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Original Research Article

Dietary supplementation of grape seed proanthocyanidins improves growth performance, carcass traits, and meat quality in growing-finishing pigs

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ABSTRACT

Grape seed proanthocyanidin (GSP) is a type of plant polyphenol with a wide variety of biological activities, such as antioxidant properties. This study investigated the effects of GSP supplementation on growth performance and meat quality in growing-finishing pigs. A total of 180 pigs (with an initial average body weight of 30.37 ± 0.66 kg) were randomly assigned to five treatments: a control diet or a control diet supplemented with GSP at 15, 30, 60, and 120 mg/kg. Each treatment group comprised six replicate pens (6 pigs per pen). Results showed that GSP supplementation linearly increased the average daily gain ($P = 0.048$) and quadratically decreased the feed intake to gain ratio ($P = 0.049$) with the lowest values at 30 and 60 mg/kg GSP. Serum concentrations of immunoglobulins (Ig) (IgA, IgG, IgM), total antioxidative capacity, catalase, and total superoxide dismutase were elevated with the peak levels at 30 mg/kg GSP ($P < 0.05$). Serum glutathione peroxidase increased and malondialdehyde decreased quadratically ($P < 0.05$), with peak and trough levels at 120 and 60 mg/kg GSP, respectively. The GSP also improved dressing percentage and muscle redness ($a^*_{45\ min}$) with optimal levels at 30 and 60 mg/kg ($P < 0.05$). Additionally, GSP supplementation quadratically reduced the muscle yellowness ($b^*_{24\ h}$) and shear force ($P < 0.05$), with the lowest values at 120 mg/kg. The expression level of myosin heavy chain I in muscle was quadratically increased with maximum expression at 30 and 60 mg/kg ($P = 0.015$). Furthermore, the expression levels of fatty acid synthase, phosphoenolpyruvate carboxykinase (*PEPCK*), and glucokinase in the muscle were decreased quadratically ($P < 0.05$) with the lowest values at 120 mg/kg. Additionally, GSP supplementation at 60 mg/kg upregulated the expression of hepatic hormone-sensitive triglyceride lipase and *PEPCK* ($P < 0.05$). These results suggest that GSP enhances carcass characteristics and meat quality in growing-finishing pigs, potentially through improved antioxidative capacity, modified muscle fiber type distribution, and altered glucose-lipid metabolism in muscle and liver.

1. Introduction

Pork is a highly prevalent meat product in global consumption. Intensive farming practices have resulted in the high level of oxidative stress in pigs, which may lead to the oxidation of lipids and proteins in pork, significantly affecting its color and flavor (Chauhan et al., 2021; Yu et al., 2017). Moreover, the tireless pursuit of leanness and growth rate is often associated with a decrease in

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pork tenderness and a reduction in flavor compounds (Ba et al., 2019). Accumulating evidence shows that modifying the nutrient composition of pig diets can improve meat quality traits. For instance, low-protein diets can improve meat quality while sustaining optimal growth by affecting the intestinal microbiome and regulating genes related to lipid metabolism (Zhu et al., 2022). Additionally, vitamin D_3 addition in drinking water before slaughter enhances pork quality by reducing oxidative damage and alleviating physiological stress (Rey et al., 2020).

Proanthocyanidin is a kind of water-soluble natural polyphenolic compound that is abundant in natural plants and fruits (Milinčić et al., 2021). Derived from grape seeds, grape seed proanthocyanidin (GSP) is made up of C4–C6 or C4–C8 linkages connecting catechin, epicatechin gallate, and epigallocatechin (Unusan, 2020). It may be found in both monomeric and polymeric forms (Trad et al., 2017). Multiple studies have shown that GSP has a diverse range of biological characteristics. For instance, GSP has been reported to act as a stronger antioxidant than vitamin E in vitro (Debasis et al., 2000). It also has obesity-inhibiting (Pascual-Serrano et al., 2018), anti-cancer (Zheng et al., 2015), and anti-inflammatory (Tyagi et al., 2013) properties. Recently, GSP has been utilized as a feed additive in animal nutrition and feed industry. For instance, under heat stress conditions, dietary supplementation with grape pomace rich in polyphenolic compounds can increase feed intake and loin area in finishing pigs (Ospina-Romero et al., 2023). Moreover, short-term dietary supplementation with GSP extract can promote skeletal muscle fiber type transformation in finishing pigs, which helps improve pork tenderness (Li et al., 2024). Studies have also shown that GSP can increase high-density lipoprotein levels in the blood while lowering blood lipid levels in finishing pigs (Feng et al., 2023).

Although multiple investigations have revealed the advantageous impact of GSP on animal productivity, the precise correlation between the dosage and effects of GSP remains uncertain. Furthermore, the underlying processes responsible for the GSP-regulated biological events are still not well understood. The purpose of this study was to evaluate the effect of increasing the level of GSP supplementation on growth performance, antioxidant capacity, and meat quality of growing-finishing pigs, thereby further validating its potential application in animal nutrition and the feed industry.

2. Materials and methods

2.1. Animal ethics statement

The research underwent submission and approval by the Committee on Animal Care Advisory of Sichuan Agricultural University, with the authorization number SICAU-2021-007. The experiment procedures were conducted in accordance with the Guidelines for the Care and Use of Laboratory Animals.

2.2. Preparation of GSP

The GSP were supplied by Fengpeng Biotechnology Co., Ltd. (Guilin, China). These proanthocyanidins were derived from dried grape seeds predominantly sourced from Xinjiang, China. It contains 86.81% proanthocyanidin oligomers, 1.52% catechin, 2.41% epicatechin, and 0.98% proanthocyanidin B_2, with a total proanthocyanidin purity of 96.58%.

2.3. Experimental design and diets

A total of 180 pigs (Duroc × Landrace × Yorkshire) with an initial body weight (BW) of 30.37 ± 0.66 kg (90 barrows and 90 gilts) were allocated to five treatments based on a randomized complete block design. Each treatment group comprised six replicate pens (6 pigs per pen). For each treatment, three replicate pens were utilized to house the barrows, and another three pens were utilized to house the gilts (pigs of the same sex were housed in a pen). The treatments were a control diet formulated to meet the requirements from NRC (2012) nutrient requirements (Table 1) with no addition of GSP, and the control diet with four increasing levels of GSP (15, 30, 60, 120 mg/kg). During the experimental period, feeders were refilled three times a day (08:00, 14:00 and 20:00). The experiment lasted for 103 days. In the feeding experiment, pigs were weighed, and daily feed consumption was recorded, with calculations performed as follows:

Average daily gain (ADG) = (total body weight at the end of the experiment − total body weight at the beginning of the experiment)/(number of pigs × number of experimental day);

Average daily feed intake (ADFI) = (daily feed amount per pen − daily remaining feed per pen)/(number of pigs per pen × number of experimental day);

Feed to gain ratio (F:G) = ADFI/ADG.

