

Reproductive performance and its association with *ESR*, *PRLR*, *FSHB* genes in indigenous “I” pigs

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Abstract

Improving the reproductive performance of sows plays an important role in the pig industry, and it applies not only to commercial pigs but also to indigenous pigs. In this study, the polymorphisms of three genes, namely *estrogen receptor* (*ESR*), *prolactin receptor* (*PRLR*), and *follicle-stimulating hormone beta subunit* (*FSHB*) in the “I” pig population were investigated, and their associations with reproductive performance were evaluated. Ear tissue samples were collected from 151 fattening pigs and 126 sows across breeding farms in Vietnam for polymorphisms of the *ESR*, *PRLR* and *FSHB* genes. Three genotypes (AA, AB, and BB) were detected at the *ESR* T1665G and *FSHB* T212C loci, whereas the AA genotype was not observed at the *PRLR* G1789A locus. Consequently, genotype frequencies of *ESR* and *FSHB* were in Hardy-Weinberg equilibrium, while *PRLR* deviated significantly ($P < 0.001$). The *ESR* genotypes and parity showed no significant effects on the reproductive traits. The *PRLR* G1789A polymorphism showed a significant effect only on BWB, with sows carrying the BB genotype exhibiting more favorable values than those with the AB genotype. However, most of the traits differed across years, except age at first mating (AFM) and farrowing interval (FRI). The *FSHB* genotypes significantly affected reproductive performance, excluding AFM, age at first farrowing (AFF), FRI, and piglet birth weight (BWB). Sows with the *FSHB*^{AA} genotype had a higher number of total piglets born and greater piglet body weight at birth and weaning than those carrying *FSHB*^{AB}. These findings indicate that the *FSHB*^{AA} genotype may serve as a useful genetic marker for enhancing reproductive traits in the endangered “I” pig population.

Keywords: *ESR*, *FSHB*, indigenous pig, *PRLR*, reproductive performance

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Introduction

The “I” pig is a Vietnamese indigenous breed, characterized as having black hair, short legs and a low-hanging belly (Nguyen *et al.*, 2017). The representative characteristics of the indigenous “I” were presented in Figure 1. The indigenous “I” pig represents a unique genetic resource characterized by adaptation to local environmental conditions and disease resistance (Nguyen *et al.*, 2017). However, population decline following the introduction of commercial breeds has raised concerns regarding genetic erosion, highlighting the need for molecular characterization to support conservation breeding strategies (NIAS, 2015; Nguyen *et al.*, 2017).



Figure 1 The indigenous “I” pig breed; A = “I” boar; B = “I” sow.

Reproductive traits are regulated by complex endocrine pathways involving estrogen signaling, follicular development, and prolactin-mediated reproductive physiology. Candidate genes within these pathways, such as *estrogen receptor (ESR1)*, *follicle stimulating hormone beta subunit (FSHB)*, and *prolactin receptor (PRLR)*, have been widely investigated in commercial pig populations (Isler *et al.*, 2002; Bidanel, 2011; Repeto, 2020; Yurina *et al.*, 2021). However, polymorphisms of the *ESR*, *PRLR*, and *FSHB* genes in “I” pigs have not yet been studied.

In pigs, the *estrogen receptor gene (ESR)*, which is associated with reproductive traits is located on chromosome 1 (Balatsky *et al.*, 2012), and there are two types of *ESR*, namely *ESRa* (encoded by *ESR1*) and *ESR β* (encoded by *ESR2*) (Vega *et al.*, 2018). There are different variants of the *ESR1* gene, but *PvuII* is the most studied variant (Balatsky *et al.*, 2012; Vega *et al.*, 2018). *PvuII* polymorphisms of the *ESR* gene associated with the total number born (TNB), number born alive (NBA), and teat number (TN) were found in some commercial breeds (Landrace and Large White) (Rothschild *et al.*, 1996; Short *et al.*, 1997; van Rens and van der Lende, 2002), and indigenous pigs (Meishan, Tongcheng and Doom) (Zhu *et al.*, 2004; Rahman *et al.*, 2021; Yurina *et al.*, 2021). In recent years, the *ESR* T1665G mutation has been very important and associated with female reproductive traits, and sows with the BB genotype have been shown to have a higher number of piglets compared to other genotypes, however the polymorphisms in the *ESR* genes to improve litter size in pigs of certain lines, breeds, and populations may differ (Balatsky *et al.*, 2012). Similarly,

Reproductive traits generally exhibit low heritability due to their polygenic nature, strong environmental influence, and sex-limited expression, which reduce the efficiency of traditional phenotypic selection approaches (Soller, 1994; Goliášová and Wolf, 2004; Distl, 2007). Therefore, genomic and molecular approaches, including marker-assisted selection (MAS), offer opportunities to accelerate genetic improvement by identifying favorable alleles at early life stages. The combination of marker-assisted selection and traditional breeding techniques allows producers to detect individuals carrying potential alleles at an early age with more accuracy and quicker to increase the genetic improvement of specific traits (Zhao *et al.*, 1998; Drogemuller *et al.*, 2001).

the follicle stimulating hormone (*FSH*) consists two subunits (alpha and beta), and Zhao *et al.* (1998) choose the *FSH beta gene (FSHB)* to control litter size in pigs. The genotypes of the *FSHB* gene also were reported to be related to litter size in some popular commercial pigs such as Landrace and Large White (Zhao *et al.*, 1998; Wang *et al.*, 2006; Humpolicek *et al.*, 2007; Yurina *et al.*, 2021). Besides the above two genes, the polymorphisms of *PRLR* have been identified as potential candidates related to age at puberty (AP), gestation length (GL), TNB, and NBA in Large White, Landrace, Duroc, Large White/Meishan and synthetic line sows (Vincent *et al.*, 1998; Drogemuller *et al.*, 2001; van Rens and van der Lende, 2002; Korwin-Kossakowska *et al.*, 2003).

In previous studies, the associations between *ESR*, *FSHB*, *PRLR* and reproductive traits have been investigated in commercial or crossed commercial breeds and in some famous indigenous breeds from China and India (Meishan, Tongcheng and Doom). To date, polymorphism patterns and their association with reproductive performance have not been characterized in the Vietnamese indigenous “I” pig, limiting the application of genomic assisted breeding in this population. Therefore, the evaluation of the relationships between polymorphisms of these candidate genes and reproductive traits in “I” breed was important not only for Vietnam, but also for the diversity of pig populations around the world. Especially, it could propose potential approaches for the conservation of the “I” breed, which would contribute to biodiversity protection around the world. The aims of the study were to examine the

polymorphisms of the *ESR*, *PRLR*, and *FSHB* genes and their associations with the reproductive performance of “I” pigs.

