the phenotypic mean were discarded. Moreover, only sows with valid performances for NBA, NSB, NWP and PM were kept for statistical analyses. Finally, performances recorded in farrowing batches with less than 18 sows were removed from the dataset. In total, litter size and piglet mortality records were available for 21 719 sows, having 2.8 litters on average, and 59% of these litters were purebred. Descriptive statistics for sow reproduction traits are summarised in Table 1.

Growth, feed efficiency and digestibility coefficients

The dataset comprised feed efficiency and digestive efficiency traits recorded on 4 643 non-castrated Large White male pigs tested since 2015 in 88 successive batches at the INRAE UE3P – France Génétique Porc phenotyping station (Le Rheu, France, https://doi.org/10.15454/1.5573932732039927E12). These pigs had dams and half-sisters with reproductive performances, and some full sisters. A fraction of these animals (n = 1 391) also had digestibility coefficients predicted for energy, organic matter and nitrogen and corresponded to the experimental design described by Déru et al. (2020 and 2021). Piglets arrived at the phenotyping station just after weaning at three weeks of age. They were allotted in groups of 14 animals. These groups remained unchanged from postweaning to slaughter. During the postweaning period, all piglets arrived in the same week were kept in the same room until nine weeks of age and were fed with a standard two-phase postweaning dietary sequence. Then, they were transferred to the growing-finishing facilities in which all pens contained a single-place electronic feeder equipped with a weighing scale (GenStar, Skiold ACEMO, Pontivy, France). The test period started when the pigs reached a BW of 35 kg and lasted until market weight (120 kg BW). During the growing-finishing phase, pigs were fed a two-phase dietary sequence. A growing type of diet was first distributed, then a five-day transition was organised at 16 weeks of age (65 kg BW on average), and finally, a finishing diet was provided until the end of the test. Most pigs received a conventional two-phase diet. This diet had a net energy content of 9.6 MJ/kg and a NDF of 13.90% and was formulated mainly based on wheat, barley, corn and soybean meal. As described in Déru et al. (2020), 801 pigs, representing half of the batches for 35 batches, were offered an alternative diet with larger dietary fibre content. The high fibre diet had a net energy content of 8.2 MJ/kg and NDF content of 23.95%. It was formulated based on wheat, barley, wheat bran, soybean hulls and sugar beet pulp. It thus contained both insoluble and soluble dietary fibres. The ratio digestible lysine/net energy was identical in both conventional and high fibre dietary sequences, to 0.94 g/MJ net energy in the growing phase and to 0.81 g/MJ net energy in the finishing phase. Feed formula can be found in Supplementary Table S1, and further details can be found in Déru et al. (2020 and 2021).

Average daily gain (**ADG**) was estimated using the weights at the beginning and end of the test period. Based on electronic feeders' data, DFI was calculated along with FCR (FCR = DFI/ADG). To determine digestibility coefficients, a spot collection of faeces (about 50 g) was carried out at 16 weeks of age (65 kg BW on aver-

Table 1
Descriptive statistics of sow reproduction traits.

Variable	Unit	n sows	n litter	Mean	SD
NBA		21 719	61 601	15.11	3.35
NSB		21 719	61 601	1.20	1.48
NWP		21 719	61 601	13.17	3.07
PM	%	21 719	61 601	12.17	11.46
MBW	Kg	14 048	32 518	1.38	0.22
CVBW	%	14 048	32 518	20.38	6.35
LWB	Kg	13 346	28 943	20.25	4.15
PPL1K	%	13 238	28 594	15.18	14.60

Abbreviations: NBA = number of born alive; NSB = number of stillborn; NWP = number of weaned piglets; PM = piglet mortality; MBW = mean birth weight; CVBW = CV of piglet birth weight; LWB = litter weight at birth; PPL1K = proportion of live-born piglets lighter than 1 kg.

age), just before the transition between the growing and finishing diets, for a subsample of 1 781 pigs born in 2017 and 2018, in batches where both the high fibre and conventional diets were distributed. Faecal samples were manually homogenised and then stored at −20 °C. Before analysis, samples were freeze-dried and ground with a grinder (Grindomix GM200, Retsch). Ground samples were analysed three times with a NIRS device (MPA Bruker Optik), and the resulting average spectrum was used to predict DC of energy, organic matter and nitrogen following methods developed by Labussière et al. (2019). Altogether, measures were available for 4 643 pigs, including 801 fed the high fibre diet, and 1 391 with DC predictions. Descriptive statistics concerning growth rate, feed efficiency and DC traits are given in Table 2 for both diets.

