·综 述·

酚类化合物在猪脂肪沉积中的作用

王亚鑫，田学凯，杨公社，于太永*

西北农林科技大学动物科技学院 陕西省动物遗传育种与繁殖重点实验室 动物脂肪沉积与肌肉发育实验室，陕西 杨凌 712100

王亚鑫，田学凯，杨公社，于太永. 酚类化合物在猪脂肪沉积中的作用[J]. 生物工程学报, 2024, 40(5): 1486-1497.
WANG Yaxin, TIAN Xuekai, YANG Gongshe, YU Taiyong. The impact of phenolic compounds on pig fat deposition[J]. Chinese Journal of Biotechnology, 2024, 40(5): 1486-1497.

摘 要：脂肪沉积的数量和部位是影响猪肉品质的重要因素。近年来的研究表明，天然成分在降低皮下和内脏脂肪沉积、提高肌内脂肪沉积方面具有重要作用。并且，天然产物具有绿色、安全、无添加和无残留等优势。而从水果、蔬菜以及草本类植物中提取的酚类化合物是天然成分中的重要一员。本文对酚类化合物在猪脂肪沉积中的作用研究进行了综述，可为利用酚类化合物调控脂肪沉积，改善猪肉品质提供借鉴和参考。
关键词：酚类化合物；猪；脂肪沉积；肉品质

The impact of phenolic compounds on pig fat deposition

WANG Yaxin, TIAN Xuekai, YANG Gongshe, YU Taiyong*

Key Laboratory of Animal Genetics, Breeding and Reproduction of Shaanxi Province, Laboratory of Animal Fat Deposition and Muscle Development, College of Animal Science and Technology, Northwest A&F University, Yangling 712100, Shaanxi, China

Abstract: The quantity and distribution of fat deposits are crucial factors that impact the quality of pork. Recent studies have indicated that the utilization of natural ingredients plays a significant role in decreasing subcutaneous and visceral fat deposits, as well as enhancing intramuscular fat. Moreover, natural products possess several advantages including being environmentally friendly, safe, free of additives, and leaving no residue. Phenolic compounds derived from fruits, vegetables and herbs constitute of vital component of these natural ingredients. This article examines the influence of phenolic compounds on pig fat deposition, aiming to provide guidance on the utilization of such compounds to regulate fat deposition and

资助项目：国家重点研发计划(2021YFD1301205)
This work was supported by the National Key Research and Development Program of China (2021YFD1301205).
*Corresponding author. E-mail: yutaiyong310@nwsuaf.edu.cn
Received: 2023-07-07; Accepted: 2023-10-09; Published online: 2023-10-20

enhance pork quality.
Keywords: phenolic compounds; pig; fat deposition; meat quality

随着我国经济的发展和人民生活水平的提高，人们对肉品质的要求越来越高。而脂肪作为家畜育种中的重要经济性状，其在体内的分布比例是决定猪肉品质优劣的关键因素。脂肪是储存和供给能量的主要来源，脂肪组织可以对内脏器官起到支撑作用，皮下脂肪组织具有隔热保温的作用。脂肪细胞是由多能干细胞分化而来，经过增殖、分化最终形成成熟的脂肪细胞。脂肪细胞中脂滴过多则会导致脂肪沉积，猪体内皮下和内脏脂肪沉积过多不仅影响猪肉口感，还影响猪肉生产效率[1]。酚类化合物本质上是一种植物次生代谢产物[2]，是一类由羟基(−OH)直接与芳香烃基团结合而成的化合物，由植物和微生物产生。由于酚类化合物广泛存在于人类的食物中以及植物的叶、花、茎和皮中等，因此它们在人类健康和疾病中的作用被广泛研究。近年来，大量研究表明酚类化合物在调控猪脂肪沉积和改善肉品质上发挥了重要作用。本团队一直从事猪脂肪沉积的研究，如天然化合物和酚类化合物影响猪脂肪沉积等方面。本文对酚类化合物在猪脂肪沉积中的作用进行了综述，旨在进一步了解与猪脂肪沉积相关的酚类化合物的调控机制，为改良猪肉品质奠定理论基础。