Materials and Methods

Animal ethics: The study was conducted in accordance with the regulations stated in Article No. 72. Law on Animal Husbandry (Vietnam National Assembly, 2018). Ethics approval was granted by the Faculty Council from the Faculty of Animal Science, Vietnam National University of Agriculture (Approval Number FAS-VNUA-2019/08).

Experimental design: The experiment was carried out on the “I” pigs at two farms in northern Vietnam belonging to the Dabaco pig breeding company from January 2019 to May 2022. From January 2019 to December 2020, all the experimental pigs were raised at the farm located in Bac Ninh province. Due to the reconstruction of the farm, on the first day of January 2021, all the pigs were moved to another farm in Phu Tho province where the animals were kept until the end of May 2022. The condition between two farms (closed housing systems, same feed, and subjected to standardized care and management protocols established by the Dabaco Group) were similar. Two main objectives of this study were carried out. Firstly, the genotypes of the *ESR*, *PRLR* and *FSHB* genes were identified from the ear tissues of 151 fattening pigs (47 males and 104 females) born from January 2019 to March 2021. Then, genotypic and allelic frequencies were calculated and used for the Hardy-Weinberg equilibrium (HWE) test. Secondly, the associations of the candidate gene polymorphisms and reproductive traits were analyzed based on the data from 126 “I” sows from the first to fourth parities with 269 litters. The studied traits were the age at first mating (AFM, day), age at first farrowing (AFF, day), farrowing interval (FRI, day), total number of piglets born/ litter (TNB, piglet), number of piglets born alive/ litter (NBA, piglet), number of piglets born and reared/ litter (NBR, piglet), number of piglets weaned/ litter (NPW, piglet), litter weight at birth (LWB, kg), individual bodyweight of piglets at birth (BWB, kg), litter weight at weaning (LWW, kg) and individual bodyweight of piglets at weaning (BWW, kg). Sows were reared in a closed building with a concrete floor and fed with commercial feed. The compositions of the feed for each period met the requirements for indigenous sows in Vietnam (Table 1). The gilts and

sows in nonproductive days were reared in groups of 6-8 individuals for detection of estrus and service. The sows in heat were serviced by a single mating with an “I” boar. One week before farrowing, sows were moved into individual farrowing pens. The ear tissues of 126 “I” sows were collected and then genotyped for the *ESR*, *PRLR* and *FSHB* genes. The associations between the three tested candidate genes (*ESR*, *PRLR* and *FSHB*) and reproductive performance were analyzed. The polymorphisms of candidate genes in the “I” pig population was investigated and completed prior to the study examining the associations of the candidate gene polymorphisms and reproductive traits. Therefore, 126 “I” sows included in the subsequent analysis comprised both individuals from the first experiment and additional animals introduced into the herd as their subsequent-generation offspring.

Ear tissue collection: The ear tissue of each animal was collected, put into Eppendorf tubes, and immediately placed on dry ice and transported to the Genetic Laboratory, Faculty of Animal Science, Vietnam National University of Agriculture, Hanoi, Vietnam. The tissue samples were stored at -20°C until DNA isolation and genotype identification.

Identification of polymorphic variants of the *ESR*, *PRLR*, and *FSHB* genes: Genomic DNA was isolated from ear tissue using the standard protocol described by Green and Sambrook (2012), with minor modifications to accommodate laboratory conditions. DNA concentration and purity were quantified using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA) and then evaluated by agarose gel electrophoresis. Samples that were of good quality (A260/A280 ratio between 1.8 and 2.0) and had a concentration higher than 50 ng/μL were used for genotyping. Genomic DNA of each sample was diluted with dd H₂O to get the concentration of 50 ng/μL, which was used as a template for PCR amplification. Polymorphisms were genotyped by PCR-RFLP, including the SNP T1665G in the *ESR* gene (Short *et al.*, 1997; Vega *et al.*, 2018), the SNP T212C in the *FSHB* gene (Rohrer *et al.*, 1994; Magotra *et al.*, 2015) and the SNP G1789A in the *PRLR* gene (Drogemuller *et al.*, 2001; Lyubov *et al.*, 2016). The information about PCR product sizes, restriction enzymes, allele sizes, and references is presented in Table 2. The reagents and thermal cycles for the PCR reactions of each gene were different (Tables 3 and 4).

Table 1 Diet compositions for sows at different stages.

Diet composition	Gilts and sows in non-productive days	Gestation sows	Lactation sows
Crude protein (min, %)	12	15	16
ME (min, Kcal/kg)	2800	2800	3000
Crude fat (min, %)	3.0	3.0	5.0
Calcium (%)	0.8-1.0	1.0-1.2	0.9-1.0
Phosphorus (%)	0.6	0.8	0.7
Sodium chloride (%)	0.4-0.6	0.4-0.6	0.4-0.6
Moisture (max, %)	14.0	14.0	14.0
Crude fiber (max, %)	6.0	7.0	7.0

Table 2 Primer sequences, PCR product size, restriction enzymes, allele sizes for identification of polymorphic variants.

Gene	Poly-morphism	Primer sequences (5'-3')	PCR product size (bp)	Restriction enzyme	Allele sizes (bp)	References
<i>ESR</i>	<i>T1665G</i>	F: CCTGTTTTTACAGTGACTTTTACAGAG R: CACTTCGAGGGTCAGTCCAATTAG	120	<i>PvuII</i>	A:120 B: 55,65	Short et al. (1997)
<i>FSHB</i>	<i>T212C</i>	F: AGTTCGAAATGATTTTTTCGGG R: TTGCCATTGACTGTCTTAAAGG	624	<i>HaeIII</i>	A: 208, 173, 159, 84 B: 332, 208, 84	Rohrer et al. (1994)
<i>PRLR</i>	<i>G1789A</i>	F: CGT GGC TCC GTT TGA AGA ACC R: CTGAAAGGAGTGCATAAAGCC	163	<i>AluI</i>	A: 85, 59, 19 B: 104, 59	Drogemuller et al. (2001)

Note: F = Forward, R = Reverse

Table 3 The reagents for the PCR reaction.

Reagents	Original concentration	Volume (μL)
Buffer PCR	10x	2.5
dNTP	2mM	0.5
Forward Primer	5μM	0.5
Reverse Primer	5μM	0.5
Taq - Polymerase	5U/μL	0.2
DNA template	-	2.0
H ₂ O	-	18.8

Table 4 The thermal cycles for the PCR reaction.