Statistical analyses

Reproduction traits were analysed with the following animal linear mixed model accounting for repeated performances across parities:

$$Y = \mathbf{X} + \mathbf{Zu} + \mathbf{Tperm} + \mathbf{e},$$

where **y** is the vector of phenotypes for a given trait, **β** is the vector of fixed effects comprising the sow parity (with six modalities: one level per parity from parities 1 to 5 and one extra level for 6th and higher parities) and the farrowing batch (1 247 levels) for all traits, the type of litter with two modalities (purebred/crossbred) for NBA, NSB, NWP and PM, and the age at weighing (two modalities: on the day of birth or on the day following birth) for MBW, CVBW, LWB and PPL1K. **X** is the incidence matrix relating observations to fixed effects. $\mathbf{u} \sim N(0, \mathbf{A}\,\sigma^2_u)$ is the vector of additive genetic effects for the considered trait, where **A** is the pedigree relationship matrix and σ^2_u is the additive genetic variance. **Z** is the incidence matrix of the additive genetic effects. $\mathbf{perm} \sim N(0, \mathbf{I}\,\sigma^2_{perm})$ is the random effect of the permanent environment of the sow, and **T** is the incidence matrix relating performances to the random effect **perm**. Finally, $\mathbf{e} \sim N(0, \mathbf{I}\,\sigma^2_e)$ is the residual random effect, and **I** is the identity matrix of appropriate size.

Because low genetic × diet interactions were estimated for all production traits, including DC traits (Déru et al., 2020 and 2021), all pigs fed the conventional and high fibre diets were kept in the subsequent statistical analyses to maximise the amount of available data and hence the accuracy of estimates. Production traits recorded with both diets were considered as single traits, and diet was modelled as an environmental factor of variation. Production traits were analysed with the following animal linear mixed model:

$$y = X + Zu + Wpen + Vc + e,$$

where **y** is the vector of phenotypes for a given trait, **β** is the vector of fixed effects depending on the trait considered: diet, batch and DFI within diet for DC traits, as recommended by Déru et al. (2021), diet, batch and weight at the end of postweaning phase for ADG and FCR, diet, batch and weight at the end of test for DFI. **X** is the incidence matrix relating observations to fixed effects. $\mathbf{u} \sim N(0, \mathbf{A}\,\sigma^2_u)$ is the vector of additive genetic effects for the considered trait, where **A** is the pedigree relationship matrix. **Z** is the incidence matrix of the additive genetic effects. $\mathbf{pen} \sim N(0, \mathbf{I}\,\sigma^2_{pen})$ is the random effect of the pen effect nested within batch and diet with variance σ^2_{pen}, and **W** is the incidence matrix relating performances to the random effect **pen**. $\mathbf{c} \sim N(0, \mathbf{I}\,\sigma^2_c)$ is the random effect of the common litter applied only for ADG, DFI and FCR. **V** is the incidence matrix relating performances to common litter effects. Finally, $\mathbf{e} \sim N(0, \mathbf{I}\,\sigma^2_e)$ is the residual random effect. Homogeneity of residual variances across diets was tested using the Levene test. Residual variances were significantly different between diets only for DFI ($P = 0.004$), FCR ($P < 0.001$) and DC of nitrogen ($P < 0.001$). Thus, heterogeneity in the residual variance due to the diet was considered for these three traits.

Variance components and covariances were estimated using bivariate analyses for all combinations of production and reproduction traits. For analyses between a production and a reproduction trait, the residual covariance was fixed to zero, because no individual had both production and reproduction records. The populations of growing pigs and sows with reproduction performances were well genetically connected because they stemmed from a

Table 2
Descriptive statistics of growth, feed and digestive efficiency traits of growing pigs.

