Jurnal Ilmu Produksi dan Teknologi Hasil Peternakan
ISSN 2303-2227 eISSN 2615-594X
Accredited by National Journal Accreditation No. 105/E/KPT/2022

Vol. 14 No. 2 June 2026, Page: 44-54
DOI: https://doi.org/10.29244/jipthp.14.2.44-54
Available online at https://journal.ipb.ac.id/index.php/ipthp/index

Single-marker and Haplotype-based Analyses of *POU1F1* and *GH1* Reveal Stage-dependent Effects on Growth Traits in Goats

N. T. Ngu[1], N. Thiet[1], T. T. Trung[1], N. T. A. Thu[2], T. H. Diep[3], A. Gunawan[4], L. H. Anh[1], L. M. Thanh[1], T. T. H. Mo[5], & L. T. Kien[1,*]

[1]Faculty of Animal Sciences, College of Agriculture, Can Tho University, Vietnam.
[2]Department of Animal Science and Veterinary Medicine, School of Agriculture and Aquaculture, Tra Vinh University, Vietnam.
[3]Faculty of Agriculture and Food Technology, Tien Giang University, Vietnam.
[4]Department of Animal Production and Technology, Faculty of Animal Science, IPB University, Indonesia.
[5]Tay Do University, 68 Tran Chien Street, Thanh My Area, Cai Rang Ward, Can Tho City, Vietnam.
*Corresponding author: letrungkien@ctu.edu.vn

(Received 19-04-2026; Revised 03-05-2026; Accepted 29-06-2026)

ABSTRACT

This study investigated the association between growth traits in goats and polymorphisms in the POU1F1 (*Alu*I and *Pst*I) and GH1 (*Hae*III) genes using both single-marker and haplotype-based approaches. A total of 79 goats were genotyped, and growth performance was evaluated based on body weight (BW), average daily gain (ADG), and relative growth rate (RGR) across developmental stages. All loci were polymorphic; however, the POU1F1/*Pst*I locus deviated from Hardy-Weinberg equilibrium (P=0.003). Association analyses revealed that the POU1F1/*Pst*I locus was significantly associated with ADG and RGR in a stage-dependent manner, including ADG3-6 (P=0.024), ADG3-10 (P=0.023), and RGR0-3 (P=0.003). In contrast, the POU1F1/*Alu*I locus showed limited and stage-dependent effects, with significant associations confined to later stages, particularly for body weight at 6 and 10 months and cumulative post-weaning gain (P<0.05), while no effects were detected during early growth. The GH1/*Hae*III locus showed no significant associations with any growth traits (P>0.05). Additive and dominance models further supported the contribution of the POU1F1/*Pst*I locus to growth rate variation. In addition, four haplotypes were identified with T-T being the most frequent (71.2%) and tending to show more favorable post-weaning growth performance. Overall, POU1F1, particularly the *Pst*I polymorphism and linked haplotypes, showed stronger associations with goat growth traits than GH1. Because the population was small and some genotype classes were unbalanced, these results remain preliminary and require validation in larger, diverse populations before practical use in selection programs.

Keywords: *GH1* gene, goat, growth traits, haplotype, *POU1F1* gene

ABSTRAK

Penelitian ini menyelidiki hubungan antara sifat pertumbuhan pada kambing dan polimorfisme pada gen POU1F1 (*Alu*I dan *Pst*I) dan GH1 (*Hae*III) menggunakan pendekatan penanda tunggal dan berbasis haplotip. Sebanyak 79 kambing dianalisis genotipnya, dan performa pertumbuhan dievaluasi berdasarkan berat badan (BW), pertambahan berat harian rata-rata (ADG), dan laju pertumbuhan relatif (RGR) di seluruh tahapan perkembangan. Semua lokus bersifat polimorfik; namun, lokus POU1F1/*Pst*I menyimpang dari kesetimbangan Hardy-Weinberg (P=0,003). Analisis asosiasi menunjukkan bahwa lokus POU1F1/*Pst*I secara signifikan terkait dengan ADG dan RGR secara bergantung pada tahapan, termasuk ADG3-6 (P=0,024), ADG3-10 (P=0,023), dan RGR0-3 (P=0,003). Sebaliknya, lokus POU1F1/*Alu*I menunjukkan efek yang terbatas dan bergantung pada tahap pertumbuhan, dengan asosiasi signifikan yang terbatas pada tahap selanjutnya, khususnya untuk berat badan pada usia 6 dan 10 bulan dan pertambahan berat badan kumulatif setelah penyapihan (P<0,05), dengan tidak adanya efek yang terdeteksi selama pertumbuhan awal. Lokus GH1/HaeIII tidak menunjukkan asosiasi signifikan dengan sifat pertumbuhan apa pun (P>0,05). Model aditif dan dominansi lebih lanjut mendukung kontribusi lokus POU1F1/*Pst*I terhadap variasi laju pertumbuhan. Selain itu, empat haplotip diidentifikasi dengan T-T sebagai yang paling sering (71,2%) dan cenderung menunjukkan kinerja pertumbuhan setelah penyapihan yang lebih baik. Secara keseluruhan, POU1F1, khususnya polimorfisme *Pst*I dan haplotip terkait, menunjukkan asosiasi yang lebih kuat dengan sifat pertumbuhan kambing daripada GH1. Karena populasinya kecil dan beberapa kelas genotipe tidak seimbang, hasil ini masih bersifat sementara dan memerlukan validasi pada populasi yang lebih besar dan beragam sebelum digunakan secara praktis dalam program seleksi.

Kata kunci: Gen GH1, kambing, sifat pertumbuhan, haplotip, gen *POU1F1*

INTRODUCTION

Growth traits are economically important in meat goat production and are therefore widely used as key selection criteria. In Vietnam, crossbreeding between Boer goats and the indigenous Bach Thao breed has been widely applied to improve meat yield while maintaining adaptation to local production conditions. Among these crossbreds, F2 (Boer × Bach Thao) goats represent a practical genetic resource for commercial meat production. Previous studies in Vietnam have shown that Boer-derived crossbreds generally outperform local goats in growth traits, although the magnitude of improvement may vary with genetic background and management conditions (Mui and Hai 2010; Hung *et al.* 2014). Similar observations have been reported in other crossbred goat populations, where growth performance and feed utilization differed across F1, F2, and backcross groups, indicating the need for population-specific evaluation (Mustefa *et al.* 2019; Predith *et al.* 2020).