Gene	Stage					
	Starting period (94°C)	Denaturation (94°C)	Annealing	Extension (72°C)	Number of cycles	Ending period (72°C)
<i>ESR</i>	3 min	1 min	57°C-1 min	45 sec	31	7 min
<i>FSHB</i>	3 min	1 min	62°C-1 min	2 min	32	10 min
<i>PRLR</i>	3 min	1 min	58°C-1 min	2 min	32	10 min

Statistical analysis: All data were analyzed using SAS® OnDemand for Academics. HWE was evaluated using a χ^2 goodness-of-fit test with one degree of freedom, comparing observed genotype frequencies with expected frequencies calculated from observed allele frequencies or the Fisher exact test when at least one expected count was less than 5. However, in the SAS software the degree of freedom is set to 2 instead of 1. Therefore, the *P*-values of the χ^2 were recalculated using one degree of freedom with the CHISQ function in Microsoft Excel. The *P*-values ≥ 0.05 were considered as consistent with HWE.

The effects of the fixed and random factors on the reproductive traits were performed using the statistical mixed model using REML method, except AFM and AFF. These last two traits were analyzed with fixed model due to only single an observation for each.

$$Y_{ijklmn} = \mu + ESR_i + PRLR_j + FSHB_k + Parity_1 + Year_m + SowID_n + \varepsilon_{ijklmno}$$

where: $Y_{ijklmno}$ = studied variables; μ = overall mean; ESR_i = fixed effect of *ESR* genotypes (AB, BB); $PRLR_j$ = fixed effect of the *PRLR* genotypes (AB, BB); $FSHB_k$ = fixed effect of *FSHB* genotypes (AA, AB); $Parity_1$ = fixed effect of parity (1, 2, 3, 4); $Year_m$ = fixed effect of farrowing year (2019, 2020, 2021, 2022), $SowID_n$ = random effect of sow and $\varepsilon_{ijklmno}$ = residual error. The coefficient of determination (R^2) was calculated from residual variances of full (σ^2_{full}) and null (σ^2_{null}) models according to the formula $R^2 = 1 -$

($\sigma^2_{full}/\sigma^2_{null}$); where σ^2_{full} = residual variance from the full model including fixed and random effects, σ^2_{null} = residual variance from the null model with only random effect. The statistical parameters were sample size (*n*), least square mean (LSM), and standard error of the mean (SE). The Tukey test was used for pairwise comparisons between LSMs.

Result

Genotypic and allelic frequencies of the *ESR* T1665G, *PRLR* G1789A, and *FSHB* T212C SNPs in the 'I' pig population: Among the 151 fattening pigs, three genotypes (AA, AB, and BB) were identified at the *ESR* T1665G and *FSHB* T212C loci, whereas only two genotypes (AB and BB) were detected at the *PRLR* G1789A locus in the 'I' pig population (Table 5). The frequency of the AA genotype at the *ESR* T1665G locus was particularly low, occurring in only one individual (0.8%), and this genotype was absent at the *PRLR* G1789A locus. At the *FSHB* T212C locus, the AA genotype was most frequent (64.2%), with the A allele (81.7%) prevailing over the B allele (18.3%). In contrast, the B allele dominated at the *ESR* T1665G (86.1%) and *PRLR* G1789A (77.2%) loci. The frequency of the homozygote BB (0.543) at the *PRLR* G1789A (77.2%) loci was higher than the heterozygote AB (0.457). Genotype distributions at *ESR* T1665G ($P = 0.255$) and *FSHB* T212C ($P = 0.064$) conformed to HWE, whereas *PRLR* G1789A deviated significantly ($P < 0.001$).

Effects of candidate genes, parity number and farrowing year on the reproductive performance of the "I" sows: The effects of the *ESR* T1665G, *PRLR* G1789A, and *FSHB* T212C genotypes, parity and farrowing year on the reproductive performance of the 'I' sows were analyzed. The *ESR* T1665G genotypes did not affect the reproductive performance of the "I" sows significantly (Table 6). The *PRLR* G1789A genotypes affected only BWB, where the sows having the BB genotype showed higher BWB (5.30 kg) than those with the AB genotype (5.03 kg; $P < 0.05$). Especially, the *FSHB* T212C genotypes affected many reproductive traits ($P < 0.05$), with the exception of AFM, AFF, FRI, and BWB (Table 6). Sows carrying the *FSHB*^{AA} genotype demonstrated significantly higher values for TNB, NBA, NBR, NPW, LWB, LWW, and BWB compared with those carrying the *FSHB*^{AB} genotype (Table 7).

Parity did not significantly affect reproductive performance, whereas farrowing year had significant effects on most traits, except AFM and AFI (Table 8). In 2019, the data on body weight and litter weight at birth and weaning were not recorded. Similarly, AFM and AFF were not observed in 2022. The reproductive performance of the "I" sows gradually reduced each year from 2019 to 2022.

Although the evaluation of reproductive performance in I sows was not the primary objective of this study, there have been no recent publications reporting on the reproductive capacity of the "I" breed under conservation rearing conditions. Therefore, we monitored and analyzed several statistical parameters related to the reproductive performance of I sows. The results are presented in Table 9.

Table 5 Genotypic and allelic frequencies of *ESR*, *PRLR*, and *FSHB* genes.

Gene	n		Genotypes			alleles		χ^2	P
			AA	AB	BB	A	B		
<i>ESR</i>	133	Observed count	1	35	97	37	229	1.298	0.255
		Frequency	0.008	0.263	0.729	0.139	0.861		
<i>PRLR</i>	151	Observed count	0	69	82	69	233	13.242	0.000
		Frequency	0	0.457	0.543	0.228	0.772		
<i>FSHB</i>	120	Observed count	77	42	1	196	44	3.420	0.064
		Frequency	0.642	0.35	0.008	0.817	0.183		

Table 6 Effects of *ESR*, *PRLR*, *FSHB* genes, parity and the farrowing year on reproductive performance of "I" sows.

Variables	<i>ESR</i>	<i>PRLR</i>	<i>FSHB</i>	Parity	Year	R ² (%)
AFM	0.2560	0.4073	0.2421	-	0.4166	6.30
AFF	0.2731	0.4163	0.5203	-	0.0417	13.45
FRI	0.1277	0.9963	0.4179	0.3775	0.0586	9.26
TNB	0.4812	0.3812	0.0006	0.7034	0.0011	3.94
NBA	0.3987	0.9034	0.0137	0.4939	<0.0001	15.07
NBR	0.4555	0.7909	0.0016	0.9515	<0.0001	13.65
NPW	0.0930	0.9249	0.0019	0.3691	<0.0001	4.99
LWB	0.8941	0.7571	0.0417	0.4895	0.0052	5.30
BWB	0.8759	0.9001	0.2622	0.6193	<0.0001	39.64
LWW	0.3469	0.2342	0.0039	0.7121	0.0006	4.96
BWW	0.7657	0.0276	0.0137	0.1265	0.0429	10.96

Values in the table are *P*-values (level of significance), R²: coefficient of determination, -: Data was not available.