2.4. Chemical analysis and calculation

The diet was evaluated for crude protein (CP) (method 976.05; AOAC, 2007) and ether extract (EE) (method 922.06; AOAC, 2007). An automated oxygen bomb calorimeter (Model 6400, Parr, USA) was used to evaluate the gross energy (GE) of diet. The diet was analyzed for calcium and total phosphorus content by inductively coupled plasma spectroscopy (method 985.01 A, B, and C; AOAC, 2007). The calculated nutrient levels of the diet were obtained from the Feed Database in China (2020).

2.5. Sample collection

At the end of the experiment, following a 12-h fasting period, 30 pigs were selected for slaughter. One pig was chosen from each pen, with selections made based on weights that approximated the average weight within each pen. Before slaughtering the pigs, 15 mL of blood was drawn from the anterior vena cava, and the serum was prepared by centrifuging the blood for 20 min at 3000 × *g*. At 08:00, the pigs were transported to the slaughterhouse, which was about 300 m away. After that, at 15 min intervals, one pig was exsanguinated after being electrically shocked for 3 s at a voltage of 300 V. Following the procedures outlined by Zhang et al. (2015), the carcass was dehaired, peeled, dissected, and then split along the midline into left and right sides. The longissimus thoracis and liver were collected from the left side within 20 min post-mortem. The longissimus thoracis of the 10th and 11th thoracic vertebrae was taken and packed into sample bags, and stored at −20 °C to determine the conventional nutrient value and amino acid composition. The liver and muscle samples that remained were kept at −80 °C for further investigation of parameters.

2.6. Serum biochemical, antioxidant, and immunoglobulin parameters

Serum biochemical parameters measured by automated olympus analyzer (Shanghai, China) include alanine aminotransferase (ALT), aspartate aminotransferase (AST), alkaline phosphatase (ALP), albumin (ALB), total protein (TP), glucose (GLU),

Table 1
Control diet ingredients and nutrient levels (air-dried matter basis, %).

Item	25 to 50 kg	50 to 75 kg	75 to 100 kg	100 to 135 kg
Ingredients				
Corn	72.58	76.91	80.94	89.23
Soybean meal	17.93	15.93	12.10	8.54
Bran	2.50	2.50	2.70	
Fish meal	2.50			
Soybean oil	2.00	1.90	1.80	
Limestone	0.69	0.69	0.59	0.55
Dicalcium phosphate	0.58	0.78	0.63	0.48
Salt	0.30	0.30	0.30	0.30
L-Lysine HCl	0.31	0.34	0.31	0.28
DL-Methionine	0.03	0.04	0.02	0.01
L-Threonine	0.07	0.09	0.09	0.09
L-Tryptophan	0.01	0.02	0.02	0.02
Choline chloride	0.15	0.15	0.15	0.15
Vitamin premix[1]	0.05	0.05	0.05	0.05
Mineral premix[2]	0.30	0.30	0.30	0.30
Total	100.00	100.00	100.00	100.00
Analyzed nutrient levels				
Gross energy, MJ/kg	18.95	18.38	18.42	17.83
Crude protein	18.48	17.23	15.45	15.34
Ether extract	3.12	2.99	3.04	2.52
Calcium	0.71	0.64	0.50	0.48
Total phosphorus	0.47	0.41	0.41	0.37
Calculated nutrient levels[3]				
Digestible energy, MJ/kg	14.23	14.23	14.23	13.98
Crude protein	15.88	13.82	12.43	11.09
Ether extract	5.08	4.89	4.89	3.25
Calcium	0.66	0.59	0.52	0.46
Total phosphorus	0.51	0.42	0.43	0.38
Available phosphorus	0.31	0.27	0.24	0.21
SID lysine	0.98	0.85	0.73	0.61
SID methionine + cystine	0.50	0.44	0.39	0.34
SID threonine	0.59	0.52	0.46	0.40
SID tryptophan	0.17	0.15	0.13	0.11

SID = standardized ileal digestibility.
[1] Vitamin premix provided the following per kilogram of diets: vitamin A 15,000 IU, vitamin D_3 5000 IU, vitamin E 40.0 IU, vitamin K 5.0 mg, vitamin B_1 5.0 mg, vitamin B_2 12.5 mg, vitamin B_6 6.0 mg, vitamin B_{12} 0.06 mg, nicotinic acid 50.0 mg, pantothenic acid 25.0 mg, folic acid 2.5 mg, biotin 0.25 mg.
[2] Mineral premix provided the following per kilogram of diets: 25 to 50 kg, Fe (as ferrous sulfate) 60.0 mg, Cu (as copper sulfate) 4.0 mg, Zn (as zinc sulfate) 60.0 mg, Mn (as manganese sulfate) 2.0 mg, I (as KI) 0.14 mg, Se (as Na_2SeO_3) 0.2 mg. 50 to 75 kg, Fe (as ferrous sulfate) 50.0 mg, Cu (as copper sulfate) 3.5 mg, Zn (as zinc sulfate) 50.0 mg, Mn (as manganese sulfate) 2.0 mg, I (as KI) 0.14 mg, Se (as Na_2SeO_3) 0.15 mg. 75 to 135 kg, Fe (as ferrous sulfate) 40.0 mg, Cu (as copper sulfate) 3.0 mg, Zn (as zinc sulfate) 50.0 mg, Mn (as manganese sulfate) 2.0 mg, I (as KI) 0.14 mg, Se (as Na_2SeO_3) 0.15 mg.
[3] Calculated nutrient levels of the diets were obtained from the Feed Database in China (2020).

triglycerides (TG), total cholesterol (T-CHO), creatine kinase (CK), creatinine (CREA), urea, and lactate dehydrogenase (LDH). Commercial kits from Nanjing Jiancheng Bioengineering Institute (Nanjing, Jiangsu, China) were utilized to measure the concentrations of total antioxidative capacity (T-AOC) (Cat. No. A015-1-2), glutathione peroxidase (GSH-Px) (Cat. No. A005-1-2), catalase (CAT) (Cat. No. A007-1-1), total superoxide dismutase (T-SOD) (Cat. No. A001-1-1), and malondialdehyde (MDA) (Cat. No. A003-1-2). The T-AOC, CAT, T-SOD, and MDA measurements were performed using undiluted serum, with intra-assay coefficients of variation (CVs) of $\leq$3.6%, $\leq$1.7%, $\leq$1.7%, and $\leq$2.3%, respectively. For GSH-Px measurement, serum samples were diluted with saline at a 1:2 ratio (serum: saline), yielding an intra-assay CV of $\leq$3.5%. Utilizing ELISA kits (MEIMIAN, Yancheng, Jiangsu, China), the concentrations of immunoglobulins (Ig) A (MM-090502), IgG (MM-040302), and IgM (MM-040202) were measured. The intra-assay CVs for the measurement of serum IgA, IgG, and IgM concentrations were all $\leq$10%.