1 脂肪组织发育调控

1.1 脂肪组织的分类

脂肪组织不仅是重要的能量贮库，还是保持内环境稳定及分泌激素和细胞因子的重要内分泌器官。根据脂肪在动物机体内的位置可以划分为皮下脂肪和内脏脂肪，其主要部位及功能如表 1 所示。

脂肪组织根据颜色、形态、代谢功能和基因表达模式分为 3 种截然不同的脂肪，即白色脂肪、棕色脂肪和米色脂肪[8]，其形态与功能见表 2。而大多数哺乳动物出生时都含有棕色脂肪组织，存在于胸部和肾脏周围。而猪却不同于其他哺乳动物，其体内不含棕色脂肪组织。

1.2 脂肪组织的形成过程

脂肪组织的形成是一个动态的过程，脂肪细胞在能量平衡中起着关键作用，通常被认为

表 1 两种脂肪组织在动物中的主要部位及功能
Table 1 The main parts and functions of two types of adipose tissues in animals

Adipose tissue	Main parts	Primary function	References
Subcutaneous fat	Subcutaneous abdomen, back and extremities	Participate in energy metabolism, thermoregulation, and store energy	[3-5]
Visceral fat	Mesenteric and peritoneal anterior and posterior	Closely associated with obesity-related diseases and secretory function	[6-7]

表 2 三种脂肪细胞在动物中的形态与功能
Table 2 The morphology and function of three types of adipocytes in animals

Adipocytes	UCP1 expression	Mitochondrial density	LD morphology	Primary function	References
White adipocytes	Negative	Low	Uni-locular	Energy storage, endocrine	[9]
Brown adipocytes	Positive	High	Multi-locular	Thermogenesis, endocrine	[10]
Beige adipocytes	Positive	Medium	Multi-locular	Thermogenesis, endocrine	[11]

由中胚层的多能干细胞逐步分化发育而来，其分化过程如图 1 所示。在细胞汇合后发生生长抑制，多能干细胞定向分化为脂肪母细胞，随后分化为前体脂肪细胞。生长抑制后，前体脂肪细胞继续分化，此时细胞开始出现脂滴。在分化过程中，细胞由成纤维样转变为圆形，前体脂肪细胞变化形成多室脂肪细胞，含有许多小脂滴。最后多室脂肪细胞随着脂类在细胞中的沉积，脂滴充满细胞的大部分，形成成熟的脂肪细胞[12-13]。

1.3 脂肪组织的沉积过程

脂肪沉积是一个动态平衡过程，主要包括脂肪的合成、分解和运输。这些过程主要发生在脂肪组织、肝脏和肌肉中[14]。在动物生长发育早期，一般以细胞增殖为主，后期则以细胞肥大为主。而猪脂肪细胞的生长主要依赖于细胞体积的增加，早期本团队杨公社教授等曾证实，脂肪型猪在 5 月龄时脂肪细胞数达到最高，瘦肉型猪在 8 月龄时脂肪细胞数目最高，脂肪型猪和瘦肉型猪在 5、6.5、8 月龄时细胞增殖的作用最小，而脂肪细胞的肥大占主导地位，且脂肪细胞的体积越大，脂肪沉积能力越强[15-17]。脂肪沉积是生猪生产中重要的经济考虑因素。猪体内脂肪沉积量过多会严重影响生产效率、质量和繁殖性能，同时也影响消费者对猪肉的选择。