In marker-assisted selection, candidate genes involved in endocrine regulation are of particular interest because of their potential effects on growth-related phenotypes. Among them, POU class 1 homeobox 1 (POU1F1) and growth hormone (GH1) genes are considered important functional candidates in goats (Supakorn 2009; Getaneh and Alemayehu 2022). The POU1F1 gene encodes a pituitary-specific transcription factor that regulates the expression of GH1, prolactin, and thyroid-stimulating hormone β, and previous studies have reported associations between POU1F1 polymorphisms and several production traits in goats. For example, an *Alu*I polymorphism was associated with milk yield and birth weight in Chinese native goats, while other POU1F1 variants were linked to litter size in Jining Grey goats and to growth and body measurement traits in Shaanbei White Cashmere goats (Lan *et al.* 2007; Feng *et al.* 2012; Zhu *et al.* 2019). The POU1F1/*Pst*I locus has also been reported as polymorphic in Egyptian and Saudi goat breeds, although its direct association with growth performance remains less clear (Alakilli *et al.* 2012). Likewise, the GH1 gene plays a central role in postnatal growth, muscle development, and metabolism, and GH1 polymorphisms have been examined in relation to body weight and growth-related traits in different goat populations. *Hae*III variants were polymorphic in Sirohi and Barbari goats but showed no significant association with chest girth or paunch girth from birth to 180 days, whereas a G505C variant in exon 5 was associated with body weight in Boer does (Singh *et al.* 2015; Rashijane *et al.* 2022). Taken together, these findings suggest that the associations of POU1F1 and GH1 variants with growth-related traits may vary according to breed, genetic background, developmental stage, and the specific trait examined.

Although a substantial number of studies have investigated candidate genes in goats, most have focused on purebred or exotic populations, whereas crossbred goats remain less studied. In Vietnam, information linking POU1F1 and GH1 polymorphisms with actual growth performance in Boer-derived crossbreds is still limited. Little is known about the combined relevance of POU1F1/*Alu*I, POU1F1/*Pst*I, and GH1/*Hae*III polymorphisms in F2 (Boer × Bach Thao) goats. This study was therefore conducted to characterize these polymorphisms and to evaluate their associations with growth traits in this population, with the aim of providing a basis for the future use of molecular markers in goat breeding programs in Vietnam.

MATERIALS AND METHODS

Animals and Management

A total of 79 F2 crossbred goats (Boer × Bach Thao), including 26 males and 53 females, were used in this study. All animals were raised on a farm located in Vinh Long province (9.6183° N, 106.4719° E), under semi-intensive production conditions. The herd was managed under uniform environmental and husbandry practices throughout the experimental period. Routine vaccination and parasite control programs were implemented in accordance with local veterinary guidelines. All experimental procedures were approved by the Animal Ethics Committee of Can Tho University (CTU-AEC2403.1).

Feeding Regime

All animals were fed a basal diet consisting of fresh forage (natural grasses and locally available green fodder) supplemented with a concentrate diet over a 7-month period. The concentrate included both commercially available and locally formulated sources based on common ingredients (e.g., rice bran, coconut meal, soybean meal, and mineral supplements) and was formulated to meet the nutritional requirements for growth.

Concentrate was provided at approximately 400 g/head/day (equivalent to 1.0-1.5% of body weight on a dry matter basis) and offered twice daily, while fresh forage was supplied *ad libitum*. Animals always had free access to clean drinking water. Feeding conditions were maintained to ensure nutritional consistency across animals and to minimize environmental variation in growth performance.

DNA Extraction

Blood samples were collected from the ear vein of each animal into anticoagulant tubes and stored under chilled conditions. Genomic DNA was extracted using a commercial kit (TopPURE®, ABT, Vietnam) following the manufacturer's instructions. Extracted DNA was stored at -20°C until further analysis.

PCR Amplification and Genotyping

Genotyping was performed for three loci: POU1F1 (*Alu*I and *Pst*I) and GH1 (*Hae*III). For POU1F1, a 450 bp fragment covering exon 6 and the 3′UTR was amplified using primers reported by Lan *et al.* (2007) and Feng *et al.* (2012) (forward: 5′-CGATCATCTCCCTTCTT-3′; reverse: 5′-AATGTACAATATGCCTTCTGAG-3′). PCR conditions included an initial denaturation at 94°C for 5 min, followed by 35 cycles (94°C for 30 s, 54.5°C for 30 s, 72°C for 30 s), and a final extension at 72°C for 10 min. For GH1, a 654 bp fragment was amplified using primers described by Rashijane *et al.* (2022) (forward: 5′-ACACCCAGGTTGCCTTCTGC-3′; reverse: 5′-GTCCGAGGTGCCAAACACCA-3′), with PCR

Figure 2. Graph of THI values during 5 to 12th week of rearing

conditions of 94°C for 5 min, followed by 32 cycles (95°C for 30 s, 54°C for 45 s, 72°C for 1 min), and a final extension at 72°C for 5 min.

Statistical Analysis

Statistical analyses were performed using R (R Foundation for Statistical Computing, Vienna, Austria). Growth traits were analyzed using a general linear model (GLM): $Y_{ijk} = \mu + G_i + S_j + e_{ijk}$; where Y_{ijk} is the observed trait, μ is the overall mean, G_i is the effect of genotype or haplotype, S_j is the effect of sex, and e_{ijk} is the residual error.

Least square means were compared using Tukey's test when significant effects were detected. Additive and dominance effects were estimated using standard genotype contrasts. Haplotype frequencies were inferred using the expectation-maximization (EM) algorithm implemented in the *haplo.stats* package. Haplotypes with frequencies below 5% were excluded from association analysis. Statistical significance was declared at $P \leq 0.05$.

RESULTS AND DISCUSSION

Growth Performance of F2 (Boer × Bach Thao) Crossbred Goats across Developmental Stages

Body weight increased progressively with age in both sexes (Figure 1A), with males generally heavier than females, particularly from 3 months of age onward ($P<0.05$). This pattern reflects the normal accumulation of body mass during postnatal growth, as early tissue development is followed by greater muscle and skeletal growth. Genetically, F2 Boer × Bach Thao goats may retain Boer-derived additive effects for larger frame size and meat-type growth, combined with Bach Thao adaptation to local conditions. The increasing male advantage suggests sex-dependent expression of this growth potential, likely through endocrine regulation favoring lean-tissue deposition in males (Van Niekerk and Casey 1988; Mahgoub *et al.* 2004; Brand *et al.* 2017).