2.7. Carcass traits

The methods for measuring carcass traits were based on Li et al. (2018), with appropriate modifications. There was a cut made in the middle of the carcass, dividing it in two, and all carcass characteristics were measured within 30 min after slaughter. The hot carcass weight was recorded within 5 min after slaughter to calculate the dressing percentage by dividing the carcass weight by the live weight. Carcass length was determined from the first rib to the articulation of the pelvis. The backfat depth was measured on the initial, tenth, and last ribs. To determine the area of the loin muscle, a 2-cm-thick slice was cut from the tenth to the thirteenth rib. The carcass's tenth rib loin muscle form was measured and drawn onto paper using a planimeter. The left hindquarter of the carcass was removed and weighed to estimate the weight of the left hip and leg. The skin, perirenal fat and leaf lard were separated, and weighed to calculate the percentage of skin and perirenal fat.

2.8. Muscle physical traits

Measurement of muscle pH was performed using a pH meter (pH-STAT, SFK-Technology, Herlev, Denmark). The CR-300 Minolta Chroma Meter (Minolta Co., Ltd., Osaka, Japan) equipped with an 8 mm aperture, D65 illuminant, and 10° permanent observer was employed to measure the values of lightness (L*), redness (a*), and yellowness (b*). The fresh side of the muscle was evaluated for marbling score (NPPC, 1999) after the longissimus thoracis was refrigerated at 4 °C for 24 h.

The drip loss was determined using the method developed by Honikel (1987) with modifications. A 30 g sample of longissimus thoracis was cut into 3 cm × 2 cm × 1 cm pieces along the muscle

fibers. The initial weight of these pieces was recorded as W_1. The samples were then hung using metal hooks, sealed in plastic bags, and stored at 4 °C for 24 h. After removing surface water, the weight was recorded as W_2.

$$\text{Drip loss (\%)} = (W_1 - W_2)/W_1 \times 100.$$

The methodology for evaluating cooking loss was based on the procedure outlined in Honikel (1998). Longissimus thoracis muscle weighing about 100 g was sliced into 25 mm thick pieces and its weight was measured as W_1. In order to cook the muscle samples, they were sequentially put into a water bath that was heated to 75 °C, and their central internal temperature was measured using a thermometer. Upon reaching 70 °C, the muscle samples were removed. The samples were then cooled at 4 °C for 30 min. Afterward, the samples were drained and their weight was measured again, denoted as W_2.

$$\text{Cooking loss (\%)} = (W_1 - W_2)/W_1 \times 100.$$

The methods for measuring shear force were based on Zhang et al. (2015) with appropriate modifications. In short, a longissimus thoracis sample of at least 12 cm × 6 cm × 6 cm was used. All tendons, membranes, and surface fat were removed from the muscle sample before analysis. The sample bag was filled and placed in an ice box, with the temperature of 4 °C for 24 h. The sample was subsequently heated in a water bath at 80 °C until the internal temperature reached 70 to 75 °C. It was then removed and cooled to 4 °C. Following this, the sample was sheared along the muscle fibers using a knife blade set at a 60° angle and with a thickness of 1.016 mm. The texture analyzer (Stable Micro System, Godalming, UK) was used for this process. With a preload force of 2 N and a crosshead speed of 200 mm/min, the average of each sample's six measurements was used to capture the shear force values.

2.9. Chemical analysis of muscle and liver

After removing the fascia covering the longissimus thoracis from a 40 g back, the muscle was chopped into tiny pieces and placed in a freeze dryer (FDU-2110, Tokyo Physical and Chemical Instrument Co., Ltd., Japan) set to −50 °C for 48 h. Next, using a high-speed pulverizer, the samples of muscle were finely powdered and put through 0.45 pm filters then stored in a −20 °C freezer. According to the conventional nutrient analysis method of AOAC (2007), the CP (method 976.05; AOAC, 2007) and EE (method 922.06; AOAC, 2007) of longissimus thoracis samples were determined. Commercial kits from Nanjing Jiancheng Bioengineering Institute (Nanjing, China) were utilized to assess the concentrations of T-CHO (Cat. No. A111-1-1), TG (Cat. No. A110-1-1), and glycogen (Cat. No. A043-1-1) in longissimus thoracis and liver. The longissimus thoracis and liver samples were homogenized with saline at a 1 g to 9 mL ratio, adding 9 times the volume of saline. Homogenization was conducted on ice, followed by centrifugation at 3000 × *g* for 10 min. Supernatants were used to measure T-CHO and TG. The intra-assay CVs were ≤3% for T-CHO and ≤5% for TG in both longissimus thoracis and liver samples. For glycogen measurements, the intra-assay CVs were ≤1.7%.

2.10. Muscle amino acid composition analysis

Based on Xie et al. (2023), the methods for measuring muscle amino acid composition were implemented with appropriate modifications. About 100 mg of freeze-dried longissimus thoracis powder was transferred into a hydrolysis tube and added with 10 mL of 6 mol/L hydrochloric acid. The tube was filled with nitrogen and the sample was hydrolyzed at 110 °C for 24 h. After hydrolysis, each hydrolysate was transferred to a volumetric bottle with a capacity of 50 mL and fixed. The mixture was then passed via 0.45 μm membrane filters. Next, an L-8900 automatic amino acid analyzer (Hitachi, Tokyo, Japan) was used.

2.11. Real-time quantitative PCR (RT-qPCR)

The frozen longissimus thoracis and liver samples were weighed and then quickly transferred to a pre-cooled mortar with liquid nitrogen, where they were ground into a powder. For RNA extraction, RNAiso Plus reagent (TaKaRa, Dalian, China) was used to extract the total RNA, and prepared for transcription into cDNA by a PrimeScript RT reagent kit with gDNA eraser (TaKaRa, Dalian, China) according to the instructions of the manufacturer. RT-qPCR was carried out by a 7900 HT Real-time PCR System (384-well standard block) (Applied Biosystems, Foster, CA, USA). The PCR reaction (10 μL total volume) was conducted using a Bio-Rad iQ6 instrument (Bio-Rad, Hercules, CA, USA) with the following protocol: 95 °C for 30 s, followed by 40 cycles of 95 °C for 5 s and 60 °C for 30 s. The reaction mixture included 5 μL of TB Green Premix Ex Taq (2 ×) (Tli RNaseH Plus), ROX plus, 0.4 μL of forward and reverse primers, 1 μL of cDNA, and 3.2 μL of RNase-Free water. Target gene fragments were amplified using primers created using Primer 5 software (Table S1). The mRNA levels of genes were calculated by the $2^{-\Delta\Delta Ct}$ method.