1.4 脂肪组织生长发育的调控因子及机制

许多研究证明前体脂肪细胞在向脂肪细胞分化的过程中受多种激素、基因及转录因子的调控，最终形成成熟的脂肪细胞。研究证明许多转录因子(PPARs、C/EBPs、aP2、LPL 和 SREBP1 等)参与脂肪细胞的分化过程[18-20]。目前，已确定过氧化物酶体增殖物激活受体(peroxisome proliferator-activated receptorγ, PPARγ)、CCAAT/增强子结合蛋白(CCAAT/enhancer-binding proteins, C/EBP)是其分化与沉积中最重要的转录因子[21]。PPARγ 是脂肪细胞分化过程中被诱导的因子，早在 1994 年就被确定为脂肪细胞分化的主要调节因子，这些研究表明 PPARγ 被诱导并参与脂肪生成[22-23]；C/EBPs 属于亮氨酸拉链转录因子大家族，有 3 个成员：C/EBPα、C/EBPβ 和 C/EBPδ，在脂肪生成过程中，C/EBPβ 被早期诱导，然后反式激活 PPARγ 和 C/EBPα，它们协同诱导 C/EBPβ 表达产生成熟脂肪细胞表型的基因[24]。C/EBP 家族在脂肪细胞分化过程中都起着关键的调控作用，而 C/EBP 的激活是脂肪细胞分化过程中 PPARγ 最重要的下游效应之一[25]，PPARγ 和 C/EBP 之间的脂肪转录合作对于完全激活成熟脂肪细胞的编程至关重要[26-27]。它们直接或间接地调控脂肪细胞发育相关基因的表达[12]，在脂肪细胞分化过程中的复杂转录级联中起关键作用。

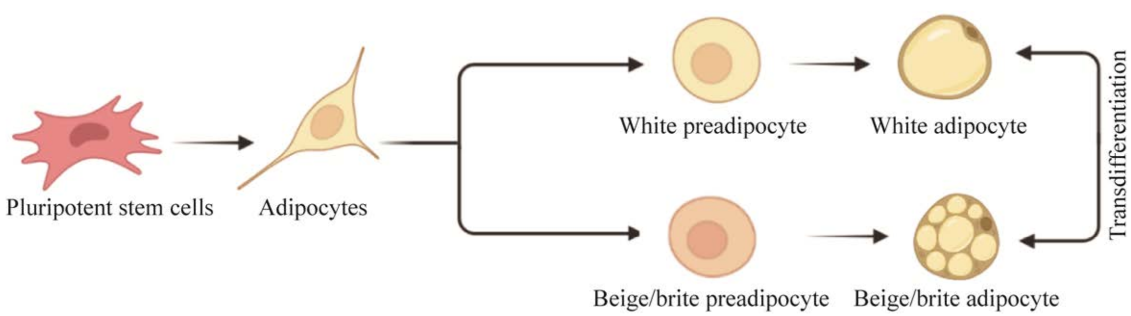

图 1 脂肪细胞分化过程

Figure 1 Adipocyte differentiation process.

2 酚类化合物

2.1 酚类化合物的分类

酚类化合物是以多羟基苯环为基本化学结构，并与多种活性官能团如羟基、羧基、甲氧基等相连[28]。根据多环芳烃核的数量以及与各官能团的结合方式,可以将酚类化合物分为 3 大类，包括多酚类、黄酮类和丹宁类[29-30]，图 2 列举了酚类化合物的分类、主要食物来源及常见酚类化合物的分子结构。

2.2 酚类化合物的生物活性

酚类化合物作为次生代谢物广泛分布于自然界的食物和植物中。抗氧化是酚类化合物最为重要的功能活性。脂肪沉积过程中会产生大量的活性氧，酚类化合物通过抑制活性氧，激活体内抗氧化酶系来抑制脂肪沉积[28,31-32]。同时，酚类化合物可以显著降低由高脂膳食引起的肥胖、血清甘油三酯、胆固醇、游离脂肪酸以及低密度脂蛋白与高密度脂蛋白的比值；并调节脂肪的合成、参与脂肪的分解，进而表现出减肥和降血脂的功效。而多酚类、黄酮类等酚类化合物可以有效降低由氧化应激所导致的一系列慢性疾病[33-34]，防止蛋白质的不良修饰和信号通路的异常激活[35-37]，对预防和治疗相