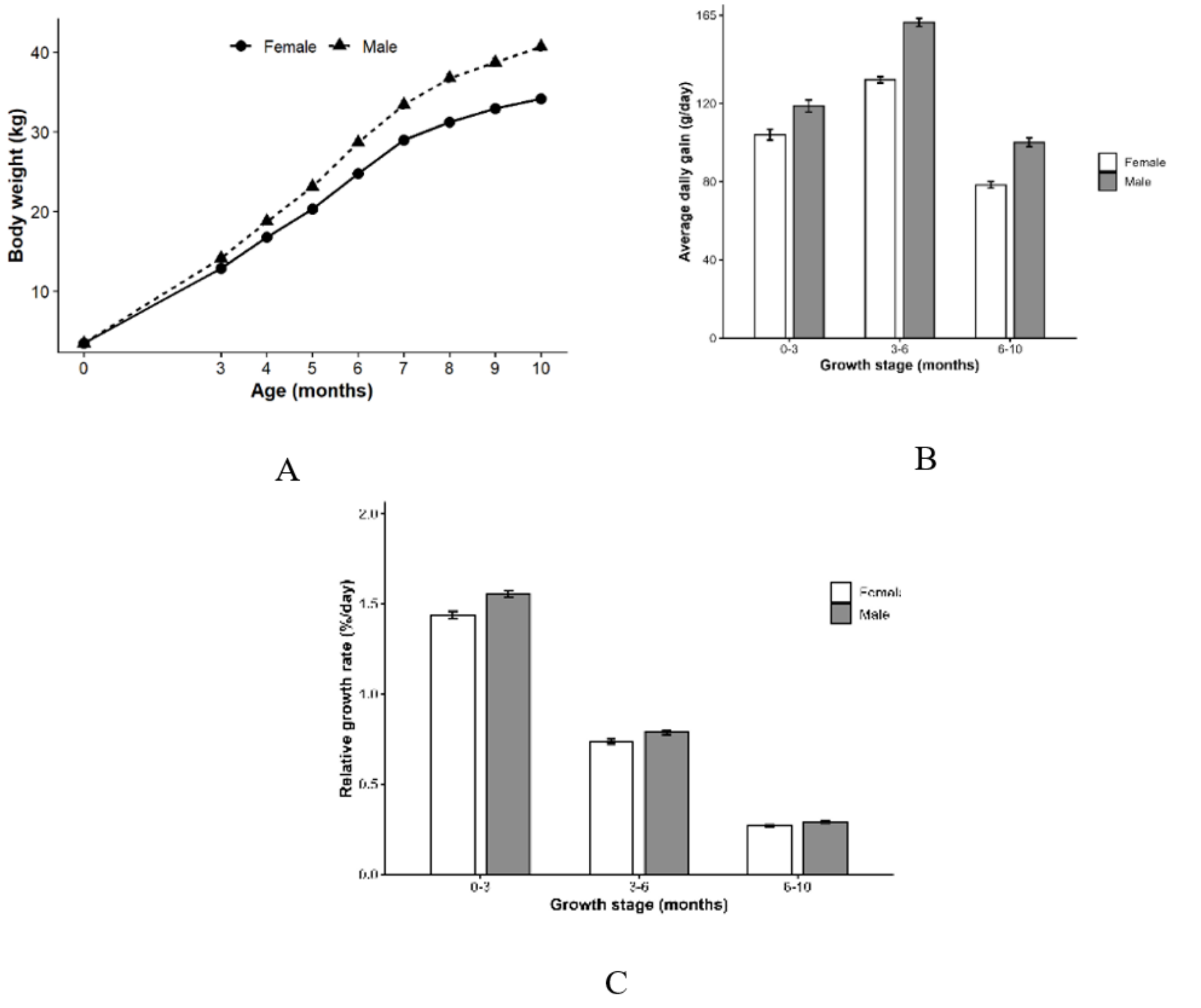

Figure 1. Growth performance of F2 goats (Boer × Bach Thao) at different growth stages; (A) body weight (BW), (B) average daily gain (ADG), and (C) relative growth rate (RGR).

Similarly, ADG showed a typical curvilinear pattern (Figure 1B), increasing from 0-3 months to a peak at 3-6 months (P<0.05), followed by a decline during 6-10 months. This indicates a developmental transition: before three months, gain may be limited by milk dependence and immature digestive function; after weaning, improved rumen activity, feed intake and nutrient use allow genetic potential for lean growth to be expressed more fully. Thus, higher ADG observed in males across all stages explains the widening BW difference between sexes, and notably, the 3-6 months period appears to be the most critical phase contributing to final body weight.

In contrast, relative growth rate (RGR) was highest during the early stage (0-3 months) and declined significantly with age (P<0.01) (Figure 1C). Because RGR is scaled to existing body weight, this decline indicates lower proportional gain as animals become heavier, not poorer growth. The weaker sex effect on RGR suggests similar proportional maturation in both sexes, whereas males differed mainly in absolute tissue accretion.

Previous studies provide useful context for interpreting these results. Peak ADG values (132-161 g/day), which are within the range reported for Boer-derived crossbreds and close to Boer × Bach Thao F1 goats (~130 g/day), support the biological plausibility of the present performance (Hai and Binh 2019; Bezerra *et al.* 2019; Fernández *et al.* 2021). Overall, BW and ADG were strongly influenced by sex because they reflect absolute growth and lean-tissue deposition, whereas RGR was less affected because it reflects proportional growth efficiency. Practically, 3-6 months is key for maximizing body weight gain, while 0-3 months represents the stage of highest relative growth efficiency.

Population Genetic Parameters of the *POU1F1* and *GH1* Loci

Genotype distribution, allele frequencies, and Hardy-Weinberg equilibrium (HWE) for the POU1F1/*Alu*I, POU1F1/*Pst*I, and GH1/*Hae*III loci are presented in Table 1. All loci were polymorphic, although the level of genetic variation differed among them. These loci are best considered as markers within the pituitary–somatotropic growth axis, because POU1F1 regulates pituitary hormones including GH, whereas GH is directly involved in postnatal growth and metabolism. At the POU1F1/*Alu*I locus, the TT genotype predominated (74.7%), followed by TC (20.3%) and CC (5.06%), with a high T allele frequency (84.8%); although a slight heterozygote deficit was observed (Ho = 0.203 vs. He = 0.258), the locus did not deviate significantly from HWE (P = 0.069), indicating relative genetic stability in this population.

At the POU1F1/*Pst*I locus, a comparable allelic distribution was observed, with TT again being the most frequent genotype (72.2%) and the T allele reaching 81.6%; however, this locus showed a significant deviation from Hardy-Weinberg equilibrium (P=0.003), associated with a marked deficit of heterozygotes (Ho=0.189 vs. He=0.299). In an F2 crossbred population, this pattern is biologically meaningful because recombination after breed crossing may reveal unequal parental allele contributions, mating structure, or selection acting on linked genomic regions. Therefore, the observed departure from HWE in this study likely reflects the genetic structure of the F2 (Boer × Bach Thao) population rather than methodological bias. Nevertheless, this deviation should be considered when interpreting genotype-phenotype associations, as it may influence the distribution of genetic effects (Supakorn 2009; Getaneh and Alemayehu 2022).