2.12. Statistical analysis

The data were analyzed using IBM SPSS 27.0 (SPSS, Inc., USA). Growth performance was assessed using every pen as the experimental unit, whereas other data measurements were conducted with every pig serving as the experimental unit. An analysis was conducted on the growth performance data using a linear mixed model (LMM), considering dietary treatment and sex as fixed effects, and pen as a random effect. The mathematical model for the LMM is as follows:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + P_k + \epsilon_{ijk},$$

where Y_{ijk} is the dependent variable; μ is the overall mean; α_i is the fixed treatment effect; β_j is the fixed sex effect; $(\alpha\beta)_{ij}$ is the interaction between treatment and sex; P_k is the random effect of pen; ϵ_{ijk} is the error term. A general linear model (GLM) was used to assess other data, the mathematical model for the GLM is as follows:

$$Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \epsilon_{ij},$$

where Y_{ij} is the dependent variable; μ is the overall mean; α_i is the fixed treatment effect; β_j is the fixed sex effect; $(\alpha\beta)_{ij}$ is the interaction between treatment and sex; ϵ_{ij} is the error term. For all data, no significant interaction effects between dietary treatment and sex were observed ($P > 0.05$). To determine the effects of elevating GSP addition on the assessed characteristics, both linear and quadratic impacts were examined. The one-way analysis of variance (ANOVA) was performed to assess the effect of the treatments. Results are presented as mean and standard error of the mean (SEM), with a significance threshold of $P < 0.05$ and a tendency defined as $0.05 \leq P < 0.10$.

3. Results

3.1. Growth performance

Based on the information shown in Table 2, GSP supplementation linearly increased ADG ($P = 0.048$) and quadratically decreased the F:G ($P = 0.049$), with the lowest values observed at 30 and 60 mg/kg of GSP, while an increase in the F:G ratio was noted at 120 mg/kg of GSP.

3.2. Serum biochemical indicators

Table 3 shows that GSP addition did not affect the biochemical indicators in serum, including ALT, AST, CK, and TP. However, the serum GLU concentrations increased quadratically ($P = 0.006$), with the highest value observed at 30 mg/kg of GSP supplementation.

3.3. Serum immunoglobulins and antioxidative capacity

With dietary GSP supplementation, the serum levels of IgA, IgG, and IgM increased quadratically ($P < 0.05$, Table 4), with the highest values observed at 120, 30, and 60 mg/kg of GSP, respectively. Moreover, MDA level in serum decreased quadratically by dietary GSP supplementation ($P = 0.036$), with the lowest value observed at 60 mg/kg of GSP, while an increase was noted at 120 mg/kg of GSP. Meanwhile, with GSP supplementation, the serum concentrations of T-SOD, CAT, and T-AOC increased quadratically ($P < 0.05$), with the highest values observed at 60, 120, and 30 mg/kg of GSP, respectively.

3.4. Carcass traits

Table 5 indicates that the dressing percentage increased quadratically ($P = 0.017$), reaching its highest value at 30 mg/kg of GSP, and gradually decreased with further increase in GSP supplementation. Moreover, the percentage of perirenal fat decreased quadratically with GSP supplementation ($P = 0.022$), reaching its lowest value at 15 mg/kg, and slightly increased with further increase in GSP levels.

3.5. Muscle physical traits

Table 6 shows that supplementation of GSP quadratically enhanced the redness ($a^*_{45\ min}$) of the longissimus thoracis ($P = 0.014$), reaching its highest value at 60 mg/kg of GSP, followed by a decrease at the 120 mg/kg supplementation level. In contrast, the yellowness ($b^*_{24\ h}$) decreased quadratically by GSP supplementation ($P = 0.012$), with the lowest value at 120 mg/kg of GSP. Moreover, the longissimus thoracis' shear force decreased quadratically with GSP supplementation ($P < 0.001$), showing the lowest value at 120 mg/kg dosage.

3.6. Muscle conventional nutrient contents

The crude protein and amino acid content in the longissimus thoracis did not show significant changes when GSP was supplemented ($P > 0.05$, Table 7). Nevertheless, the supplementation of GSP quadratically decreased the ether extract of the longissimus thoracis ($P = 0.009$), with the lowest value observed at 120 mg/kg of GSP.

3.7. Gene expression levels for muscle fiber types

According to the data shown in Fig. 1, longissimus thoracis supplemented with GSP showed a quadratic increase in *MYHC I* expression ($P = 0.015$), peaking at 30 and 60 mg/kg of GSP, followed by a decline at the 120 mg/kg supplementation level. *MYHC IIa* expression levels were decreased quadratically by dietary GSP supplementation ($P = 0.010$), reaching the lowest value observed at 120 mg/kg of GSP. Moreover, GSP supplementation quadratically reduced *MYHC IIx* ($P = 0.010$) and *MYHC IIb* ($P < 0.001$) expression levels, with the lowest values observed at 120 mg/kg GSP for both.

3.8. Glucose-lipid metabolisms in the muscle and liver

With dietary GSP supplementation, the concentrations of TG and T-CHO in the muscle decreased quadratically ($P = 0.003$ and $P = 0.005$, Table 8), with the lowest values observed at 60 mg/kg GSP for both. Moreover, GSP supplementation also quadratically decreased the liver TG concentration ($P = 0.021$), with the lowest values observed at 30 and 120 mg/kg of GSP.

Interestingly, GSP supplementation quadratically decreased the fatty acid synthase (*FASN*), acetyl-CoA carboxylase (*ACC*), phosphoenolpyruvate carboxykinase (*PEPCK*), and glucokinase (GCK) expression in the longissimus thoracis ($P < 0.05$, Fig. 2), with the lowest values observed at 120 mg/kg GSP for all four. Moreover, the liver expression level of *FASN* was quadratically decreased by GSP ($P < 0.001$), with the lowest value observed at 120 mg/kg of GSP. Additionally, GSP supplementation quadratically elevated the liver hormone-sensitive lipase (*HSL*) and *PEPCK* expression levels ($P = 0.004$ and $P = 0.003$), showing the highest values at 120 and 60 mg/kg of GSP, respectively.

4. Discussion

Currently, plant extracts including the GSP have gained significant global attention because of their diverse range of biological activities. First, the GSP exhibits potent antioxidant properties, effectively scavenging free radicals and mitigating oxidative stress

Table 2
Effect of dietary GSP supplementation on the growth performance of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		LMM	Linear	Quadratic
Initial weight, kg	30.39	30.29	30.42	30.33	30.42	0.661	0.754	0.984	0.999
Final weight, kg	127.63^{b}	127.73^{b}	131.79^{a}	131.73^{a}	130.63^{ab}	0.764	0.049	0.063	0.104
ADFI, kg/d	2.67	2.64	2.65	2.65	2.70	0.010	0.111	0.442	0.125
ADG, kg/d	0.94^{b}	0.95^{b}	0.98^{a}	0.98^{a}	0.97^{ab}	0.007	0.017	0.048	0.073
F:G	2.84^{a}	2.80^{a}	2.69^{b}	2.69^{b}	2.78^{ab}	0.023	0.025	0.137	0.049

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; LMM = linear mixed model; ADFI = average daily feed intake; ADG = average daily gain; F:G = feed to gain ratio.
[a, b] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