Note: AFM = age at first mating, AFF = age at first farrowing, FRI = farrowing interval, TNB = total number of piglets born/ litter, NBA = number of piglets born alive/ litter, NBR = number of piglets born reared/ litter, NPW = number of piglets weaned/ litter, LWB = litter weight at birth, BWB = individual bodyweight of piglet at birth, LWW = litter weight at weaning and BWW = individual bodyweight of piglet at weaning.

Table 7 Effects of *FSHB* gene on reproductive performance of “I” sows.

Variables	AA			AB			P-value
	n	LSM	SE	n	LSM	SE	
AFM (day)	46	325.02	15.25	25	296.61	19.42	0.2421
AFF (day)	41	419.60	14.59	25	405.23	17.56	0.5203
FRI (day)	101	191.18	9.88	54	203.52	12.34	0.4179
TNB (piglet)	172	9.74 ^e	0.20	95	8.72 ^f	0.25	0.0006
NBA (piglet)	172	8.87 ^a	0.18	95	8.21 ^b	0.23	0.0137
NBR (piglet)	172	8.30 ^c	0.19	95	7.41 ^d	0.24	0.0016
NPW (piglet)	125	7.61 ^c	0.20	64	6.76 ^d	0.26	0.0019
LWB (kg)	124	4.96 ^a	0.16	71	4.42 ^b	0.20	0.0417
BWB (kg)	124	0.61	0.01	71	0.59	0.01	0.2622
LWW (kg)	112	41.10 ^c	1.63	56	33.84 ^d	2.10	0.0039
BWW (kg)	112	5.40 ^a	0.13	56	4.93 ^b	0.16	0.0137

^{ab, cd, ef}: LSMs within a row with different superscripts are significantly different at $P < 0.05$, < 0.01 and < 0.001 , respectively. Note: AFM = age at first mating, AFF = age at first farrowing, FRI = farrowing interval, TNB = total number of piglets born/ litter, NBA = number of piglets born alive/ litter, NBR = number of piglets born reared/ litter, NPW = number of piglets weaned/ litter, LWB = litter weight at birth, BWB = individual bodyweight of piglet at birth, LWW = litter weight at weaning, and BWW = individual bodyweight of piglet at weaning.

Table 8 Effects of year on reproductive performance of “I” sows.

Variables	2019			2020			2021			2022			P-Value
	n	LSM	SE	n	LSM	SE	n	LSM	SE	n	LSM	SE	
AFM (day)	17	318.59	23.81	26	290.21	20.26	28	323.64	18.09	-	-	-	0.4166
AFF (day)	14	428.50 ^{ab}	23.75	25	375.06 ^b	17.95	27	433.68 ^a	16.63	-	-	-	0.0417
FRI (day)	18	208.58	20.32	32	193.08	15.94	74	217.46	10.72	31	170.28	15.37	0.0586
TNB (piglet)	43	10.14 ^c	0.37	66	9.64 ^{cd}	0.31	126	9.09 ^d	0.22	34	8.05 ^e	0.39	0.0011
NBA (piglet)	43	9.98 ^f	0.33	66	9.59 ^f	0.28	126	8.21 ^g	0.20	34	6.38 ^h	0.35	<0.0001
NBR (piglet)	43	9.23 ^f	0.35	66	8.44 ^f	0.29	126	7.42 ^g	0.21	34	6.32 ^h	0.37	<0.0001
NPW (piglet)	13	7.95 ^f	0.47	32	8.38 ^f	0.34	125	6.83 ^g	0.17	20	5.58 ^h	0.38	<0.0001
LWB (kg)	-	-	-	43	4.58 ^d	0.27	120	5.17 ^c	0.16	34	4.32 ^d	0.27	0.0052
BWB (kg)	-	-	-	43	0.46 ^g	0.02	120	0.68 ^f	0.01	34	0.66 ^f	0.02	<0.0001
LWW (kg)	-	-	-	29	46.77 ^f	2.72	125	34.63 ^g	1.32	15	31.02 ^g	3.25	0.0006
BWW (kg)	-	-	-	29	5.10 ^{ab}	0.21	125	4.87 ^b	0.10	15	5.52 ^a	0.25	0.0429

^{ab, cd, efg}: LSMs within a row with different superscripts are significantly different at $P < 0.05$, < 0.01 , and < 0.001 , respectively.

Note: AFM = age at first mating, AFF = age at first farrowing, FRI = farrowing interval, TNB = total number of piglets born/ litter, NBA = number of piglets born alive/ litter, NBR = number of piglets born reared/ litter, NPW = number of piglets weaned/ litter, LWB = litter weight at birth, BWB = individual bodyweight of piglet at birth, LWW = litter weight at weaning, and BWW = individual bodyweight of piglet at weaning.

Table 9 Reproductive performance of I sows.

Variables	n	Mean	SD
AFM (day)	71	314.44	93.93
AFF (day)	66	412.25	88.06
FRI (day)	155	207.05	85.64
TNB (piglet)	269	9.31	2.34
NBA (piglet)	269	8.59	2.39
NBR (piglet)	269	7.92	2.32
NPW (piglet)	190	7.05	1.87
LWB (kg)	197	4.91	1.57
BWB (kg)	197	0.64	0.14
LWW (kg)	169	38.86	13.61
BWW (kg)	169	5.10	1.05

n: sample size, SD: standard deviation. Note: AFM = age at first mating, AFF = age at first farrowing, FRI = farrowing interval, TNB = total number of piglets born/litter, NBA = number of piglets born alive/ litter, NBR = number of piglets born and reared/litter, NPW = number of piglets weaned/ litter, LWB = litter weight at birth, BWB = individual bodyweight of piglets at birth, LWW = litter weight at weaning, and BWW = individual bodyweight of piglets at weaning.