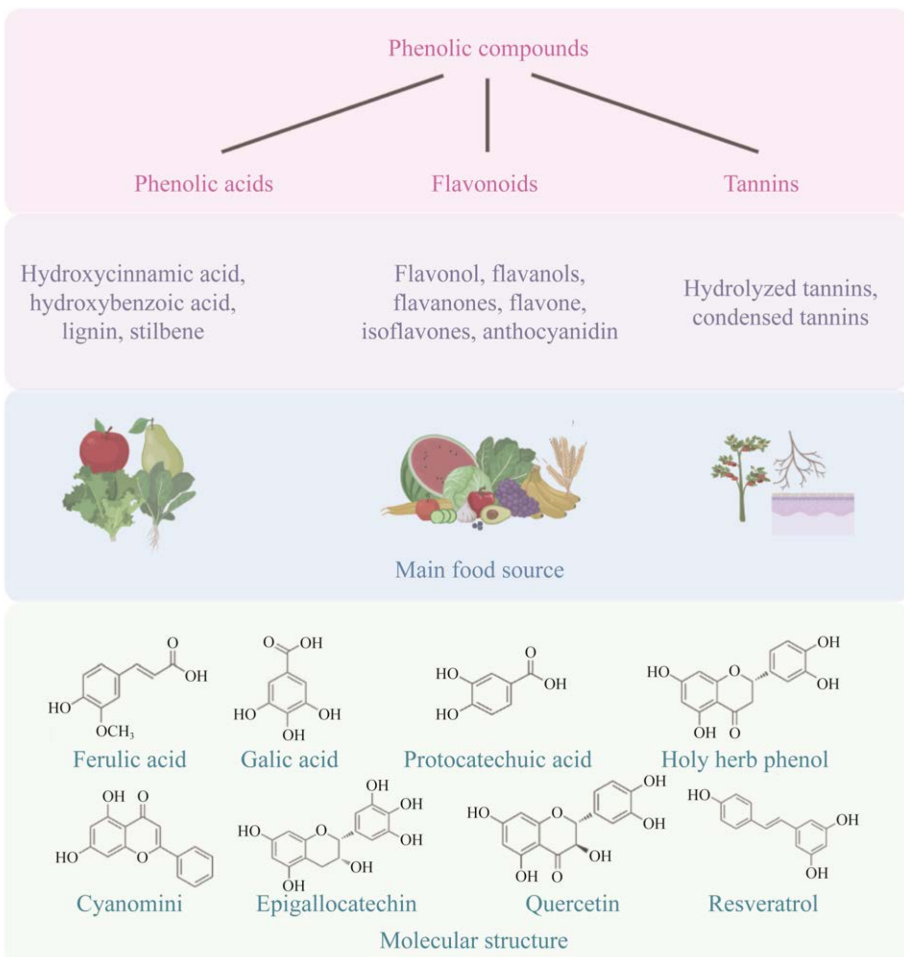

图 2 酚类化合物的分类及分子结构

Figure 2 Classification and molecular structure of phenolic compounds.

关疾病具有一定的效果。酚类化合物还能够通过清除自由基和活性羰基化合物、螯合金属离子、防止蛋白结构修饰等多种机制抑制高级糖化终末产物(advanced glycation end-products, AGEs)的生成[38-40]。大量研究表明，由于酚类化合物羟基取代的高反应性和其吞噬自由基的能力，使其具有抗衰老、抗氧化和抗菌等生物学功能，且来源安全性高，不会产生抗药性[41]。表 3 列举了一些酚类化合物的生物活性功能。

3 酚类化合物在猪脂肪沉积中的作用研究

3.1 酚类化合物调控猪脂肪细胞的增殖分化

近年来，越来越多研究表明酚类化合物可以抑制猪脂肪细胞的增殖分化，可能是这些酚类化合物下调了某些脂肪细胞转录因子(C/EBP, PPAR, ADD1/SREBP1)的 mRNA 表达量，上调某些脂解基因(*ATGL*, *HSL*, *PGC1α*)的 mRNA 表达量(图 3)，或通过某些信号通路来抑制脂肪细胞的分化，从而减少了脂肪在体内的积聚量，进一步揭示猪脂肪沉积的不同调控机制[52-53]。