Table 3
Effect of dietary GSP supplementation on serum biochemical indexes of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
ALT, U/L	54.77	51.94	55.44	48.44	44.56	2.048	0.503	0.099	0.199
AST, U/L	24.41	23.85	26.44	23.70	21.70	0.843	0.547	0.360	0.340
ALP, U/L	120.17	124.00	111.17	100.83	107.33	4.846	0.406	0.158	0.368
ALB, g/L	34.13	33.34	32.76	35.00	32.75	0.542	0.708	0.779	0.962
TP, g/L	60.45	60.64	59.98	61.41	60.17	0.814	0.983	0.971	0.993
GLU, mmol/L	4.12^{bc}	4.31^{ab}	4.51^{a}	4.15^{ab}	3.79^{c}	0.076	0.004	0.126	0.006
TG, mmol/L	0.29	0.27	0.34	0.31	0.27	0.018	0.734	0.994	0.600
T-CHO, mmol/L	2.20	2.16	2.25	2.28	2.16	0.065	0.972	0.921	0.908
CK, U/L	24.41	23.85	26.44	23.70	21.70	0.843	0.547	0.360	0.340
CREA, μmol/L	129.52	134.83	129.01	126.72	136.13	2.325	0.624	0.762	0.806
Urea, mmol/L	3.09	3.82	3.47	3.10	3.13	0.128	0.223	0.493	0.341
LDH, U/L	356.37	365.63	345.40	345.68	348.82	9.197	0.963	0.599	0.868

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model; ALT = alanine aminotransferase; AST = aspartate aminotransferase; ALP = alkaline phosphatase; ALB = albumin; TP = total protein; GLU = glucose; TG = triglyceride; T-CHO = total cholesterol; CK = creatine kinase; CREA = creatinine; LDH = lactate dehydrogenase.
[a-c] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

Table 4
Effect of dietary GSP supplementation on serum immunoglobulins and antioxidative capacity of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
IgA, μg/mL	21.80^{c}	23.27^{bc}	27.66^{a}	26.82^{ab}	29.05^{a}	0.753	0.005	<0.001	<0.001
IgG, μg/mL	265.00^{b}	388.86^{a}	488.86^{a}	434.32^{a}	470.91^{a}	22.311	0.005	0.002	<0.001
IgM, μg/mL	6.34^{c}	8.36^{bc}	10.72^{ab}	11.39^{a}	10.30^{ab}	0.499	0.001	<0.001	<0.001
MDA, nmol/mL	2.72	2.64	2.40	2.11	2.36	0.076	0.065	0.017	0.036
T-AOC, U/mL	1.97^{b}	2.77^{ab}	3.52^{a}	3.37^{a}	3.25^{a}	0.185	0.041	0.013	0.007
CAT, U/mL	3.30^{d}	5.15^{c}	8.25^{b}	8.79^{b}	10.67^{a}	0.553	<0.001	<0.001	<0.001
GSH-Px, U/mL	937.73^{b}	950.66^{b}	969.72^{b}	984.70^{ab}	1,063.08^{a}	14.265	0.046	0.003	0.006
T-SOD, U/mL	135.91^{b}	143.22^{ab}	152.52^{a}	159.34^{a}	156.94^{a}	2.802	0.026	0.002	0.005

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model; IgA = immunoglobulin A; IgG = immunoglobulin G; IgM = immunoglobulin M; MDA = malondialdehyde; T-AOC = total antioxidant capacity; CAT = catalase; GSH-Px = glutathione peroxidase; T-SOD = total superoxide dismutase.
[a-c] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

Table 5
Effect of dietary GSP supplementation on carcass traits of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
Carcass weight, kg	85.37^{b}	90.40^{a}	91.13^{a}	88.23^{ab}	87.30^{ab}	0.667	0.048	0.789	0.955
Carcass straight length, cm	92.83	95.50	92.50	94.00	94.08	0.515	0.344	0.725	0.014
Dressing percentage, %	66.68^{b}	70.95^{a}	72.31^{a}	69.70^{ab}	69.41^{ab}	0.609	0.037	0.336	0.017
Tenth rib backfat thickness, mm	41.17	38.50	40.00	36.50	40.50	2.722	0.988	0.866	0.926
Mean backfat thickness, mm	43.61	43.33	41.83	42.11	42.67	1.987	0.998	0.829	0.958
Loin eye area, cm^2	69.84	70.04	68.46	70.55	69.78	1.392	0.995	0.969	0.989
Hip and leg weight, kg	14.49	14.98	14.87	14.57	14.93	0.173	0.801	0.711	0.893
Hip and leg percentage, %	33.97	33.17	32.61	33.05	34.20	0.362	0.359	0.893	0.276
Skin weight, kg	6.83	7.01	6.46	6.89	6.82	0.116	0.640	0.858	0.887
Skin percentage, %	8.00	7.77	7.10	7.81	7.81	0.138	0.264	0.740	0.268
Perirenal fat weight, g	30.28^{a}	19.03^{b}	22.65^{b}	20.78^{b}	21.15^{b}	1.291	0.022	0.069	0.044
Perirenal fat percentage, %	0.04^{a}	0.02^{b}	0.02^{b}	0.02^{b}	0.02^{b}	0.002	0.009	0.063	0.022
Leaf lard weight, kg	1.16	1.60	1.47	1.36	1.27	0.082	0.426	0.989	0.332

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model.
[a, b] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

in animals (Keser et al., 2013). Possessing antimicrobial and antiviral properties, GSP can disrupt microbial cell membrane structures and inhibit protein synthesis in microorganisms (Al-Mousawi et al., 2020; Saeloh and Visutthi, 2021). Additionally, GSP exerts anti-inflammatory effects by inhibiting the production of pro-inflammatory cytokines and modulating the activity of inflammation-related enzymes (Chu et al., 2024). This research examined the impact of adding GSP to the diet on growth and pork quality in the growing and finishing stages. The results of our investigation revealed that the inclusion of GSP in the diet achieved the lowest value of F:G at inclusion levels of 30 and 60 mg/kg, indicating a significant improvement in feed efficiency. The result is in line with earlier research on the weaning and growing stages of pigs (Li et al., 2020; Park et al., 2014). The increased feed efficiency

Table 6
Effect of dietary GSP supplementation on meat quality of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
$pH_{45\ min}$	6.19	6.12	6.18	6.14	6.26	0.045	0.860	0.615	0.669
$pH_{24\ h}$	5.43	5.45	5.44	5.47	5.44	0.011	0.841	0.472	0.652
L^*_{45min}	42.24	42.83	44.00	42.68	43.04	0.283	0.362	0.478	0.370
$a^*_{45\ min}$	6.36^{b}	6.67^{b}	7.19^{ab}	7.66^{a}	6.68^{b}	0.139	0.027	0.094	0.014
$b^*_{45\ min}$	5.54	5.37	5.39	5.51	5.21	0.069	0.630	0.290	0.560
$L^*_{24\ h}$	56.55	55.00	54.09	53.66	53.12	0.548	0.346	0.032	0.088
$a^*_{24\ h}$	10.20	11.59	10.33	10.57	10.33	0.239	0.441	0.661	0.628
$b^*_{24\ h}$	8.87	8.48	8.22	8.22	8.07	0.097	0.082	0.005	0.012
Cooking loss, %	32.65	30.65	31.09	31.01	32.01	0.433	0.432	0.849	0.672
Drip loss, %	3.59	2.61	2.73	2.74	3.05	0.165	0.241	0.421	0.143
Shear force, N	61.25^{a}	58.25^{ab}	58.05^{ab}	55.59^{bc}	52.01^{c}	0.820	0.004	<0.001	<0.001
Marbling score	2.33	2.67	2.50	2.50	2.17	0.104	0.633	0.505	0.333