Discussion

Genotypic and allelic frequencies of the ESR T1665G, PRLR G1789A, and FSHB T212C SNPs in the “I” pig population

ESR gene: Three genotypes (AA, AB, and BB) were identified at the *ESR* T1665G locus, with BB and AB predominating and the AA genotype occurring at a very low frequency. This distribution, characterized by a high frequency of the B allele, is consistent with findings in Vietnamese indigenous pig breeds such as Lung Pu, Ban, Hung, Lung, Meo, and O Lam pigs (Van Hau, 2008; Duyen and Bien, 2016), as well as in Meishan pigs (Gibson *et al.*, 2002). In contrast, a higher frequency of the A allele has commonly been reported in commercial breeds, including Black Slavonian (Kabalin *et al.*, 2013), Landrace (Noguera *et al.*, 2003), Large White (Wang *et al.*, 2006), and Myrhorod and Poltava pigs in Ukraine (Matiuk, 2025). Some studies have reported an absence of the BB genotype (Linville *et al.*, 2001; Kmiec and Terman, 2004), whereas only the AA genotype was observed in Philippine native pigs (Tabon *et al.*, 2022). Estrogen receptor signaling plays a central role in follicular development, ovulation, and uterine function. Previous studies demonstrated that sows carrying the BB genotype at the *ESR1 Pvull* locus produced larger litters than those with the AB or AA genotypes, although the effect varied among breeds and populations (Balatsky *et al.*, 2012). Thus, the analysis of allelic frequencies of *ESR* T1665G in the “I” population is important to improve this specific breed. These findings suggest that the A allele tends to be more prevalent in commercial breeds, whereas the B allele is more frequently observed in indigenous pig populations in Vietnam. These breed-dependent effects indicate that *ESR* polymorphisms should be evaluated within specific genetic backgrounds, and the present allele frequency data provide important baseline information for the genetic management of the “I” pig population.

PRLR gene: At the *PRLR* G1789A locus, only the AB and BB genotypes were detected, and the genotype distribution deviated significantly from Hardy-Weinberg equilibrium. A predominance of the B allele has been reported in several Vietnamese indigenous breeds, including Ban, Hung, Meo, Lung, O Lam (Duyen and Bien, 2016), and Mong Cai pigs (Van Hau, 2008). Similar patterns have been observed in some commercial populations such as Landrace and Yorkshire (Thanh *et al.*, 2019), as well as Polish Large White and Polish Landrace pigs (Ziółkowska *et al.*, 2010), although higher A allele frequencies have also been reported in Landrace and Yorkshire pigs (Barreras Serrano *et al.*, 2009). Considerable variation among breeds was further documented by Matiuk (2025), who reported differences in allele predominance among Myrhorod, Welsh, and Poltava pigs. While the AA genotype of the *PRLR* gene has been associated with increased TNB in commercial pig populations (Vincent *et al.*, 1997; Vincent *et al.*, 1998; Kmiec and Terman, 2004), it was absent in the “I” pig population. Therefore, the use of the AA genotype of the *PRLR* gene as a marker for selection may have

contributed to its high frequency in commercial pig breeds. In contrast, the limited application of marker-assisted selection in indigenous pig populations has likely resulted in the low frequency or absence of the AA genotype in these breeds. In the “I” pig population, the genotypic frequency of the *PRLR* gene deviated from HWE. This finding is consistent with the results of Matiuk *et al.* (2025), who also reported deviations from HWE in the genotypic distribution of *PRLR* among Myrhorod and Poltava pig populations. The limited size of the initial herd may increase the risk of inbreeding in indigenous pig populations, leading to reduced genetic diversity, the absence of expected genotypes, and a deviation of the *PRLR* genotypic frequencies from HWE. **FSHB gene:** At the *FSHB* T212C locus, the A allele predominated, with the AA genotype being most frequent and the BB genotype detected in only one individual. This pattern is consistent with findings in Yorkshire boars in Vietnam (Luc *et al.*, 2022) but contrasts with reports in several commercial breeds, where higher B allele frequencies were observed (Korwin-Kossakowska *et al.*, 2003; Humpolicek *et al.*, 2007). For example, Kowalewska *et al.* (2024) reported a predominance of the BB genotype in Polish Large White × Polish Landrace crossbred sows and in Yorkshire sows. Follicle-stimulating hormone is essential for follicular development and reproductive performance, and variation in the *FSHB* gene has been associated with litter size differences. The skewed genotype distribution observed in the present study likely reflects reduced effective population size and genetic drift rather than deliberate selection. As stated in Methods section, the genotypes of the *ESR*, *PRLR* and *FSHB* genes were identified from the ear tissues of 151 fattening pigs. However, during the course of the study, genotyping failed for a number of individuals; consequently, the sample size varied among the genes analyzed (Table 5).

As mentioned above, the “I” pig breed is currently classified as being at risk of extinction. The small initial herd size likely increases the risk of inbreeding within the population. As a result, genetic diversity has been reduced, leading to the absence of several expected polymorphisms in candidate genes (the AA genotype of the *PRLR* gene) or the presence of certain genotypes at extremely low frequencies, sometimes detected in only a single individual (the AA genotype of the *ESR* and the BB genotype of the *FSHB* genes). Additionally, the genotype distribution of the *PRLR* gene deviated from HWE, which may suggest a potential reduction in genetic variability within the population. From a practical perspective, these findings highlight the need for conservation-oriented breeding programs that maintain genetic diversity while using candidate gene information cautiously to support future improvement of reproductive performance in this indigenous pig population.

Effects of candidate genes, parity, and the farrowing year on the reproductive performance of the “I” sows

ESR gene: The association between *ESR* gene polymorphisms and reproductive traits has been reported to vary considerably among pig breeds (Matiuk *et al.*, 2025). The absence of significant

associations observed in the present study is consistent with findings in Black Slavonian sows (Kabalin *et al.*, 2013), Doom pigs (Rahman *et al.*, 2021), crossbred pigs (Gibson *et al.*, 2002; Noguera *et al.*, 2003), Indian native pig breeds (Vashi *et al.*, 2021), and Myrhorod pigs (Matiuk *et al.*, 2025). Nevertheless, significant associations between ESR polymorphisms and reproductive traits have been documented in other populations. For example, Yorkshire sows with the AA genotype showed lower TNB and NBA but higher BWB and BWW than the AB or BB genotypes (Thanh *et al.*, 2021), while AA sows exhibited lower LWW in Indian native pigs (Vashi *et al.*, 2021). In contrast, beneficial effects of the A allele have been reported in several studies, with AA sows showing higher TNB, NBA, and NPW than the BB or AB genotypes (van Rens *et al.*, 2002; Goliášová and Wolf, 2004; Pang *et al.*, 2018). Taken together, these inconsistent results across breeds suggest that the effects of ESR polymorphisms on reproductive performance are strongly breed dependent. The lack of significant associations in the "I" pig population indicates that ESR T1665G is unlikely to be a reliable marker for improving reproductive traits in this breed.