Regarding the GH1/*Hae*III locus, only AA (83.5%) and AB genotypes were detected, resulting in a low B allele frequency and the absence of BB individuals. Although GH is functionally important for growth, the very low B allele frequency limits the observable genetic contrast at this marker. Consequently, the lack of significant associations observed in this study may partly reflect insufficient genetic variability rather than the absence of a biological effect. Despite this, the locus conformed to HWE (P=1.000), likely due to the very low expected frequency of the BB genotype. The low expected heterozygosity (He=0.151) further indicates limited informativeness of this marker in the studied population.

Overall, polymorphism in the pituitary-growth regulatory pathway was retained in the F2 Boer × Bach Thao population, but the usefulness of each marker depends on allele balance, heterozygosity, and HWE status. In comparison, the POU1F1 loci exhibited greater genetic variability than GH1/*Hae*III, supporting their stronger potential for association analysis. However, because growth traits are polygenic and influenced by gene-environment interactions, these markers should be regarded as supportive genetic indicators for selection rather than independent determinants of performance.

Table 1. Genotype distribution. allele frequencies and Hardy-Weinberg equilibrium of three loci in goats

Locus	N	Genotype (n. %)	Allele frequency (%)	Ho	He	HWE (P-value)
POU1F1/AluI	79	CC: 4 (5.06) TC: 16 (20.3) TT: 59 (74.7)	C: 15.2 T: 84.8	0.203	0.258	0.069
POU1F1/PstI	79	CC: 7 (8.86) TC: 15 (18.9) TT: 57 (72.2)	C: 18.4 T: 81.6	0.189	0.299	0.003
GH1/HaeIII	79	AA: 66 (83.5) AB: 13 (16.5) BB: 0 (0.00)	A: 91.8 B: 8.20	0.165	0.151	1

Note: Ho: observed heterozygosity; He: expected heterozygosity; HWE: Hardy-Weinberg equilibrium tested using exact test; Values in parentheses represent percentages (%)

Association of the POU1F1/AluI Polymorphism with Growth Traits

Associations between POU1F1/*Alu*I genotypes and growth traits are presented in Table 2. This locus showed a stage-dependent effect, becoming more evident at later developmental stages. No significant differences among genotypes were observed for body weight at birth (BW0) or at 3 months (BW3) (P>0.05); this suggests that early growth may have been more influenced by prenatal development, maternal effects, milk intake and early environmental conditions, which could reduce the detectable effect of genotype. However, significant variation emerged at later stages. At 6 months, animals with the TT genotype had higher BW (26.9±0.3 kg) than TC individuals (P=0.009), while CC showed intermediate values, and a similar pattern was observed at 10 months, where TT animals reached the highest BW (37.8±0.3 kg), significantly exceeding TC (P=0.001). Because the *Alu*I polymorphism represents a silent variant in POU1F1, its association should be interpreted mainly as a marker-linked effect, possibly reflecting linkage with functional variants or haplotypes affecting the pituitary-somatotropic pathway, rather than as direct evidence of a causal amino-acid change.

For growth rate, no significant genotype effects were detected for short-term ADG intervals (ADG0-3, ADG3-6, ADG6-10) (P>0.05). However, cumulative post-weaning gain differed among *Alu*I genotypes (ADG3-10; P=0.020), with TT animals showing significantly higher values than CC and TC animals. This suggests that the *Alu*I effect was not clearly expressed within individual short intervals but became detectable when growth was evaluated across the full post-weaning period. With respect to RGR, no significant differences were found across stages (P>0.05), although a slight, non-significant tendency toward higher RGR0-3 was observed in CC individuals (P=0.068). Overall, the POU1F1/*Alu*I polymorphism appeared to influence cumulative absolute gain more than relative growth efficiency.

The later appearance of genotype-related differences is consistent with the role of POU1F1 as a pituitary transcription factor involved in regulating GH, PRL and TSHβ, which are related to growth, metabolism and tissue development. As kids mature, especially after weaning, digestive capacity, voluntary feed intake and endogenous hormonal regulation become more important; therefore, genotype-related differences are more likely to become detectable at BW6 and BW10, and across the cumulative ADG3-10 period. This interpretation is supported by previous studies reporting associations between POU1F1 polymorphisms and growth or production traits in goats (Lan *et al.* 2007; Supakorn 2009; Zhu *et al.* 2019), but these comparisons should be considered supportive rather than the primary explanation.

The significant pairwise separation for ADG3-10 indicates that TT animals had more favorable cumulative post-weaning gain than CC and TC animals. However, the very low frequency of the CC genotype (n=4) still limits reliable inference on dominance or allele-dose effects. Therefore, the TT advantage should be interpreted as a moderate marker-associated effect on late-stage growth rather than evidence that this single locus independently determines growth performance. Collectively, the POU1F1/*Alu*I locus appears to have a moderate influence on late-stage growth, although its application in marker-assisted selection requires validation in larger populations.

Table 2. Least squares mean (±SE) of body weight, average daily gain, and relative growth rate according to POU1F1/*Alu*I genotypes in goats

Trait	CC (n=4)	TC (n=16)	TT (n=59)	P-value
Body weight (kg)				
BW0	3.4±0.1	3.5±0.0	3.5±0.0	0.606
BW3	13.7±0.9	12.7±0.4	13.6±0.2	0.095
BW6	26.8±0.9ab	25.6±0.5^{b}	26.9±0.3a	0.009
BW10	36.8±1.0ab	35.9±0.5^{b}	37.8±0.3a	0.001
Average daily gain (g/day)				
ADG0-3	114±9.2	103±4.7	113±2.5	0.085
ADG3-6	145±5.7	144±2.9	148±1.6	0.143
ADG6-10	84±6.0	86±3.1	91±1.6	0.093
ADG3-10	110±4.2b	111±2.2b	115±1.2a	0.02
Relative growth rate (%/day)				
RGR0-3	1.54±0.06	1.44±0.03	1.51±0.02	0.068
RGR3-6	0.75±0.05	0.79±0.02	0.76±0.01	0.715
RGR6-10	0.27±0.02	0.28±0.01	0.28±0.01	0.733
RGR3-10	0.47±0.03	0.50±0.01	0.49±0.01	0.872

Notes: Values are least-squares means±standard errors adjusted for sex. P-values indicate the overall effect of genotype in the model. Different superscripts within the same row indicate significant pairwise differences among genotypes based on Tukey's test at P≤0.05. BW0, BW3, BW6, and BW10 denote body weight at birth, 3, 6, and 10 months of age, respectively; ADG=average daily gain; RGR=relative growth rate.