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model; L* = lightness; a* = redness; b* = yellowness.
[a-c] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

Table 7
Effect of dietary GSP supplementation on conventional nutrient contents and amino acid composition in the muscle of growing-finishing pigs (%).[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
CP	86.84	86.88	85.47	85.96	86.63	0.355	0.739	0.605	0.495
EE	8.67^{a}	8.34^{ab}	8.42^{ab}	7.09^{bc}	6.82^{c}	0.245	0.029	0.002	0.009
Lys	7.17	7.28	7.10	7.19	7.02	0.060	0.732	0.346	0.547
Phe	3.04	3.06	3.00	3.02	3.02	0.031	0.977	0.655	0.896
Met	2.31	2.39	2.31	2.33	2.26	0.022	0.399	0.253	0.276
Thr	3.95	4.01	3.91	3.96	3.85	0.034	0.689	0.320	0.482
Val	3.89	3.91	3.81	3.85	3.73	0.034	0.519	0.121	0.266
Leu	6.67	6.74	6.58	6.67	6.50	0.057	0.749	0.318	0.544
Ile	3.57	3.62	3.53	3.60	3.51	0.034	0.856	0.540	0.782
Arg	5.42	5.67	5.54	5.49	5.21	0.056	0.098	0.136	0.029
His	3.44	3.53	3.44	3.53	3.38	0.031	0.572	0.674	0.466
EAA	42.25	42.99	41.94	42.39	41.19	0.365	0.666	0.301	0.440
Asp	7.72	7.85	7.68	7.75	7.55	0.064	0.710	0.369	0.504
Glu	13.03	13.29	12.94	13.07	12.70	0.112	0.591	0.278	0.402
Gly	3.53	3.54	3.47	3.51	3.48	0.025	0.889	0.483	0.780
Ala	4.52	4.60	4.50	4.55	4.46	0.036	0.769	0.490	0.642
Pro	3.27	3.32	3.26	3.27	3.19	0.031	0.762	0.336	0.507
Ser	3.47	3.48	3.41	3.44	3.36	0.032	0.766	0.270	0.525
Tyr	2.80	2.79	2.72	2.76	2.73	0.025	0.814	0.336	0.599
Cys	0.45	0.36	0.45	0.46	0.46	0.017	0.338	0.290	0.485
TAA	78.22	79.43	77.63	78.44	76.39	0.656	0.704	0.325	0.485
FAA	41.62	42.43	41.44	41.77	40.61	0.351	0.604	0.287	0.386

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model; CP = crude protein; EE = ether extract; EAA = essential amino acids; FAA = flavorful amino acids.
[a-c] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

may be linked to enhanced immune function and increased antioxidative capability after supplementation with GSP (Hao et al., 2021; Hoseinifar et al., 2015). This research found that supplementing GSP at a dosage of 30 mg/kg in feed led to near-peak levels of IgA, IgG, and IgM in the serum. Previous studies indicated that GSP can prevent UV radiation-induced immunosuppression by altering immunomodulation-related cytokines and by stimulating the repair of damaged DNA (Katiyar, 2015). Moreover, GSP could inhibit nuclear factor kappa-light-chain-enhancer of activated B cells (NF-κB) translocation, downregulate the expression of inducible nitric oxide synthase (iNOS) and the generation of nitric oxide (NO) and prostaglandin E2 (PGE2) in stimulated macrophages, hence modulating their inflammatory response, and thus has potential health benefits under inflammatory conditions (Terra et al., 2007).

Interestingly, we found that the addition of GSP to the diet, at 15 and 30 mg/kg dosage, resulted in significant increases in both carcass weight and dressing percentage. The findings align with a prior investigation on chlorogenic acid, a polyphenolic compound that has been shown to effectively improve dressing percentage (Xie et al., 2023). Moreover, we found that GSP supplementation reduced the perirenal fat percentage, which can be used as an indicator to evaluate fat deposition, reflecting the extent to which visceral fat contributes to overall fat deposition (Ricci et al., 2018). Both results suggested that GSP may have excellent anti-obesity properties and significantly reduced fat deposition (Ibars et al., 2017).

The antioxidative capacity of growing-finishing pigs is critical for meat quality, and excess reactive oxygen species (ROS) may lead to the oxidation of unsaturated muscle proteins and fatty acids, and DNA damage, which subsequently affects the pork's color, tenderness, and flavor (Serao et al., 2020). In the last decades, various antioxidants have been tentatively utilized to enhance pork quality (Zhang et al., 2013; Kone et al., 2016). For instance, exogenous

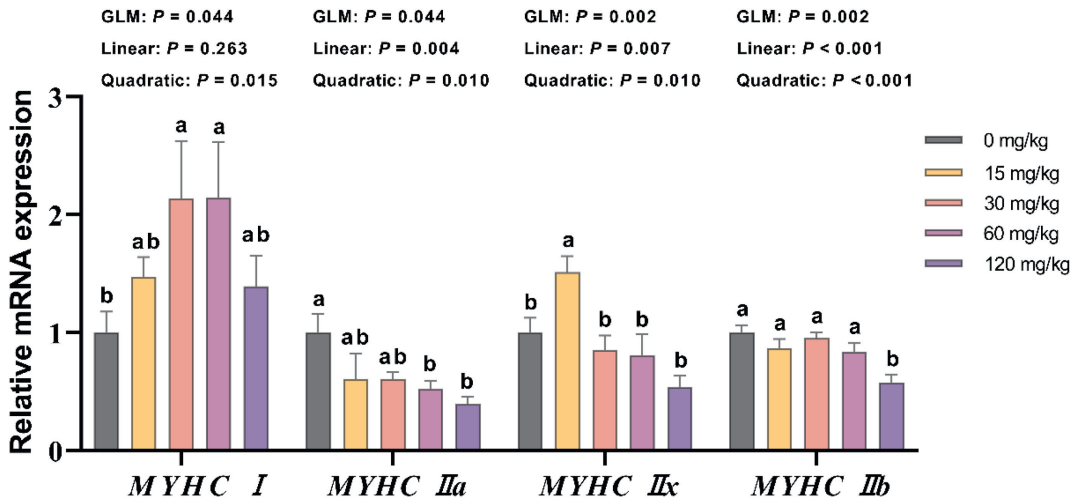

Fig. 1. Effect of GSP on expression patterns of the muscle-fiber types. The right-side legend shows the dosage of GSP in the diet. GSP = grape seed proanthocyanidin; *MyHC I* = myosin heavy chain I; *MyHC IIa* = myosin heavy chain IIa; *MyHC IIx* = myosin heavy chain IIx; *MyHC IIb* = myosin heavy chain IIb; GLM = general linear model. [a, b]Different letters indicate significant differences ($P < 0.05$). Means ± standard error of the mean (SEM) ($n = 6$) are used to express the data.