PRLR gene: The present study showed that "I" sows carrying the BB genotype at the PRLR G1789A locus had significantly higher BWW than those with the AB genotype ($P < 0.05$). This observation is consistent with previous reports indicating beneficial effects of the BB genotype on reproductive traits. For instance, sows carrying the BB genotype showed higher TNB and NBA in specific parities compared with AB sows (Menčík *et al.*, 2015). Breed-specific effects of PRLR polymorphisms on BWB and LWW have also been reported in Myrhorod, Poltava, and Welsh pigs (Matiuk *et al.*, 2025). In contrast, several studies in commercial pig breeds have reported more favorable reproductive performance associated with the AA genotype. In particular, the AA genotype has been linked to higher TNB, NBA, NBR, NPW, LWB, BWB, and BWW in Landrace and Yorkshire sows (Chen *et al.*, 2000; Terman *et al.*, 2016; Thanh *et al.*, 2021) and in 990-line sows (Terman *et al.*, 2016). These contradictory findings indicate that the influence of PRLR polymorphisms on reproductive performance is highly dependent on breed and genetic background. In the present study, the absence of the AA genotype and the deviation from HWE observed in the PRLR genotypic distribution (Table 5) further indicate limited genetic variation at this locus in the studied population. These factors may limit the statistical power of correlation analyses and hinder the interpretation of gene-trait associations. The lack of an association between the PRLR gene polymorphism and almost reproductive performance of the "I" breed herein suggests that PRLR is not a potential candidate gene for improving the reproductive performance of the "I" breed. However, the limited genetic variation at this locus may reduce the statistical power to detect meaningful associations, and the absence of significant effects may reflect population-specific constraints rather than a true lack of biological relevance. Overall, the lack of significant associations between PRLR polymorphism and most reproductive traits in "I" sows suggests that this gene

may not be a strong candidate marker for improving reproductive performance in this breed. Nevertheless, the restricted genetic variation detected at this locus may have limited the ability to identify meaningful associations. Therefore, the absence of significant effects in the present study should be interpreted cautiously, as it may reflect population-specific genetic constraints rather than a true lack of biological relevance.

FSHB gene: In contrast to ESR and PRLR, the FSHB T212C polymorphisms showed significant effects on most of the reproductive traits in the "I" sows. These results are consistent with previous studies reporting favorable effects of the AA genotype in Landrace sows (Bo *et al.*, 2021) and in crossbred and Yorkshire herds (Kowalewska *et al.*, 2024). Conversely, some studies reported higher reproductive performance in BB sows (Humpolicek *et al.*, 2007; Pang *et al.*, 2018), while others found no significant associations between FSHB polymorphisms and reproductive traits (Korwin-Kossakowska *et al.*, 2003; Polasik *et al.*, 2016). The discrepancies among studies may be explained by differences in breed, genetic background, and population structure. In this study, the distribution of FSHB genotypes was markedly unbalanced, as the BB genotype was represented by only a single individual. Consequently, the association analysis was effectively restricted to comparisons between the AA and AB genotypes. This imbalance may reduce statistical power and robustness, thereby increasing the likelihood that the observed significant differences are partially attributable to unequal allele frequencies. Replication studies in populations with larger genetically diverse population are warranted to reinforce the conclusion regarding the significant effect of FSHB gene polymorphism on the reproductive performance of "I" sows. Nevertheless, the consistent and significant associations observed in the present study indicate that FSHB T212C is a promising candidate gene for improving reproductive performance in the "I" pig population, particularly through the selection of sows carrying the AA genotype.

Effect of parity and farrowing year: Parity is associated with physical changes in the bodies of animals, so it may affect the function of the reproductive tract of sows. The reproductive performance in sows normally increases from 3 to 5 parities and then decreases steadily thereafter (Leigh, 1977). However, the reproductive performance of the "I" sows was not significantly different from parities 1 to 4. The decrease of the reproductive performance of the "I" sows from 2019 to 2022 with remarkable differences between years were noticeable results. Although environmental and management-related factors may influence sow reproductive performance and potentially confound genetic effects, the animals were maintained under relatively standardized conditions throughout the experiment. Specifically, the sows were housed in a closed housing system and fed with commercial diet, while management and care protocols were consistently applied according to the standards of the Dabaco Group. Weather data during the experimental

period were not recorded; therefore, there is no evidence indicating substantial fluctuations in environmental or management conditions among the years of the study. The risks of increased inbreeding in the population may contribute to the reduced vitality and productivity of “I” pigs in the next generations. Of the three examined genes in this study, statistically significant effects of polymorphisms were observed for *PRLR* on only BWW and the *FSHB* gene on several reproductive traits, suggesting that reproductive performance is a complex, polygenic trait influenced by interactions among multiple genes. This complexity reduces the individual impact of specific polymorphisms, making it difficult to isolate their effects (Matiuk *et al.*, 2025). Conversely, differences in reproductive potential across breeds may be attributed to the combined influence of multiple polymorphic loci, which together shape breed-specific genetic profiles. From a practical perspective, the present findings suggest that selection based on *FSHB* T212C polymorphisms may contribute to improving reproductive performance in the endangered “I” pig breed, while conservation-oriented breeding strategies remain essential to preserve genetic diversity.

In conclusion, three genotypes (AA, AB, and BB) were identified at the *ESR* T1665G and *FSHB* T212C loci in indigenous “I” pigs, whereas only two genotypes (AB and BB) were observed at the *PRLR* G1789A locus. Moreover, the B allele was more frequent in the *ESR* and *PRLR* genes, while the A allele predominated in the *FSHB* gene. No significant associations were found between the *ESR* T1665G polymorphism and the reproductive traits of the “I” sows. The *PRLR* G1789A polymorphism showed a significant effect only on BWW, with sows carrying the BB genotype exhibiting more favorable values than those with the AB genotype. In contrast, the AA genotype at the *FSHB* T212C locus was positively associated with several reproductive performance traits, namely TNB, NBA, NBR, NPW, LWB, LWW, and BWW. These results suggest that the *FSHB*AA genotype may serve as a potential genetic marker for improving reproductive performance in indigenous “I” pigs. These findings can help improve the “I” population in Vietnam and contribute to biodiversity protection worldwide.

Statement of Author Contributions

Do Duc Luc: Project administration, Conceptualization, Supervision, Visualization, Investigation, Formal analysis, Writing – review and editing. **Nguyen Thai Anh:** Data curation, Writing – review and editing. **Nguyen Hoang Thinh:** Data curation, Writing – review and editing. **Do Thi Hue:** Visualization, Writing – review and editing. **Phan Thi Tuoi:** Writing – original draft, Investigation, Data curation, Writing – review and editing.