		Diet					
		Conventional			High fibre		
Variable	Unit	*n*	Mean	SD	*n*	Mean	SD
ADG	g/d	3 842	1039.46	87.19	801	968.23	86.36
DFI	kg feed/d	3 842	2.56	0.23	801	2.69	0.25
FCR	kg feed/kg	3 842	2.47	0.16	801	2.79	0.18
DCE	%	674	84.28	3.22	663	77.89	3.29
DCOM	%	725	83.81	2.91	666	77.99	2.59
DCN	%	711	78.94	3.31	651	73.67	2.85

Abbreviations: ADG = average daily gain; DFI = daily feed intake; FCR = feed conversion ratio; DCOM = digestibility coefficient of organic matter; DCE = digestibility coefficient of energy; DCN = digestibility coefficient of nitrogen.

common panel of sires representative of the French Large White population. For instance, growing pigs with DC traits had on average 34.7 ± 37.9 half-sisters with at least one NBA record and 18.1 ± 20.9 half-sisters with at least one MBW record. The pedigree relationship matrix was constructed tracing back five generations upwards and considering altogether growing pigs and breeding sows with performances. The pedigree file contained in total 32 326 individuals. Variance components were estimated by Restricted Maximum Likelihood using the ASREML 3.0 software (Gilmour et al., 2009).

Results

Genetic parameters estimated across sow reproductive traits

Heritabilities, genetic and phenotypic correlations estimated among reproductive traits are reported in Table 3. Estimated heritabilities were low for NBA, NSB, NWP and PM (0.08 ± 0.01 to 0.11 ± 0.01) and low to moderate for litter weight characteristics (0.14 ± 0.02 to 0.38 ± 0.01).

Although genetic and phenotypic correlations were high between NBA and NWP (0.86 ± 0.02), both traits had different sets of genetic correlations with other reproductive traits. NBA was moderately and unfavourably correlated with PM but also with MBW, CVBW and PPL1K (0.31 ± 0.05 to 0.44 ± 0.04 in absolute values). Due to the genetic antagonism between NBA and MBW, the genetic correlation between NBA and litter weight was moderate (0.34 ± 0.04). Interestingly, NWP was lowly genetically correlated with PM, MBW, CVBW and PPL1K (0.05 ± 0.06 to 0.16 ± 0.05 in absolute values). As a result, the genetic correlation between NWP and LWB (0.51 ± 0.04) was higher than between NBA and LWB (0.34 ± 0.04), although the phenotypic correlation was identical between LWB and both NBA and NWP. Genetic and phenotypic correlations between NSB and other traits were generally low, although significant and unfavourable with NBA (0.16 ± 0.05), and significant and favourable with PM (0.27 ± 0.05). Finally, most genetic correlations among litter weight characteristics were moderate to high (0.24 ± 0.05 to 0.94 ± 0.01 in absolute values). MBW was favourably correlated with CVBW and litter weight. PPL1K was highly and favourably correlated with MBW, CVBW and LWB at the genetic level (Table 3). MBW, CVBW and PPL1K were also highly genetically correlated with piglet mortality (0.52 ± 0.04 to 0.64 ± 0.04 in absolute values).

Genetic parameters estimated across digestive and feed efficiency traits

Genetic parameters estimated for growth, feed efficiency and digestive efficiency traits are presented in Table 4. Heritability estimates of ADG, DFI and FCR were moderate to high (0.37 ± 0.04 to 0.61 ± 0.05). Genetic and phenotypic correlations were strong between ADG and DFI on the one hand, and between DFI and FCR on the other hand (0.73 ± 0.03 and 0.69 ± 0.05, respectively). The correlations between ADG and FCR were moderate at the phenotypic level for both diets (−0.37 ± 0.03 and −0.44 ± 0.03 for the conventional and high fibre diet, respectively) and much lower at the genetic level (−0.11 ± 0.07).

Genetic parameters were estimated for DC traits combining data across diets and adjusting for DFI within diet (Table 4), accounting for heterogeneity of variances for DC of nitrogen. For DC traits, heritabilities were moderate, with values between 0.26 ± 0.06 and 0.38 ± 0.07. The heritability estimated for DC of nitrogen was lower in the conventional diet than in the high fibre diet, as already reported by Déru et al. (2021). Genetic and phenotypic correlations estimated between DC traits were very high (>0.93 ± 0.07 and >0.74 ± 0.02, respectively) and could not be estimated between DC of energy and organic matter due to convergence problems.