Association of the POU1F1/PstI Polymorphism with Growth Parameters

Associations between POU1F1/*Pst*I genotypes and growth traits are presented in Table 3. Compared with the POU1F1/*Alu*I locus, POU1F1/*Pst*I showed a more pronounced but clearly stage-dependent effect, rather than a uniformly consistent effect across all growth traits. No significant differences in body weight were observed at birth (BW0), 6 months (BW6), or 10 months (BW10); however, a marginal difference was detected at 3 months (BW3; P=0.050), with CC animals tending to show higher BW than TC and TT. Because this difference was observed only at BW3 and was not maintained at BW6 or BW10, it should be interpreted as a transient difference in early growth timing rather than a persistent effect on final body size.

In terms of growth rate, ADG exhibited significant genotype effects that varied with age. During the early stage (ADG0-3), CC animals had higher gains than TT, with TC intermediate (P=0.028), whereas this pattern reversed during 3-6 months, where TT animals outperformed CC (P=0.024); over the extended post-weaning period (ADG3-10), TC and TT animals showed higher cumulative gains than CC (P=0.023). A comparable stage-dependent pattern was observed for RGR, with CC animals showing higher values during 0-3 months (P=0.003), while T allele carriers (TC and TT) exhibited higher RGR during 3-6 months (P=0.014) and over the 3-10 months period (P=0.012), and no differences were detected at 6-10 months (P>0.05), suggesting a reduction in genotypic effects at later stages. The reversal between early and post-weaning growth suggests that this locus may be associated with the timing of growth acceleration, with the C allele favoring early proportional growth and the T allele favoring post-weaning cumulative gain.

These results indicate that the POU1F1/*Pst*I polymorphism exerts a stage-dependent effect, with the C allele associated with higher growth in early life and the T allele associated with improved post-weaning performance. This pattern is consistent with the biological role of POU1F1 in endocrine regulation of growth, where genetic effects may become more evident as endogenous hormonal control increases with age (Zhu *et al.* 2019; Getaneh and Alemayehu 2022), and similar stage-specific associations have been reported in other livestock populations (Lan *et al.* 2007; Feng *et al.* 2012). The TC genotype generally showed intermediate or relatively favorable values, particularly for cumulative traits (ADG3-10, RGR3-10), suggesting possible non-additive effects; however, the limited number of CC individuals (n=7) reduces the power to precisely estimate allelic effects. Thus, the POU1F1/*Pst*I locus appears to be a potentially informative candidate locus for growth traits, although validation in larger populations is required.

Association of the *GH1/Hae*III Locus with Growth Parameters

Associations between GH1/*Hae*III genotypes and growth traits are presented in Table 4. Compared with POU1F1, no significant associations were detected between GH1/*Hae*III genotypes and BW, ADG, or RGR across all developmental stages (P>0.05). Although minor numerical differences were observed (e.g., AA slightly higher at later ages and AB at 3 months), these variations were inconsistent and not statistically significant, and no clear genotypic patterns were detected for ADG or RGR. Therefore, this result should be interpreted as no detectable marker effect under the present allelic distribution, rather than evidence that GH1 is biologically irrelevant to growth. Functionally, GH1 remains an important growth-related

Table 3. Least squares mean (±SE) of body weight, average daily gain, and relative growth rate according to POU1F1/*Pst*I genotypes in goats

Trait	CC (n=7)	TC (n=15)	TT (n=57)	P-value
Body weight (kg)				
BW0	3.40±0.1	3.50±0.0	3.50±0.0	0.615
BW3	14.7±0.7	12.8±0.5	13.5±0.2	0.05
BW6	27.1±0.7	26.0±0.5	26.8±0.3	0.129
BW10	37.1±0.8	37.0±0.6	37.5±0.3	0.188
Average daily gain (g/day)				
ADG0-3	125±6.9^{a}	103±4.8^{b}	111±2.5a^{b}	0.028
ADG3-6	137±4.2b	147±2.9^{a}	148±1.5^{a}	0.024
ADG6-10	84±4.6	92±3.2	90±1.7	0.296
ADG3-10	107±3.2b	115±2.2^{a}	115±1.2^{a}	0.023
Relative growth rate (%/day)				
RGR0-3	1.62±0.05^{a}	1.42±0.03b	1.50±0.02ab	0.003
RGR3-6	0.68±0.03b	0.80±0.02a	0.77±0.01a	0.014
RGR6-10	0.26±0.02	0.29±0.01	0.28±0.01	0.238
RGR3-10	0.44±0.02b	0.51±0.01a	0.49±0.01a	0.012

Notes: Values are least squares means±standard errors adjusted for sex. Different superscripts within the same row indicate significant differences among genotypes at P≤0.05. BW0, BW3, BW6, and BW10 denote body weight at birth, 3, 6, and 10 months of age, respectively; ADG=average daily gain; RGR=relative growth rate.

Table 4. Least squares means (±SE) of body weight, average daily gain, and relative growth rate according to GH1/*Hae*III genotypes in goats

Trait	AA (n=66)	AB (n=13)	P-value
Body weight (kg)			
BW0	3.50±0.2	3.40±0.1	0.204
BW3	13.4±0.2	13.6±0.5	0.677
BW6	26.7±0.2	26.5±0.5	0.956
BW10	37.5±0.3	36.8±0.6	0.697
Average daily gain (g/day)			
ADG0-3	110±2.4	113±5.2	0.567
ADG3-6	147±1.5	143±3.2	0.537
ADG6-10	90±1.6	86±3.4	0.505
ADG3-10	115±1.1	111±2.4	0.375
Relative growth rate (%/day)			
RGR0-3	1.49±0.02	1.52±0.04	0.333
RGR3-6	0.77±0.01	0.75±0.03	0.598
RGR6-10	0.28±0.01	0.28±0.01	0.628
RGR3-10	0.49±0.01	0.48±0.01	0.538

candidate gene because growth hormone is involved in bone formation, muscle development, body composition and metabolism; however, such biological relevance may not be statistically expressed when the tested polymorphism has low variability. The lack of association may be partly explained by the limited genetic variation at this locus, as only AA and AB genotypes were observed, with no BB individuals, resulting in a low frequency of the B allele. This allelic imbalance narrows the genetic contrast among genotype classes and reduces the power to detect small effects, which are expected for polygenic quantitative traits.

These findings are consistent with previous studies reporting inconsistent or non-significant effects of GH1 polymorphisms on growth traits in goats (Singh *et al.* 2015; Getaneh and Alemayehu 2022; Rashijane *et al.* 2022). These inconsistent findings are expected, as the usefulness of a candidate marker depends on allele frequency, linkage with functional variants, breed background, and gene-environment interactions. While the GH1 gene is biologically important, the *Hae*III polymorphism showed limited informativeness and no detectable effect on growth traits in F2 (Boer × Bach Thao) goats. Thus, future studies should evaluate larger populations and additional GH1 variants or haplotypes, preferably in combination with other growth-regulatory genes and phenotypic performance records, before considering this marker for marker-assisted selection.