多酚类化合物具有多个酚基团而得名，包括白藜芦醇、姜黄素等多酚类物质，具有抗氧化、抗炎、抗癌及心血管保护等作用。目前多酚类化合物调控猪脂肪细胞的增殖分化已在一些研究中被报道。Jiang 等[54]发现白藜芦醇可以通过 PPARα 和 C/EBPα 促进 LincRNA-ROFM 的表达，且 LincRNA-ROFM 可以结合 miR-133b，并被白藜芦醇上调，导致 AdipoQ 表达增强，从而揭示了白藜芦醇通过新的 LincRNA-ROFM/miR-133b/AdipoQ 通路抑制猪前体脂肪细胞的增殖和分化，减少猪的背膘厚度，为白藜芦醇通过调控 lncRNA 抑制脂肪沉积的下游机制提供了新的思路。而采用不同浓度的白藜芦醇进行处理，发现白藜芦醇能显著抑制猪前体脂肪细胞增殖和分化，且可以明显下调 *FoxO1* 基因和上调 *SOCS3* 基因的表达，揭示了白藜芦醇可能通过下调 *FoxO1* 基因和上调 *SOCS3* 基因的表达抑制脂肪细胞增殖分化，减少脂肪沉积[55]。而崔忆馨[52]采用不同浓度的姜黄素处理猪前体脂肪细胞，发现脂滴沉积量明显减少，且 PPARγ 和 C/EBPβ 的 mRNA 表达和 2 个重要合成酶 ACC 和 FAS 的 mRNA 表达显著下降，从而抑制猪前体脂肪细胞的增殖和成脂分化，降低脂肪沉积，为猪分子营养学调控脂肪沉积的潜在机制提供了新的见解。

表 3 酚类化合物的生物活性

Table 3 Biological activity of phenolic compounds

Phenolic compounds	Biological activity	References
Protocatechuic acid	Antioxidant, scavenges DPPH, ABTS, hydroxyl radicals and superoxide anions	[42]
Soy isoflavones	Lower cholesterol, blood pressure, blood sugar, anti-arteriosclerosis	[43]
Galic acid	Antioxidant, antibacterial, protect the liver, stop bleeding	[44]
Holy herb phenol	Antioxidant, anti-inflammatory, anticancer, neuroprotective, cardioprotective, anti-diabetic, anti-obesity	[45]
Resveratrol	Antioxidant, anti-inflammatory, improves insulin sensitivity	[46]
Proanthocyanidins	Antioxidants, free radical scavengers and lipid peroxidation inhibitors, hypoglycemia, hypolipidemia	[47]
Cyanomini	Antioxidant, antidiabetic, anti-inflammatory, anti-aging	[48]
Quercetin	Lower blood pressure, enhance capillary resistance, lower blood lipids, anti-aging	[49]
Epigallocatechin	Regulates blood lipid metabolism, anti-obesity, anti-atherosclerosis	[50]
Catechin	Reduce abdominal fat and serum triglyceride content	[51]