Phenotypic correlations between DC traits and ADG were generally low but significantly different from 0 (Table 4). Interestingly, the phenotypic correlations between ADG and DC of organic matter as well as DC of energy were slightly negative (−0.08 ± 0.04 and −0.12 ± 0.04), thus unfavourable, whereas they were positive and favourable between ADG and DC of nitrogen with slightly larger estimates in the high fibre diet (0.09 ± 0.04 and 0.20 ± 0.04, respectively). At the genetic level, DCs of energy and organic matter were moderately and unfavourably correlated with ADG, whereas the correlation between ADG and DC of nitrogen was close to zero.

Phenotypic correlations were low and negative, thus favourable, between DC traits and DFI as well as FCR. They were slightly more negative in the conventional diet than in the high fibre diet for DC of nitrogen. The genetic correlations were moderate between FCR and DC traits (<−0.20 ± 0.12), and high and significant between DFI and DC traits (−0.57 ± 0.10 to −0.59 ± 0.10).

Genetic correlations between reproductive, growth, feed efficiency and digestive efficiency traits

Genetic correlations were low between ADG and reproductive traits (Table 5). They were significantly different from zero only with MBW (0.19 ± 0.06) and PPL1K (−0.16 ± 0.07). All genetic correlations between DFI and reproductive traits were low and not significantly different from zero. Finally, FCR was significantly genetically correlated only with NSB, MBW and PPL1K. These genetic correlations were unfavourable with NSB (−0.24 ± 0.07) whereas they were favourable with MBW (−0.19 ± 0.06) and PPL1K (0.18 ± 0.07).

Genetic correlations between each of the DC traits and the reproductive traits followed similar patterns (Table 5). Genetic correlations between DC traits and NBA were slightly negative, i.e.

Table 3
Heritabilities on the diagonal (with SE), genetic correlations above diagonal (with SE) and phenotypic correlations[1] below diagonal among sow litter traits.

Variable	NBA	NSB	NWP	PM	MBW	CVBW	LWB	PPL1K
NBA	**0.10 (0.01)**	0.16 (0.05)	0.86 (0.02)	0.39 (0.05)	−0.40 (0.04)	0.31 (0.05)	0.34 (0.04)	0.44 (0.04)
NSB	−0.03	**0.11 (0.01)**	0.02 (0.05)	0.27 (0.05)	−0.07 (0.04)	−0.04 (0.05)	0.01 (0.05)	0.07 (0.05)
NWP	0.83	−0.08	**0.08 (0.01)**	−0.12 (0.06)	−0.16 (0.05)	0.05 (0.06)	0.51 (0.04)	0.14 (0.05)
PM	0.23	0.11	−0.34	**0.08 (0.01)**	−0.53 (0.04)	0.52 (0.04)	−0.24 (0.05)	0.64 (0.04)
MBW	−0.52	−0.17	−0.31	−0.36	**0.38 (0.02)**	−0.44 (0.03)	0.74 (0.03)	−0.94 (0.01)
CVBW	0.37	0.08	0.17	0.35	−0.52	**0.14 (0.01)**	−0.24 (0.05)	0.68 (0.03)
LWB	0.74	−0.15	0.74	−0.01	0.16	0.03	**0.21 (0.01)**	−0.67 (0.03)
PPL1K	0.39	0.13	0.15	0.39	0.77	0.67	−0.20	**0.25 (0.01)**

Abbreviations: NBA = Number of born alive piglets; NSB = number of stillborn piglets; NWP = number of weaned piglets; PM = piglet mortality; MBW = mean birth weight of live-born piglets; CVBW = within-litter CV of live-born piglet birth weights; LWB = litter weight at birth; PPL1K = proportion of piglets weighing less than 1 kg.
[1] Standard errors of phenotypic correlations are at most equal to 0.01.

Table 4
Heritabilities (with SE, on the diagonal), genetic correlations (with SE, above diagonal) and phenotypic correlations[1] (below diagonal) estimated among production traits measured in growing pigs.