Additive and Dominance Effects of *POU1F1* Polymorphisms on Growth Traits

Additive and dominance effects of POU1F1/*Alu*I and POU1F1/*Pst*I polymorphisms are presented in Table 5. The results indicate that the *Pst*I locus showed detectable and stage-dependent genetic effects, whereas *Alu*I had no clear additive or dominance component in the present model. For the POU1F1/*Alu*I locus, neither additive nor dominance effects were significant across traits (P>0.05); although some dominance estimates approached significance for BW6, BW10, and RGR0-3 (P≈0.06-0.08), the effects were small and inconsistent. Thus, the *Alu*I association observed in previous genotype-phenotype analysis may reflect genotype-class differences or linkage context rather than a stable allele-substitution or dominance effect.

At the POU1F1/*Pst*I locus, significant genetic effects were observed, particularly for growth rate traits. During the early stage (ADG0-3), a significant dominance effect was detected (−15.0; P=0.013), indicating deviation of the heterozygote from the homozygous mean. This negative dominance estimate indicates non-additive deviation from the additive expectation, but should not be interpreted as heterosis. At later stages, significant additive effects were identified for ADG3-6 (5.10; P=0.024) and ADG3-10 (3.90; P=0.023), suggesting that allelic substitution contributed to improved post-weaning growth. For RGR, significant additive effects were observed across stages (P<0.05), together with consistent dominance effects (P≤0.011), and notably, the direction of additive effects differed between early (RGR0-3) and later stages. This reversal supports a shift in genetic control across physiological stages, from early proportional growth to post-weaning cumulative tissue accretion.

These findings indicate that the POU1F1/*Pst*I polymorphism is influenced by both additive and non-additive genetic components, whereas *Alu*I shows limited genetic contribution, a pattern consistent with the regulatory role of POU1F1 in growth-related endocrine pathways (Lan *et al.* 2007; Feng *et al.* 2012; Getaneh and Alemayehu 2022). The POU1F1/*Pst*I locus demonstrates stage-dependent and partly non-additive genetic architecture, suggesting potential relevance for selection; however, its application should consider both additive and dominance effects and requires validation in larger populations.

Table 5. Additive and dominance effects of POU1F1/*Alu*I and POU1F1/*Pst*I polymorphisms on selected growth traits in goats

Locus	Trait	Additive effect	P-value	Dominance effect	P-value
POU1F1/*Alu*I	BW6	0.1	0.883	-1.2	0.078
	BW10	0.5	0.367	-1.4	0.064
	ADG0-3	-0.8	0.863	-10.9	0.107
	ADG3-6	1.2	0.679	-2.3	0.577
	ADG3-10	2.5	0.253	-2.1	0.501
	RGR0-3	-0.02	0.636	-0.08	0.075
	RGR3-6	0.01	0.781	0.03	0.329
	RGR3-10	0.01	0.566	0.02	0.384
POU1F1/*Pst*I	BW6	-0.1	0.700	-0.9	0.135
	BW10	0.2	0.629	-0.3	0.644
	ADG0-3	-7.1	0.053	-15	0.013
	ADG3-6	5.1	0.024	4.1	0.265
	ADG3-10	3.9	0.023	4.6	0.100
	RGR0-3	-0.06	0.018	-0.13	0.001
	RGR3-6	0.04	0.014	0.07	0.011
	RGR3-10	0.02	0.016	0.04	0.007

Notes: Additive and dominance effects were estimated using linear models adjusted for sex. For genotype coding, CC, TC, and TT were assigned as −1, 0, and 1 for additive effect, and 0, 1, and 0 for dominance effect, respectively.

Haplotype Frequencies and Genetic Structure of the *POU1F1* Loci

Haplotype frequencies for the combined POU1F1/*Alu*I and POU1F1/*Pst*I loci are presented in Table 6. Four haplotypes were identified: T-T, T-C, C-T, and C-C, among which the T-T haplotype was predominant (71.2%), followed by T-C (13.6%) and C-T (10.4%), whereas C-C was rare (4.76%). The high frequency of the T-T haplotype indicates a strong co-occurrence of T alleles at both loci in this population. In this F2 Boer × Bach Thao population, the skewed haplotype distribution may reflect the retention of common parental allele combinations after crossbreeding, together with the presence of rarer recombinant haplotypes. However, as linkage disequilibrium was not formally estimated, this interpretation should be considered with caution.

Due to its low frequency (<5%), the C-C haplotype was excluded from subsequent association analyses to avoid unreliable estimates and inflated standard errors (Balding 2006), which is consistent with standard practices in haplotype-based analyses. The dominance of T-containing haplotypes is consistent with the genotypic distribution observed at individual loci (Table 1). Given the association of the PstI T allele with post-weaning growth (Tables 3 and 5), the high frequency of the T-T haplotype may indicate that a major POU1F1 allele combination is widely retained in this population; however, high frequency should not be interpreted as functional superiority without haplotype-phenotype validation. High haplotype frequency alone does not imply functional superiority, as it may also reflect demographic or sampling effects. Taken together, the POU1F1 gene showed a skewed haplotype structure, with the T-T configuration predominating. Because POU1F1 participates in pituitary regulation of growth-related hormones, haplotype analysis may better capture the combined marker background of this gene than single-marker analysis alone. Nevertheless, the main haplotypes identified here should be considered candidate genetic backgrounds for further testing, rather than confirmed causal units. Future haplotype-phenotype association analyses in larger populations are required to determine whether these POU1F1 haplotypes provide additional predictive value for growth traits beyond individual SNP effects (Hayes *et al.* 2009).