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Declaration of Artificial Intelligence Use

During the preparation of this work, the authors used ChatGPT solely for language editing. The authors take full responsibility for the integrity, accuracy, and originality of the work.

References

- Balatsky VN, Saenko AM and Grishina LP 2012. Polymorphism of the estrogen receptor 1 locus in populations of pigs of different genotypes and its association with reproductive traits of large white sows. *Cytol Genet.* 46(4): 233-237.
- Barreras Serrano A, Herrera Haro JG, Hori-Oshima S, Gutiérrez Espinosa A, Ortega Cerrilla ME, Pérez Pérez J, Lemus Flores C, Kinejara Espinosa AL, González Arangure A and Soto Avila JG 2009. Prolactin receptor (*PRLR*) gen polymorphism and associations with reproductive traits in pigs. *J Anim Vet Adv.* 8(3): 469-475.
- Bidanel JP 2011. Biology and genetics of reproduction. In: *The Genetics of the Pig*. 2nd ed. M. F. Rothschild and A. Ruvinsky (eds). Wallingford: CABI. 222-232.
- Bo HX, Trang LT, Manh TX, Hung NV and Luc DD 2021. Additive genetic effects of *FSHB* Polymorphisms on litter size in Landrace and Yorkshire sows. *JAHSST.* 269: 8-15.
- Chen KF, Huang LS, Li N, Zhang Q, Luo M and Wu CX 2000. The genetic effect of estrogen receptor (*ESR*) on litter size traits in pig. *Acta Genet Sin.* 27(10): 853-857.
- Distl O 2007. Mechanisms of regulation of litter size in pigs on the genome level. *Reprod Domest Anim.* 42: 10-16.
- Drogemuller C, Hamann H and Distl O 2001. Candidate gene markers for litter size in different German pig lines. *J Anim Sci.* 79(10): 2565-2570.
- Duyen TTB and Bien DH 2016. “Research on evaluation of genetic potential from indigenous pig breeds”. NVQG-2011/24, Vietnam National Institute of Animal Science, Hanoi, Vietnam.
- Gibson JP, Jiang Z, Robinson J, Archibald A and Haley C 2002. No detectable association of the *ESR* PvuII mutation with sow productivity in a Meishan× Large White F2 population. *Anim Genet.* 33(6): 448-450.
- Goliášová E and Wolf J 2004. Impact of the *ESR* gene on litter size and production traits in Czech Large White pigs. *Anim Genet.* 35(4): 293-297.
- Green MR and Sambrook J 2012. *Molecular Cloning: A Laboratory Manual*. 4th ed. New York: Cold Spring Harbor Laboratory Press. 448 pp.
- Humpolicek P, Urban T, Matousek V and Tvrdon Z 2007. Effect of estrogen receptor, follicle stimulating hormone and myogenin genes on the performance of Large White sows. *Czech J Anim Sci.* 52(10): 334.
- Hunyadi-Bagi Á, Balogh P, Nagy K and Kusza S 2016. Association and polymorphism study of seven