Variable	Diet[2]	ADG	DFI	FCR	DCOM	DCE	DCN
ADG	-	**0.37 (0.04)**	0.73 (0.03)	−0.11 (0.07)	−0.40 (0.11)	−0.41 (0.11)	−0.01 (0.15)
DFI	Conventional	0.88	**0.56 (0.05)**	0.69 (0.05)	−0.59 (0.10)	−0.59 (0.10)	−0.61 (0.12)
	High fibre	0.81	**0.49 (0.05)**				
FCR	Conventional	−0.37	0.51	**0.42 (0.05)**	−0.28 (0.13)	−0.20 (0.12)	−0.37 (0.13)
	High fibre	−0.44	0.54	**0.34 (0.04)**			
DCOM	-	−0.08	−0.36	−0.22	**0.38 (0.07)**	NE[3]	0.93 (0.07)
			−0.34	−0.19			
DCE	-	−0.12	−0.40	−0.19	NE[3]	**0.32 (0.06)**	0.97 (0.04)
			−0.37	−0.16			
DCN	Conventional	0.09	−0.19	−0.20	0.74	0.76	**0.26 (0.06)**
	High fibre	0.20	−0.26	−0.08	0.78	0.80	**0.35 (0.08)**

Abbreviations: ADG = average daily gain; DFI = daily feed intake; FCR = feed conversion ratio; DCOM = digestibility coefficient of organic matter; DCE = digestibility coefficient of energy; DCN = digestibility coefficient of nitrogen.
[1] Standard errors of phenotypic correlations were 0.01–0.02 among growth and feed efficiency traits. Standard errors of phenotypic correlations were 0.03–0.04 among digestibility coefficients and between digestibility coefficients traits and growth and feed efficiency traits.
[2] For traits having heterogeneous residual variances depending on diet.
[3] Not estimated due to convergence problems.

Table 5
Genetic correlations along with their SE (between brackets) between sow litter traits, and growth, feed efficiency and digestive efficiency traits in growing pigs.

Variable	ADG	DFI	FCR	DCOM	DCE	DCN
NBA	−0.07 (0.07)	−0.03 (0.07)	−0.01 (0.07)	−0.25 (0.11)	−0.26 (0.12)	−0.21 (0.13)
NSB	0.11 (0.07)	−0.11 (0.07)	−0.24 (0.07)	−0.14 (0.11)	−0.06 (0.12)	−0.01 (0.13)
NWP	−0.08 (0.08)	−0.06 (0.07)	0.04 (0.08)	−0.02 (0.13)	−0.05 (0.14)	−0.01 (0.14)
PM	0.01 (0.08)	−0.01 (0.07)	0.05 (0.07)	−0.40 (0.11)	−0.40 (0.12)	−0.38 (0.12)
MBW	0.19 (0.06)	−0.04 (0.06)	−0.19 (0.06)	0.37 (0.09)	0.37 (0.10)	0.30 (0.11)
CVBW	−0.02 (0.07)	0.07 (0.07)	0.11 (0.07)	−0.36 (0.11)	−0.41 (0.11)	−0.41 (0.12)
LWB	0.07 (0.07)	−0.13 (0.07)	−0.08 (0.07)	0.19 (0.11)	0.17 (0.12)	0.14 (0.12)
PPL1K	−0.16 (0.07)	0.06 (0.07)	0.18 (0.07)	−0.39 (0.10)	−0.45 (0.11)	−0.37 (0.11)

Abbreviations: ADG = average daily gain; DFI = daily feed intake; FCR = feed conversion ratio; DCOM = digestibility coefficient of organic matter; DCE = digestibility coefficient of energy; DCN = digestibility coefficient of nitrogen; NBA = number of born alive; NSB = number of stillborn; NWPs = number of weaned piglets; PM = piglet mortality; MBW = mean birth weight; CVBW = CV of piglet birth weight; LWB = litter weight at birth; PPL1K = proportion of live-born piglets lighter than 1 kg.

unfavourable, and were significantly different from zero for DC of organic matter and DC of energy (<−0.25 ± 0.11). Genetic correlations were slightly negative but not significantly different from zero between DC traits and NSB. On the contrary, genetic correlations were moderate and significant with MBW (>0.30 ± 0.11), CVBW (<−0.36 ± 0.11) and PPL1K (<−0.37 ± 0.11). Despite negative correlations with NBA, genetic correlations between DC traits and LWB were slightly positive though not significant (>0.14 ± 0.12). Genetic correlations between DC traits and PM were significantly negative and hence favourable (<−0.38 ± 0.12). Finally, genetic correlations between DC traits and NWP were close to zero.