Table 6. Estimated haplotype frequencies of the POU1F1/*Alu*I and POU1F1/*Pst*I polymorphisms in goats

Haplotype	Frequency	Percent (%)	Estimated count
T-T	0.712	71.2	112.5
T-C	0.136	13.6	21.5
C-T	0.104	10.4	16.5
C-C	0.048	4.76	7.53

Stage-Dependent Effects of *POU1F1* Haplotypes on Growth Performance

The effects of POU1F1 haplotypes on growth traits are illustrated in Figure 2, where animals were grouped into T-T carriers and others (T-C and/or C-T). For body weight (Figure 2A), both groups showed similar growth trajectories from birth to 10 months, and although T-T carriers tended to have slightly higher BW at later stages, the differences were not statistically significant. Thus, the T-T haplotype should not be interpreted as having a strong direct effect on absolute body weight, but rather as a potential genetic background associated with later growth tendency. With respect to growth rate, ADG exhibited a consistent stage-dependent trend (Figure 2B), with T-T carriers showing slightly lower values for 0-3 months but achieving similar

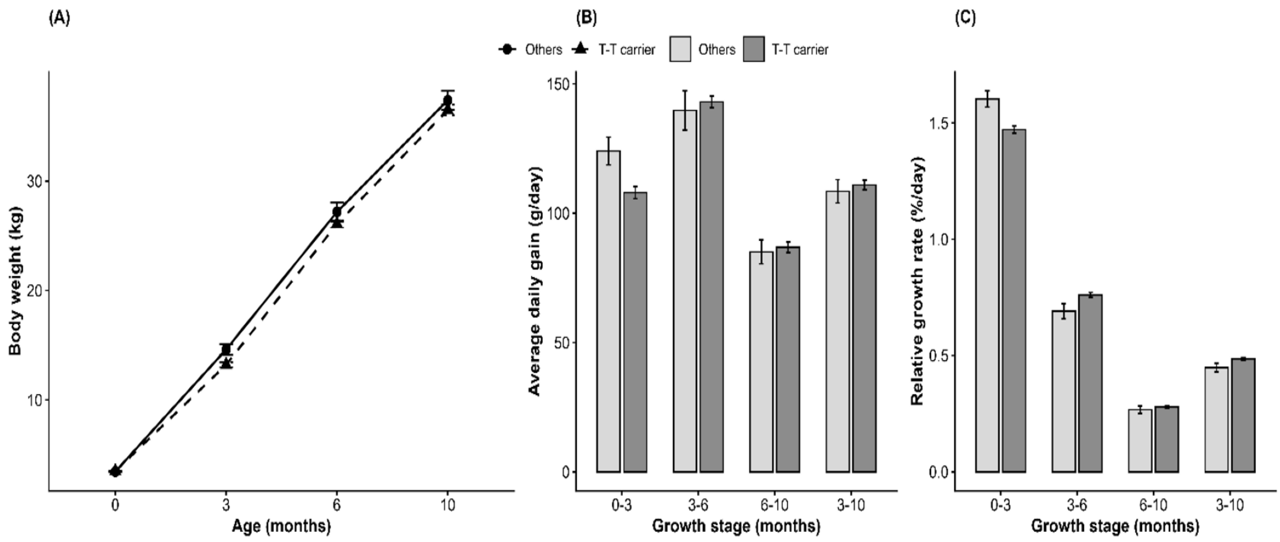

Figure 2. Effects of POU1F1 haplotype groups on growth performance in goats; (A) body weight, (B) average daily gain, and (C) relative growth rate. Values are presented as least squares means±SE, adjusted for sex. “T-T carrier” represents individuals carrying at least one T-T haplotype, whereas “Others” includes individuals carrying only T-C and/or C-T haplotype

or higher gains from 3-6 months onward, an advantage that was maintained over the cumulative 3-10 months period, suggesting improved post-weaning growth. A comparable trend was observed for RGR (Figure 2C), where T-T carriers showed lower values early (0-3 months) but higher values during 3-6 and 3-10 months. This biphasic pattern suggests that the haplotype effect, if present, may be linked more to post-weaning growth acceleration than to early-life growth, when maternal effects, milk intake and early environmental factors are more influential.

This interpretation is consistent with the role of POU1F1 in pituitary regulation of GH, PRL and TSHβ, which are involved in growth, metabolism and tissue development (Lan *et al.* 2007; Feng *et al.* 2012). Therefore, haplotype differences may become more visible after weaning, when endogenous endocrine regulation, feed intake and rumen function contribute more strongly to growth performance. From a genetic perspective, haplotype analysis may capture the combined background of linked POU1F1 variants better than single-marker analysis alone; however, this does not prove that the T-T haplotype itself is causal (Balding 2006; Feng *et al.* 2012). Taken together, the T-T haplotype showed a tendency toward more favorable post-weaning ADG and RGR, whereas its effect on BW was limited. These findings support the usefulness of haplotype-based analysis as a complementary approach, but the observed effect should be considered moderate and population-specific. Validation in larger populations, with formal haplotype-phenotype association testing and balanced haplotype frequencies, is required before practical application in marker-assisted selection, because reliable marker-based selection depends on sufficient genotype and phenotype information to estimate genetic effects accurately (Hayes *et al.* 2009).

CONCLUSION

This study demonstrates that polymorphisms in the POU1F1 gene, particularly at the *Pst*I locus, are associated with stage-dependent growth performance in F2 (Boer × Bach Thao) goats. The C allele was associated with relatively higher early growth, whereas the T allele was associated with improved post-weaning growth, and the T-T haplotype showed a similar tendency. This age-dependent pattern is biologically plausible because animal growth is not governed by a single uniform mechanism throughout development. Early growth is more strongly influenced by prenatal development, maternal effects, milk intake and rapid cellular proliferation, whereas post-weaning growth increasingly depends on rumen development, voluntary feed intake, endocrine regulation and lean-tissue accretion. Thus, the apparent shift from C-associated early growth to T-associated post-weaning growth may reflect stage-specific expression of genetic effects within the pituitary-somatotropic pathway, rather than different alleles independently controlling growth at separate ages.

In contrast, the GH1/*Hae*III polymorphism showed no significant effect, likely due to limited genetic variation at this locus in the studied population. Overall, POU1F1 may provide useful candidate genetic information for further validation in F2 Boer × Bach Thao goats. However, because growth is a polygenic trait influenced by developmental stage, endocrine status and environmental conditions, the observed associations should be considered moderate and population-specific. Validation in larger and independent populations is therefore required before practical application in marker-assisted selection.

ACKNOWLEDGMENTS

This research was conducted under the project entitled "Development of crossbreeding strategies for Boer × Bach Thao goats to improve growth performance and meat quality in Vinh Long Province". The authors would like to express their sincere gratitude to the Vinh Long Department of Science and Technology, Vietnam, for financial support.

CONFLICT OF INTEREST

The authors have stated that they have no competing interests.

REFERENCES

Alakilli, S. Y. M., K. F. Mahrous, L. M. Salem, & E. S. Ahmed. 2012. Genetic polymorphism of five genes associated with growth traits in goat. Afr. J. Biotechnol. 11(82), 14738-14748. https://doi.org/10.5897/AJB12.1642.

Balding, D. J. 2006. A tutorial on statistical methods for population association studies. Nat. Rev. Genet. 7(10), 781-791. https://doi.org/10.1038/nrg1916.

Bezerra, H., E. Santos, J. Oliveira, G. Carvalho, F. Silva, M. Cassuce, A. Perazzo, A. Zanine, & R. Pinho. 2019. Performance and ruminal parameters of Boer crossbred goats fed diets that contain crude glycerin. Animals 9(11), 967. https://doi.org/10.3390/ani9110967.