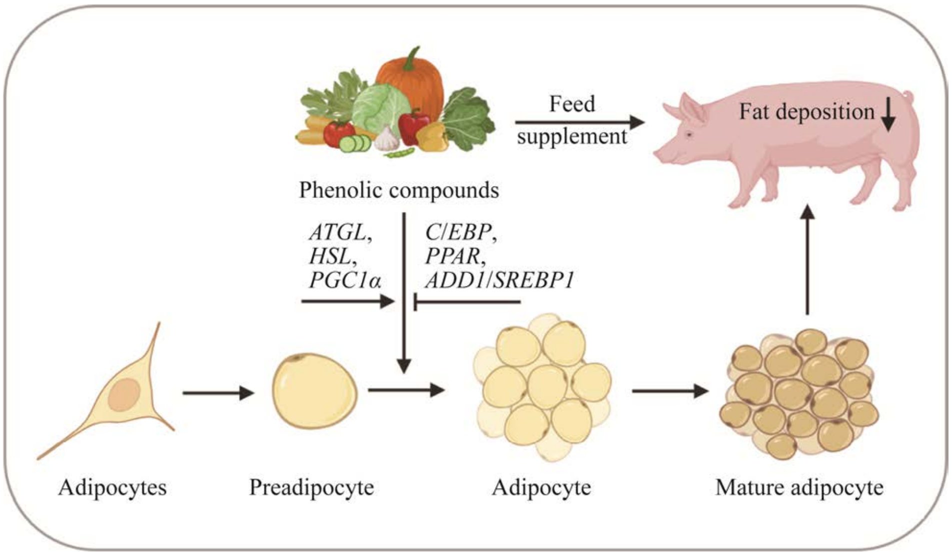

图 3　酚类化合物在猪脂肪沉积中的调控机制

Figure 3　Regulatory mechanism of phenolic compounds in pig fat deposition.

黄酮类化合物是一组具有不同酚类结构的天然物质，包括儿茶素、槲皮素、原花青素和香叶木素等，存在于水果、蔬菜、谷物、树皮、茶和葡萄酒中，具有抗氧化、抗炎以及调节关键细胞酶功能的能力。目前已有许多研究报道了黄酮类化合物在调控猪脂肪细胞增殖分化方面的作用。猪脂肪细胞的分化过程决定了猪的体脂沉积，吴睿帆[56]以猪原代前体脂肪细胞为研究对象，利用不同浓度的表没食子儿茶素没食子酸酯处理细胞，首次发现了表没食子儿茶素没食子酸酯通过靶向 FTO-m6A-YTHDF2 途径抑制 CDK2 和 CCNA2 蛋白和基因的表达，进而抑制细胞周期进程和脂肪细胞分化，为猪脂肪合理沉积的调控提供了有效的分子靶点。原花青素是一种生物类黄酮，由具有不同聚合度的儿茶素和/或表儿茶素组成[57]，Wei 等[58]采用原花青素处理猪原代前脂肪细胞，降低 PPARγ 和脂肪酸结合蛋白 4 (fatty acid-binding protein4, FABP4)的 mRNA 表达，抑制猪前体脂肪细胞分化，减少脂质堆积；同时在成熟脂肪细胞中原花青素可以降低脂质含量，提高激素敏感性脂肪酶(hormone-sensitive lipase, HSL)和脂肪甘油三酸酯脂肪酶(adipose triglyceride lipase, ATGL)等主要脂解转录因子的 mRNA 表达，表明原花青素可以抑制猪前脂肪细胞的分化和增殖并刺激成熟脂肪细胞的脂解。而利用不同浓度的原花青素处理梅山猪前脂肪细胞，发现原花青素能够抑制猪前体脂肪细胞增殖和分化，这种抑制作用可能是通过在前体脂肪细胞分化晚期，PPARγ 和 FABP4 表达下调以及 DLK1 表达上调实现的，从而为通过营养调控手段改善猪的脂肪沉积提供理论支持[53]。以上研究表明黄酮类化合物可以通过调控脂肪细胞转录因子、酶活性及靶向某些途径来抑制猪前体脂肪细胞的增殖分化，促进成熟脂肪细胞脂解，为调控猪脂肪沉积的分子机制提供新的思路和见解。