Discussion

Results presented in this study confirmed the assumption that digestive efficiency traits measured in growing pigs are genetically correlated to litter productivity of sows. Interestingly, genetic correlations suggested that breeding animals with the highest breeding values for digestive efficiency traits generally tended to have slightly lower prolificacy but heavier and more homogeneous piglets at birth with lower mortality rates during the suckling period.

In the present study, DC traits were corrected for DFI as covariate in the model to focus specifically on digestive efficiency aptitudes, independently from DFI variations. Indeed, as discussed in Déru et al. (2021), DC predictions partly captured variations in pig feed intake that influences digestibility presumably due to faster passage rates in the intestines. A negative, and hence favourable, correlation between DC traits and DFI as well as FCR was found at the genetic and phenotypic levels. The genetic correlation between DC of energy and organic matter with ADG was negative and unfavourable whereas it was close to zero between DC of nitrogen and ADG. All estimated genetic parameters of DC traits, growth and feed efficiency traits were consistent with results reported by Déru et al. (2021). Biological assumptions to interpret those results were thoroughly discussed in the latter article.

Litter size and litter weight characteristics were lowly genetically correlated with growth and feed intake traits of growing pigs. These results are consistent with the literature, as genetic correlations between production and reproduction traits are either close to zero or slightly unfavourable in pigs (for a review, see Rotschild and Ruvinsky, 2011). Among the few genetic correlations that were significantly different from zero, the correlations between ADG and MBW, and conversely PPL1K, were slightly positive. This result agrees with genetic parameters reported by Hermesch et al. (2000). Besides, the genetic correlation between FCR and NSB was slightly negative and unfavourable. To our knowledge, genetic correlations estimated between these traits have not been reported in the literature. However, no such correlated response on stillbirth had been observed in a divergent selection experiment on residual feed intake, another feed efficiency trait (Gilbert et al., 2012). All other genetic correlations between ADG (and FCR) and reproductive traits were not different from zero. Similarly, none of genetic correlations between DFI in growing pigs and sow litter productivity traits were significantly different from zero.

On the contrary, most genetic correlations estimated between DC traits, litter size at birth, litter weight characteristics and piglet mortality were significant. The genetic correlation between DC traits and NBA, PM, MBW, CVBW and PPL1K suggested that sows

closely related to growing pigs with the best digestive efficiency would produce heavier and more homogeneous piglets, with slightly smaller litter sizes at birth but better piglet survival, and hence no effect on the number of weaned piglets. These results seemed consistent because piglet weight characteristics and litter homogeneity at birth are known to be critical to their survival (Quiniou et al., 2002; Feldpausch et al., 2019). To our knowledge, the present study reports the first estimates of genetic correlations between individual digestibility coefficients and reproductive traits in pigs as well as in other livestock species. Pascual et al. (2010) had already observed that lactating does selected for larger litter size at weaning displayed higher digestive efficiency than does selected for longer productive life. In the line selected for litter size at weaning, a 12-generation selection enabled large genetic progress on the number of pups born alive (+2.06, *i.e.* a 25% relative increase) without reduction in the mean weight of pups (Quevedo et al., 2005), despite a genetic antagonism between both traits (Pascual et al., 2013). Hence, findings of the present study seemed to confirm that digestive efficiency is a lever to consider when designing breeding strategies to maintain the newborn birth weight whilst improving litter size in polytocous species.