Brand, T. S., D. A. van der Merwe, E. Swart, & L. C. Hoffman. 2017. Comparing the effect of age and dietary energy content on feedlot performance of Boer goats. Small Rumin. Res. 157, 40-46. https://doi.org/10.1016/j.smallrumres. 2017.10.009.

Castilhos, A. M. D., R. H. Branco, T. L. S. Corvino, A. G. Razook, S. F. M. Bonilha, & L. A. D. Figueiredo. 2010. Feed efficiency of Nellore cattle selected for postweaning weight. R. Bras. Zootec. 39(11), 2486-2493. https://doi.org/10.1590/S1516-35982010001100023.

Feng, T., M. X. Chu, G. L. Cao, Q. Q. Tang, R. Di, L. Fang, & N. Li. 2012. Polymorphisms of caprine POU1F1 gene and their association with litter size. Mol. Biol. Rep. 39, 4029-4038. https://doi.org/10.1007/s11033-011-1180-7

Fernández, N., J. L. Palomares, I. Pérez-Baena, M. Rodríguez, & C. J. Peris. 2021. Kid growth comparison between Murciano-Granadina and crossbred Murciano-Granadina × Boer in a mixed rearing system. Animals 11(4), 1051. https://doi.org/10.3390/ani11041051.

Getaneh, M., & K. Alemayehu. 2022. Candidate genes associated with economically important traits in dairy goats. Cogent Food Agric. 8(1), 2149131. https://doi.org/10.1080/23311932.2022.2149131.

Hai, N. T. & D. H. Binh. 2019. Growth performance and disease resistancy of Boer goat and F1 crossbred (Boer x Bach Thao) in Ho Chi Minh city. J. Sci. Tech. 99(5), 8-16. In Vietnamese.

Hayes, B. J., P. M. Visscher, & M. E. Goddard. 2009. Increased accuracy of artificial selection by using the realized relationship matrix. Genet. Res. 91(1), 47-60. https://doi.org/10.1017/S0016672308009981.

Hung, B. K., N.B. Mui, D. T. Hai, & P. K. Dang. 2014. Productivity and meat quality of grass goats and crosses between F1 (Boer × Bach Thao) and F2 (Boer × Bach Thao) male goats with grass goats raised in Bac Kan. J. Sci. Develop. 12(8), 1223-1230. In Vietnamese.

Kayser, W., J. B. Glaze, C. M. Welch, M. Kerley, & R. A. Hill. 2015. Evaluation of the effect of alternative measurements of body weight gain and dry matter intake for the calculation of residual feed intake in growing purebred Charolais and Red Angus cattle. J. Anim. Sci. 93(7), 3675-3681. https://doi.org/10.2527/jas.2014-8337.

Lan, X. Y., C. Y. Pan, H. Chen, C. L. Zhang, J. Y. Li, M. Zhao, C. Z. Lei, A. L. Zhang, & L. Zhang. 2007. An *AluI* PCR-RFLP detecting a silent allele at the goat POU1F1 locus and its association with production traits. Small Rumin. Res. 73, 8-12. https://doi.org/10.1016/j.smallrumres.2006.10.012.

Mahgoub, O., & C. D. Lu. 1998. Growth, body composition and carcass tissue distribution in goats of large and small sizes. Small Rumin. Res. 27(3), 267-278. https://doi.org/10.1016/S0921-4488(97)00055-2.

Mahgoub, O., I. T. Kadim, N. M. Al-Saqry, & R. M. Al-Busaidi. 2004. Effects of body weight and sex on carcass tissue distribution in goats. Meat Sci. 67(4), 577-585. https://doi.org/10.1016/j.meatsci.2003.12.011.

Mehrban, H., M. Naserkheil, D. H. Lee, & N. Ibáñez-Escriche. 2021. Genetic parameters and correlations of related feed efficiency, growth, and carcass traits in Hanwoo beef cattle. Anim. Biosci. 34(5), 824. https://doi.org/10.5713/ajas.20.0135

Mui, N. B. & D. T. Hai. 2010. Appearance characteristics and growth ability of Co goats, F1 (Bach Thao × Co) and Boer × F1 (Bach Thao × Co) hybrids raised in Ninh Binh. J. Sci. Develop. 8(1), 82-89. In Vietnamese.

Mustefa, A., S. Gizaw, S. Banerjee, A. Abebe, M. Taye, A. Areaya, & S. Besufekad. 2019. Growth performance of Boer goats and their F1 and F2 crosses and backcrosses with Central Highland goats in Ethiopia. Livest. Res. Rural Dev. 31(6), 89.

Owens, F. N., P. Dubeski, & C. F. Hanson. 1993. Factors that alter the growth and development of ruminants. J. Anim. Sci. 71(11), 3138-3150. https://doi.org/10.2527/1993.71113138x.

Predith, M., S. Shanmugavelu, R. M. Hifzan, & A. W. Mohd Hafiz. 2020. Pre-weaning growth performance of F1 and F2 Katjang-Boer crossbreds fed formulated creep feed. Mal. J. Anim. Sci. 23(2), 62-71.

Rashijane, L. T., V. G. Mbazima, & T. L. Tyasi. 2022. Polymorphism of growth hormone gene and its association with body measurement traits in Boer goat does. S. Afr. J. Anim. Sci. 52(1), 44-49. https://doi.org/10.4314/sajas.v52i1.6.

Singh, P. P., S. S. Tomar, M. S. Thakur, & A. Kumar. 2015. Polymorphism and association of growth hormone gene with growth traits in goats. Vet. World. 8(3), 382-387. https://doi.org/10.14202/vetworld.2015.382-387.

Supakorn, C. 2009. The important candidate genes in goats - A review. Walailak J. Sci. & Tech. 6(1), 17-36.

Van Niekerk, W. A., & N. H. Casey. 1988. The Boer goat. II. Growth, nutrient requirements, carcass and meat quality. Small Rumin. Res. 1(4), 355-368. https://doi.org/10.1016/0921-4488(88)90061-2.

Webb, E. C., N. H. Casey, & L. Simela. 2005. Goat meat quality. Small Rumin. Res. 60(1-2), 153-166. https://doi.org/10.1016/j.smallrumres.2005.06.009.

Zhu, H., Y. Zhang, Y. Bai, H. Yang, H. Yan, J. Liu, L. Shi, X. Song, L. Li, S. Dong & C. Pan. 2019. Relationship between SNPs of POU1F1 gene and litter size and growth traits in Shaanbei white cashmere goats. Animals 9(3), 114. https://doi.org/10.3390/ani9030114.