3.2　酚类化合物调控猪脂肪沉积

猪肉脂肪沉积是影响肉品质的关键因素。近年来，越来越多的研究表明酚类化合物在调

控猪脂肪沉积上发挥着重要作用。通过在猪的基础日粮中添加不同水平的酚类化合物，探究酚类化合物对育肥猪肉品质、抗氧化性能及脂肪沉积的影响。

多酚类化合物具有很强的抗氧化能力，存在于许多天然植物、水果和茶叶中，可以作为生产优质猪肉的潜在功能性饲料添加剂。没食子酸是自然界中最常见的多酚类物质，没食子酸能通过调节机体抗氧化酶活性和能量代谢，或通过影响肠道微生物，在预防或调节机体脂质代谢紊乱中发挥重要作用。研究表明，在育肥猪日粮中添加没食子酸可以显著增加猪皮下脂肪中脂解相关基因和蛋白(ATGL, HSL, PGC1α)的表达，降低脂合成相关基因和蛋白(PPARγ, ACC, LPL)的表达，同时能显著降低肝脏中脂质沉积，并显著提高超氧化物歧化酶(superoxide dismutase, SOD)蛋白表达和抗氧化酶 SOD、过氧化氢酶(catalase, CAT)的活性，从而可以提高育肥猪的抗氧化能力并增强脂质运输和代谢能力，减少育肥猪皮下脂肪生成[59]。白藜芦醇是一种具有多种生物功能的植物多酚类物质，在猪模型中评估白藜芦醇的降脂作用和作用机理，研究发现白藜芦醇通过降低 *PPARγ* 和脂肪酸合酶(fatty acid synthase, FAS) mRNA 的水平及脂蛋白脂肪酶(lipoprotein lipase, LPL)的活性，提高 *HSL*、*ATGL* 和肉碱棕榈酰转移酶-1 (carnitine palmitoyltransferase-1, CPT-1) mRNA 水平来改善血脂水平，减少体内脂肪沉积[60]。而以‘杜长大’为研究对象，饲喂不同浓度的白藜芦醇，可以上调脂解基因 *HSL*、*ATGL*，脂肪酸氧化代谢关键基因 *LPL*、*CPT1*，下调脂肪合成关键基因 *ACC*，并可以通过激活 AdiopQ-AdipoR1-AMPKα-PGC-1α 和 AdiopQ-AdipoR2-PPARα 两条信号通路调控下游脂肪代谢基因的表达，促进脂肪分解、抑制脂肪合成、减少机体脂肪沉积[61]。证明在猪日粮中添加多酚类化合物，可以减少猪皮下和内脏脂肪沉积，改善肉品质。

黄酮类化合物主要存在于茶、水果、蔬菜中，这些富含黄酮类化合物的物质也可以作为饲料添加剂加入到猪基础日粮中。绿茶中富含表没食子儿茶素没食子酸酯和儿茶素等黄酮类化合物，在育肥猪日粮中添加绿茶副产品，可以显著降低肉的粗蛋白和脂肪含量并改善肉品质[62]；且可以显著降低背膘厚度及血浆胆固醇的含量，减少脂肪沉积，提高肉品质[63]。而在日粮中添加茶预混料，脂肪内甘油三酯及胆固醇含量下降，并能显著降低与脂肪消化和吸收相关酶类基因的表达水平，降低脂肪沉积[64]。同时，绿原酸(chlorogenic acid, CGA)是一种存在于植物中的天然多酚，具有抗炎、抗氧化和代谢调节功能，在‘杜洛克×长白×约克夏’ (DLY)猪日粮中添加绿原酸，可以增加脂肪生成基因 *ACC1* mRNA 水平，降低 NT5C2 的表达水平；且降低肌肉中丙二醛(malondialdehyde, MDA)含量，增加谷胱甘肽过氧化物酶(glutathione peroxidase, GSH-Px)含量以及抗氧化基因(*HO-1*, *NQO-1*, *NRF2*) mRNA 水平，从而降低脂肪沉积、改善肉品质[65]。在日粮中加入不同浓度的肉桂醛，可以显著降低背膘厚度、剪切力，并增加 GSH-Px 含量,降低 MDA 含量和超氧化物歧化酶(superoxide dismutase, SOD)酶活性，从而改善肉品质[66]。本团队肖子通[67]以地方猪品种关中黑猪为实验对象，在基础日粮中添加葡萄渣，可以增强猪肉的抗氧化能力，并提高 *LPL* 的 mRNA 表达水平,在一定程度上降低脂质积累。本团队通过在饲料中添加香叶木素(diosmetin)饲喂育肥猪，屠宰后发现 diosmetin 可以显著降低胴体脂肪含量和背膘厚，从而改善猪胴体性状和肉品质[68]，为后期改善猪肉品质提供了理论基础和科学依据。这些研究表明天然植物也可