Table 8
Effect of dietary GSP supplementation on lipid and glycogen content in the muscle and liver of growing-finishing pigs.[1]

Item	GSP, mg/kg					SEM	*P*-value		
	0	15	30	60	120		GLM	Linear	Quadratic
Muscle									
TG, mmol/g prot	2.66[a]	1.83[ab]	1.52[b]	1.21[b]	1.85[ab]	0.149	0.029	0.031	0.003
T-CHO, mg/g prot	0.82[a]	0.76[ab]	0.58[b]	0.57[b]	0.57[b]	0.034	0.017	0.002	0.005
Glycogen, U/mg prot	4.04	2.20	4.16	2.23	3.39	0.304	0.075	0.501	0.604
Liver									
TG, mmol/g prot	0.07[a]	0.06[ab]	0.05[b]	0.06[ab]	0.05[b]	0.002	0.046	0.008	0.021
T-CHO, mg/g prot	0.07	0.07	0.07	0.05	0.06	0.004	0.511	0.427	0.678
Glycogen, U/mg prot	19.15	15.94	14.60	9.42	19.88	1.471	0.092	0.636	0.144

GSP = grape seed proanthocyanidin; SEM = standard error of the mean; GLM = general linear model; TG = triglyceride; T-CHO = total cholesterol.
[a, b] Within a row, values with different superscript letters significantly differ ($P < 0.05$).
[1] $n = 6$ replicates per treatment.

antioxidants such as vitamin E, lycopene, resveratrol, etc., were reported to attenuate ROS-induced damage, delay fat oxidation, and maintain the stability of the meat color (Xu et al., 2018; Yu et al., 2021). The GSP's chemical structure contains multiple hydroxyl groups and conjugated double-bond structures, which allows them to effectively capture free radicals and stabilize their structure (Spranger et al., 2008). By activating the nuclear factor erythroid 2-related factor 2 (Nrf2) signaling pathway, which is associated with antioxidation, GSP has the potential to reduce oxidative damage (Xu et al., 2018). This study found that the inclusion of GSP led to a significant improvement in the pigs' antioxidative capacity, as indicated by the elevated serum CAT concentration achieved with a 30 mg/kg dosage. The CAT is an extensively studied enzyme that has a crucial function in safeguarding cells from the harmful impacts of peroxide of hydrogen (Kang et al., 2012). Moreover, serum levels of T-AOC and T-SOD also reached their peak at a GSP supplementation dosage of 30 mg/kg. T-SOD is a type of metal-containing enzyme that provides a vital function in the first defense against oxidative damage products during detoxification (Kumar et al., 2020). The findings were congruent with prior research on finishing pigs, in which an improved antioxidative capacity and an activated Nrf2 signaling pathway were both observed upon GSP supplementation (Feng et al., 2023). The GSP-elevated antioxidative capacity is consistent with improving meat quality, which is usually most visualized as improved meat color (Chen et al., 2018). In this research, the inclusion of GSP resulted in a notable rise in the redness ($a^*_{45\ min}$) of the longissimus thoracis, while reducing the yellowness ($b^*_{24\ h}$).

Moreover, we observed that the crude fat content and muscle shear force were significantly reduced when GSP supplementation was given at 60 and 120 mg/kg. Xu et al. (2022) also indicated that dietary 200 mg/kg grape seed proanthocyanidin extract (GSPE) decreased the shear force of longissimus thoracis, which is consistent with the results of this study. The results also suggested an anti-obesity property of the GSP. A lower fat content may result in looser connections between muscle fibers, which may affect the tenderness of pork (Shaw et al., 2008). This research shows that GSP did not change muscle amino acid composition, which aligns with the findings of recent research conducted on finishing pigs (Xu et al., 2022). In that study, adding 50, 100, or 200 mg/kg of GSPE to the diet had no effect on the total amino acids, total essential amino acids (EAA), sum of flavor amino acids, or the EAA/non-essential amino acids (NEAA) ratio in the longissimus dorsi muscle.

Muscle fiber type plays a critical role in determining meat characteristics such as color, texture, and flavor (Joo et al., 2013). Furthermore, the types of muscle fibers may impact the nutritional value and cooking characteristics (Lee et al., 2010). MyHC isoforms divide muscle fibers into four groups: oxidative (Type I and Type IIa), intermediate (Type IIx), and glycolytic (Type IIb) fibers (Mizunoya et al., 2013). This research found that the addition of GSP at dosages of 30 and 60 mg/kg maximized the levels of *MyHC I* expression. Previous studies indicated that oxidative fiber-rich