The slight genetic antagonism between digestive efficiency and the number of born alive piglets was not expected, despite its unfavourable correlations with piglets and litter weights. It seems unlikely that an increase in the number of stillborn piglets could explain this observation, given the genetic and phenotypic correlations between DC traits and NSB. However, litter size at birth is conditioned by the proper follicular development and recruitment before ovulation, which can be affected by environmental factors especially in lactating sows (Lucy et al., 2001). During lactation, the feeding level is usually increased to supply the sow with all required nutrients and satisfy her physiological needs, approaching a situation of *ad libitum* feeding. During this period, females that can rapidly increase their voluntary feed intake could be advantaged to enable follicular development, especially in primiparous sows (Hoving et al., 2011). According to genetic and phenotypic correlations estimated in growing pigs, animals with the largest digestive efficiency have lower voluntary DFI and lower residual feed intake (Déru et al., 2021). Hence, we may hypothesise that sows with high digestive efficiency could have lower increase in voluntary feed intake during lactation that may limit follicular development and hence litter size.

Interestingly, digestive efficiency traits measured in growing pigs were in most cases more related to sow reproductive traits than DFI and FCR, although DC traits are genetically correlated with both DFI and FCR. It is known that DC traits increase with age during the growing period up to the adult stage (Noblet et al., 1994 and 2013; Le Goff and Noblet, 2001). Assuming that the variability in digestive efficiency measured in growing pigs is partly maintained up to the adult stage, at least better than DFI or FCR that would depend more on metabolic changes between physiologically different periods, a possible explanation would be that sows with more efficient digestion provide their litter with more energy or nutrients *in utero*. Indeed, sow feeding is usually restricted during gestation to cover their nutritional needs between the first days after insemination and around 90–100 days of gestation. These requirements are defined according to the sow weight, body condition score, or backfat measurement, and litter growth requirements assuming a constant digestive efficiency for all sows. At a given restricted feed intake, sows with higher DC will thus retain more nutrients at the gut level that might be used for the growth of foetuses. In all cases, amounts of circulating nutrients may not be limiting during the first 70 days of gestation where protein and energy needs to ensure foetal growth are not high yet (McPherson et al., 2004). However, during the last third of the gestation period (around 70d of gestation), protein and energy requirements increase rapidly and may not be completely fulfilled in case of large litters, although the sow feeding level is generally increased during the last three weeks before farrowing (McPherson et al., 2004; Dourmad et al., 2021). Besides, the routine use of ingredients containing more dietary fibres in sow diets, to favour satiety and welfare under restricted feeding, certainly enhances the importance of better digestive efficiency, as compared to growing-finishing diets that contain fewer dietary fibres. Therefore, these results highlight the fact that variability in digestive efficiency of sows certainly exists and should be accounted for to define more adequate feeding plans.

This study was based on an experimental dataset of limited size designed to assess the genetic variability of DC traits (Déru et al., 2021). Hence, genetic correlations were estimated with moderate accuracy, in particular between DC traits and other production traits, and must be considered with caution. Compared to the gold standard methodology used to measuring digestive efficiency, the NIRS-based methodology considered in this study makes it possible to phenotype large numbers of animals reared in groups. Thus, it should facilitate collecting larger datasets in future to refine estimates of genetic correlations. In future research, it will be also critical to finely measure feed intake and DC traits in females during both the growing and the reproductive stages, to be able to disentangle genetic and environmental effects influencing feed and digestive efficiency, and litter characteristics. In addition, measuring digestive efficiency traits in lines divergently selected for improved piglet survival could be a way to evaluate experimentally if an increase in digestive efficiency is observed as a correlated response to selection.

To conclude, data were collected in two large groups of closely related animals that were representative of the genetic variability existing in two connected French Large White commercial populations. It suggested usable genetic variation in DC to define new selection strategies in pig maternal lines. Besides, accounting for DC traits in breeding schemes could be promising to improve selection accuracy on piglet survival and piglet birth weight, because it can be obtained for gilts before candidate selection.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2021.100447.

Ethics approval

The study was conducted following the French legislation on animal experimentation and ethics as regards the experimental design led to measure digestibility coefficients. The certificate of Authorization to Experiment on Living Animals was delivered by the Ministry of Higher Education, Research and Innovation to conduct this experiment at INRAE UE3P - France Génétique Porc phenotyping station (https://doi.org/10.15454/1.5573932732039927E12) under reference number 2017011010237883. For the reproduction dataset, sow performances were recorded for routine genomic evaluations in accordance with national regulations of humane care and use of animals in agriculture defined by the Ministry of Agriculture and Food.

Data and model availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy restrictions.

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Declaration of interest

None.

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