- candidate genes with reproductive traits in three pig breeds in Hungary. *Acta Biochim Pol.* 63(2): 359-364.
- Isler B, Irvin K, Neal S, Moeller S and Davis M 2002. Examination of the relationship between the estrogen receptor gene and reproductive traits in swine. *J Anim Sci.* 80(9): 2334-2339.
- Kabalin AE, Starčević K, Menčik S, Maurić M, Sušić V and Štoković I 2013. Analysis of ESR and RBP polymorphisms in black Slavonian sows: Preliminary results. *Acta Agric Slov Supl.* 4: 10-12.
- Kmiec M and Terman A 2004. Polymorphism in the PRLR/AluI gene and its effect on litter size in Large White sows. *Anim Sci Pap Rep.* 22(4).
- Korwin-Kossakowska A, Kamyczek M, Cieślak D, Pierzchała M and Kurył J 2003. Candidate gene markers for reproductive traits in polish 990 pig line. *J Anim Breed Genet.* 120(3): 181-191.
- Kowalewska M, Terman A, Chomczyńska O, Wojdak-Maksymiec K, Polasik D and Dybus A 2024. Associations between RBP4, Fshb and Egf gene polymorphisms and reproductive traits in pigs. *Folia Pomeranae Universitatis Technologiae Stetinensis Agric Aliment Pisc Zootech.* 371(2): 45-59.
- Leigh A 1977. Litter performance characteristics of pigs in tropical south-western Nigeria 1. Breed differences and effects of some non-genetic sources of variation. *Anim Prod.* 24(3): 323-331.
- Linville R, Pomp D, Johnson R and Rothschild MF 2001. Candidate gene analysis for loci affecting litter size and ovulation rate in swine. *J Anim Sci.* 79(1): 60-67.
- Luc DD, Bo HX, Thinh NH, Thanh NC, Manh TX, Van Hung N, Tuoi PT, Ton VD and Frederic F 2022. Effect of ESR, FSHB and PRLR genes on sperm traits of landrace and yorkshire boars in the tropical environmental conditions of Vietnam. *Indian J Anim Res.* 56(2): 129-134.
- Lyubov G, Kolosov A, Leonova M, Bakoev S, Klimenko A, Vasilenko V and Radyuk A 2016. Polymorphisms in several porcine genes are associated with growth traits. *Am J Anim Vet Sci.* 11(4): 136-141.
- Magotra A, Naskar S, Das B and Ahmad T 2015. A comparative study of SINE insertion together with a mutation in the first intron of follicle stimulating hormone beta gene in indigenous pigs of India. *Mol Biol Rep.* 42(2): 465-470.
- Matiuk V, Saienko A, Vashchenko P, Slynko V, Fesenko O, Peka M and Tsereniuk O 2025. Association of polymorphisms in estrogen and prolactin receptor genes with reproductive traits in sows of rare breeds. *Regul Mech Biosyst.* 16(1): e25033-e25033.
- Matiuk VV 2025. Polymorphism of the ESR1 and PRLR genes in Myrhorod, Poltava meat and Welsh pig breeds. *Agrarian Bull Black Sea Littoral.* 114: 166-178.
- Menčik S, Vuković V, Modrić M, Špehar M, Ostović M, Sušić V, Štoković I, Samardžija M and Kabalin AE 2015. PRLR-I gene polymorphism and litter size traits in highly prolific line of topigs 20 sows. *Acta Vet.* 65(4): 463-476.
- Nguyen HD, Bui TA, Nguyen PT, Kim OTP and Vo TTB 2017. The complete mitochondrial genome sequence of the indigenous I pig (*Sus scrofa*) in Vietnam. *Asian-Australas. J Anim Sci.* 30(7): 930-937.
- NIAS 2015. Science and Technology Research Partnership for Sustainable Development (SATREPS) project establishment of cryo-bank system for Vietnamese native pig resources and sustainable production system to conserve biodiversity. National Institute of Animal Science. Hanoi, Vietnam.
- Noguera J, Varona L, Gomez-Raya L, Sánchez A, Babot D, Estany J, Messer L, Rothschild M and Perez-Enciso M 2003. Estrogen receptor polymorphism in Landrace pigs and its association with litter size performance. *Livest Prod Sci.* 82(1): 53-59.
- Pang P, Li Z, Hu H, Wang L, Sun H, Mei S and Li F 2018. Genetic effect and combined genotype effect of ESR, FSH β , CTNNAL1 and miR-27a loci on litter size in a large White population. *Anim Biotechnol.* 30(4): 287-292.
- Polasik D, Kumalska M, Sawaragi Y, Žak G, Tyra M, Urbański P and Terman A 2016. Analysis of FSHB gene polymorphism in Polish Landrace and Polish Large White x Polish Landrace sows. *Electron J Pol Agric Univ.* 19(1).
- Rahman M, Phookan A, Zaman GU, Das A, Akhtar F, Tamuly S, Choudhury H and Sarma LM 2021. Allelic variability of estrogen receptor (ESR) gene and its effect on litter traits of Doom pigs. *Trop Anim Health Prod.* 53(2): 316.
- Reproto RO 2020. Genetic selection and advances in swine breeding: A review of its impact on sow's reproductive traits. *Int J Res.* 7: 41-52.
- Rothschild M, Jacobson C, Vaske D, Tuggle C, Wang L, Short T, Eckardt G, Sasaki S, Vincent A and McLaren D 1996. The estrogen receptor locus is associated with a major gene influencing litter size in pigs. *Proc Natl Acad Sci.* 93(1): 201-205.
- Short T, Rothschild MF, Southwood O, McLaren D, De Vries A, Van der Steen H, Eckardt G, Tuggle C, Helm J and Vaske D 1997. Effect of the estrogen receptor locus on reproduction and production traits in four commercial pig lines. *J Anim Sci.* 75(12): 3138-3142.
- Soller M 1994. Marker assisted selection-an overview. *Anim Biotechnol.* 5(2): 193-207.
- Tabon G, Medina N, Uy-De Guia M and Mingala C. 2022 ESR1 Candidate marker gene associated with litter size in the Philippine native pigs (*Sus philippensis*). *Adv Anim Vet Sci.* 10(8): 1747-1751.
- Terman A, Polasik D, Korpala A, Wozniak K, Prüffer K, Žak G and Lambert B 2016. Association between prolactin receptor (PRLR) gene polymorphism and reproduction performance traits of Polish swine. *Can J Anim Sci.* 97(2): 169-171.
- Thanh NC, Manh TX, Hung NV, Trang LT, Hao PX and Ton VD 2019. Genetic structures of estrogen receptor (ESR) and prolactin receptor (PRLR) genes in Landrace and Yorkshire populations at DABACO nucleus pig breeding company. *Vietnam J Agric Sci.* 17: 379-385.
- Thanh NC, Manh TX, Hung NV, Trang LT, Hao PX and Ton V 2021. Association of estrogen receptor and

- prolactin receptor gene polymorphism with reproductive performances in Landrace and Yorkshire pigs. JAHST. 267: 6-12.
- Van Hau N 2008. On Farm Performance of Vietnamese Pigs Breeds and its Relation to Candidate Genes. Göttingen: Cuvillier Verlag. 150 pp.
- Van Rens BT, de Groot PN and Van der Lende T 2002. The effect of estrogen receptor genotype on litter size and placental traits at term in F2 crossbred gilts. Theriogenology 57(6): 1635-1649.
- van Rens BT and van der Lende T 2002. Litter size and piglet traits of gilts with different prolactin receptor genotypes. Theriogenology 57(2): 883-893.
- Vashi Y, Magotra A, Kalita D, Banik S, Sahoo NR, Gupta SK and Naskar S 2021. Evaluation of candidate genes related to litter traits in Indian pig breeds. Reprod Domest Anim. 56(4): 577-585.
- Vega RS, Castillo RMC, Barrientos NNB, Llanes-Autriz MM, de la Viña CB and Villa NO 2018. Leptin (T3469C) and estrogen receptor (T1665G) gene polymorphisms and their associations to backfat thickness and reproductive traits of large white pigs (*Sus scrofa* L.). Philipp J Sci. 147(2): 293-300.
- Vincent A, Tuggle C, Rothschild MF, Evans G, Short T, Southwood O and Plastow G 1998. The prolactin receptor gene is associated with increased litter size in pigs. Iowa State University Animal Industry Report 1(1).
- Vincent AL, Wang L, Tuggle CK, Robic A and Rothschild MF 1997. Prolactin receptor maps to pig chromosome 16. Mamm Genome. 8(10): 793.
- Wang X, Wang A, Fu J and Lin H 2006. Effects of ESR1, FSHB and RBP4 genes on litter size in a Large White and a Landrace Herd. Arch Anim Breed. 49(1): 64-70.
- Yurina A, Skovorodin E and Dolmatova I 2021. Evaluation of reproductive traits and ovarian and uterine morphology of sows with different genotypes for the estrogen receptor, prolactin receptor, and follicle-stimulating hormone subunit beta genes. Can J Vet Res. 85(3): 186-192.
- Zhao Y, Li N, Xiao L, Cao G, Chen Y, Zhang S, Chen Y, Wu C, Zhang J, Sun S and Xu X 1998. FSHB subunit gene is associated with major gene controlling litter size in commercial pig breeds. Sci China Life Sci. 41(6): 664-668.
- Zhu M, Yu M, Liu B, Zhu Z, Xiong T, Fan B, Xu S, Du Y, Peng Z and Li K 2004. Genetic status of ESR locus and other unidentified genes associated with litter size in Chinese indigenous Tongcheng pig breed after a long time selection. Asian-Australas J Anim Sci. 17(5): 598-602.
- Ziółkowska A, Bogdzińska M and Bieganski J 2010. Polymorphism of prolactin receptor gene (PRLR) in the Polish Landrace and Polish Large White swine population and reproductive traits. J Cent Eur Agric. 11(4): 443-448.