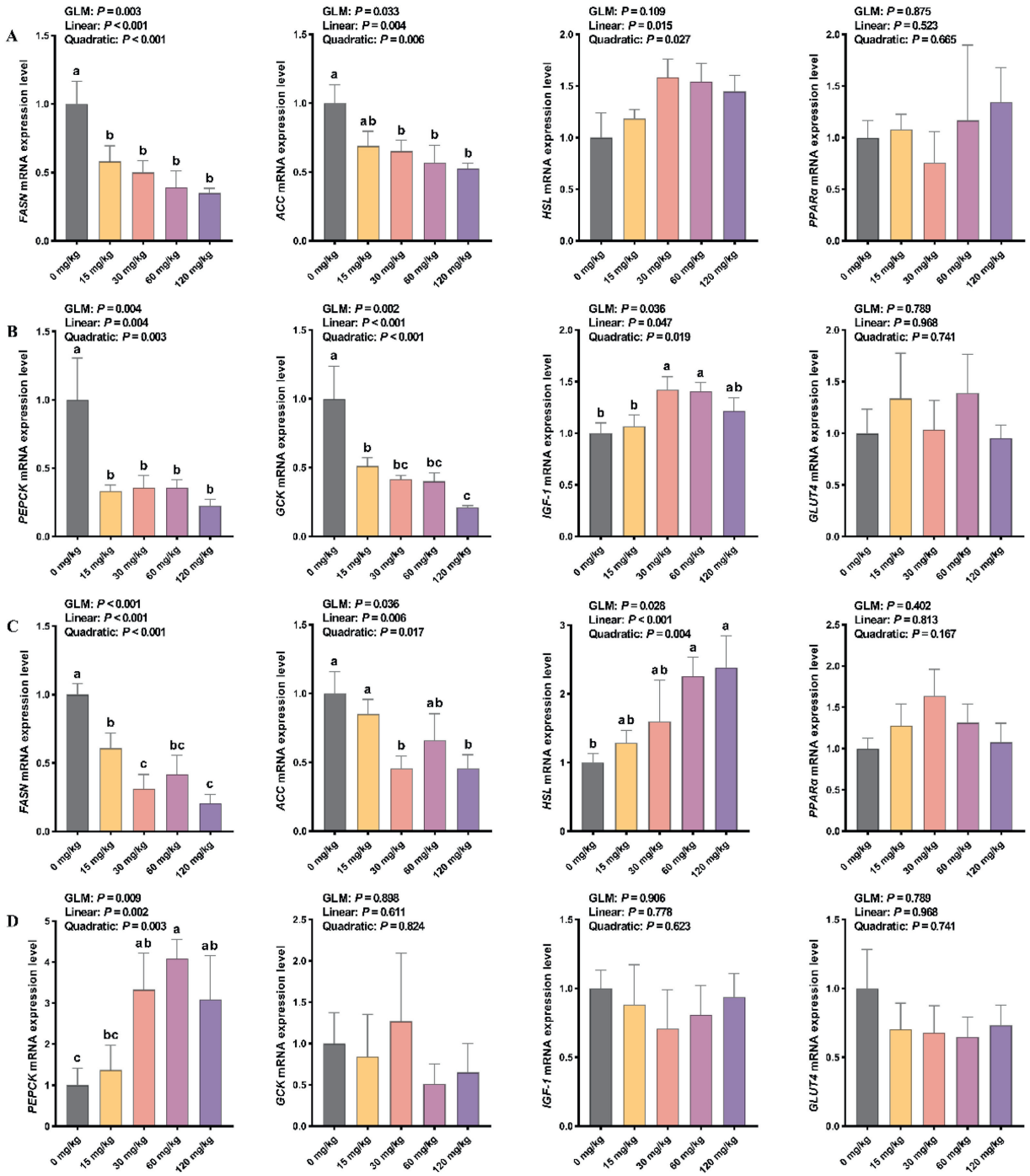

Fig. 2. Effect of GSP on expression levels of critical genes related to glucose-lipid metabolisms in longissimus thoracis (A, B) and liver (C, D). The X-axis labels show the dosage of GSP in the diet. GSP = grape seed proanthocyanidin; *FASN* = fatty acid synthase; *ACC* = acetyl CoA carboxylase; *HSL* = hormone-sensitive triglyceride lipase; *PPARα* = peroxisome proliferators-activated receptor α; *PEPCK* = phosphoenolpyruvate carboxykinase; *GCK* = glucokinase; *IGF-1* = insulin-like growth factor-1; *GLUT4* = glucose transporter 4; GLM = general linear model. $^{a\text{-}c}$ Different letters indicate significant differences ($P < 0.05$). Means ± standard error of the mean (SEM) ($n = 6$) are used to express the data.

muscle is red, contains more myoglobin, and tastes better (Kim et al., 2013; Zhang et al., 2019). The findings also align with the improvements in meat color and shear force upon GSP supplementation.

Importantly, we observed that GSP supplementation at 30 or 60 mg/kg reduced muscle TG and T-CHO levels to their minimum, while 30 mg/kg GSP minimized TG levels in the liver. The results align with an earlier study on finishing pigs, which suggested that GSP has the potential to decrease the accumulation of fat and regulate body glucose-lipid balance (Feng et al., 2023). This research demonstrated the inclusion of GSP caused the expression of *FASN*, *PEPCK*, and *GCK* in the muscle to decrease. The FASN is one of the key enzymes for fatty acid synthesis, which catalyzes the processes of fatty acid chain elongation, cyclic reactions of fatty acid synthesis, and release of acyl carriers (Lei et al., 2012), whereas, the PEPCK and GCK are key enzymes in the heterologous synthesis of glucose and the glycolytic pathway (Hu et al., 2010; Stark et al., 2014). Additionally, our findings indicate that *FASN* and *ACC* expression levels significantly decreased in response to GSP supplementation, while *HSL* expression levels increased in the liver. In

addition to its role as a crucial regulatory molecule in the process of fat storage, the ACC is accountable for the production of fatty acids from scratch (Goodwin and Taegtmeyer, 1999). The HSL serves as the enzyme that limits the rate of lipolysis, which is the process of breaking down triglycerides. It serves as the initial stage in the regulation of triglyceride decomposition (Fang et al., 2017). Both results suggested a reduction in lipid deposition in the muscle and liver.

This study shows that GSP improves feed efficiency, dressing percentage, meat color, and tenderness in growing-finishing pigs. The better feed efficiency and higher dressing percentage contribute to increased pork production (Bohrer et al., 2020), while meat quality is vital for consumer appeal (Pugliese et al., 2023). Since 30 mg/kg GSP supplementation showed beneficial effects on growth performance and meat quality, we can evaluate its economic benefits by comparing diet costs between the control and the 30 mg/kg GSP groups. Based on final weight and ADG data, pigs in the control group and the 30 mg/kg GSP group reached market weight on an average of 84.2 and 80.8 days, respectively, assuming a market weight of 110 kg. The ADFI data revealed that pigs in the 30 mg/kg GSP group consumed 10.7 kg less feed per pig to reach market weight compared to the control group. With the control diet costing $ 500.8/t and GSP priced at $ 25.00/kg (Faitury Bio-Tech Co., Ltd.), the average cost of the diet with 30 mg/kg GSP supplementation is $ 501.6/t. Therefore, the 30 mg/kg GSP treatment group saved $ 5.19 per pig in diet costs to reach market weight. Given that GSP supplementation also significantly improved dressing percentage and meat quality, it has the potential to reduce production costs and enhance economic efficiency in practical animal husbandry. However, further research is needed to validate its applicability in large-scale production systems.

5. Conclusion

In summary, dietary GSP supplementation not only increases the growth performance but also improves the carcass traits and meat quality of growing-finishing pigs. The improvement in meat quality by GSP is likely associated with improvements in serum antioxidant-related indicators, such as T-AOC, T-SOD, and CAT, and improvements in the distribution of muscle fiber types and glucose-lipid metabolisms. For commercial application, dietary supplementation of 30 and 60 mg/kg GSP may be optimal for the growing-finishing pigs. This study not only indicated a beneficial effect of GSP supplementation on pigs but also contributed to understanding the mechanisms behind the GSP-regulated biological functions such as the antioxidant activity and modulation of the metabolisms.

CRediT authorship contribution statement

Yuyang Zheng: Writing – original draft, Validation, Investigation, Formal analysis. **Yan Li:** Writing – review & editing, Visualization, Investigation, Data curation. **Bing Yu:** Visualization, Resources. **Yuheng Luo:** Supervision, Resources. **Zhingqing Huang:** Supervision, Resources. **Ping Zheng:** Supervision, Resources. **Xiangbing Mao:** Validation, Software. **Zhaolai Dai:** Software, Validation. **Jie Yu:** Validation, Software. **Hui Yan:** Supervision. **Junqiu Luo:** Formal analysis. **Jun He:** Supervision, Resources, Project administration, Methodology, Conceptualization.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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Appendix supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aninu.2024.10.006.

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