以作为新型饲料添加剂，从而降低脂肪沉积，改善肉品质。

而在猪的基础日粮中添加不同水平的酚类化合物，酚类化合物对降低脂肪沉积和改善肉品质肉质都有直接或间接的作用。有机酸和精油(1.7%麝香草酚和 1.0%香兰素)的微囊化复合物是一种微囊化饲料添加剂，添加在基础日粮中，屠宰后发现在 0.2%的水平可以改善肉的红色值，并减少断奶到育肥猪约 30%的滴水损失，改善肉品质[69]。富含多酚的黑果野樱桃渣是果汁生产的副产品，是一种有益健康的天然抗氧化剂，在断奶仔猪日粮中添加不同浓度的黑果野樱桃渣，屠宰后发现滴水损失显著减少，且猪肝脏和血清中 GSH-Px 水平增加，从而在一定程度上提升肉品质[70]。此外，0.2%水平的牛至(origanum vulgare)精油可以改善猪肉的氧化稳定性[71]。而将发酵的苹果渣饲喂给肥育猪会提高饲料利用率，提高了背部脂肪亚油酸、亚麻酸和花生酸的水平，从而影响肉质和背部脂肪的脂肪酸组成[72]。

4 展望

猪脂肪沉积与猪肉品质密切相关，酚类化合物是一种理想的调控脂肪沉积、改善肉品质的物质。许多天然植物中均含有酚类化合物，通过饲料添加剂的方式加入基础日粮中，可以有效降低猪皮下脂肪的沉积，改善肉品质。但这些结果仍然具有不一致和不完整性，需要更多的研究来证明酚类化合物在降低脂肪沉积方面的效果。而并非所有酚类化合物都一定是有益的，它们的生理作用取决于一系列因素，且应根据特定的动物物种考虑选择酚类化合物以及最佳补充水平。酚类物质的作用因不同来源、植物成分、成熟程度、剂量、提取方法、环境或饮食模式、代谢、宿主物种和化合物的生物利用度而异[73]；且酚类化合物降低猪脂质沉积的潜在机制尚不明确，相信随着研究的不断深入，人们对酚类化合物在动物脂肪沉积，特别是猪脂肪沉积调控中的作用机制将更加清晰。本综述总结了使用酚类化合物作为潜在的天然饲料添加剂对改善猪肉品质的作用，为今后酚类化合物在畜禽生产中作为饲料添加剂来提高畜禽生产性能和改善肉品质提供借鉴和参考。

REFERENCES

[1] GU T, SHI JS, LUO LH, LI ZC, ZHENG EQ, CAI GY, HONG LJ, WU ZF. Comparison of carcass traits, meat quality, and chemical composition of tissues from progeny derived from cloned and noncloned pigs[J]. Cellular Reprogramming, 2019, 21(6): 296-300.

[2] KAUFFMANN AC, CASTRO VS. Phenolic compounds in bacterial inactivation: a perspective from Brazil[J]. Antibiotics (Basel, Switzerland), 2023, 12(4): 645.

[3] STINKENS R, GOOSSENS GH, JOCKEN JWE, BLAAK EE. Targeting fatty acid metabolism to improve glucose metabolism[J]. Obesity Reviews, 2015, 16(9): 715-757.

[4] ROSEN ED, SPIEGELMAN BM. What we talk about when we talk about fat[J]. Cell, 2014, 156(1/2): 20-44.

[5] WANG LH, GU H, LIAO TC, LEI YH, QIU YH, CHEN QY, CHEN L, ZHANG SH, WANG JY, HAO XX, JIANG DM, ZHAO Y, NIU LL, LI XW, SHEN LY, GAN ML, ZHU L. tsRNA landscape and potential function network in subcutaneous and visceral pig adipose tissue[J]. Genes, 2023, 14(4): 782.

[6] TCHERNOF A, DESPRÉS JP. Pathophysiology of human visceral obesity: an update[J]. Physiological Reviews, 2013, 93(1): 359-404.

[7] ABRAHAM TM, PEDLEY A, MASSARO JM, HOFFMANN U, FOX CS. Association between visceral and subcutaneous adipose depots and incident cardiovascular disease risk factors[J]. Circulation, 2015, 132(17): 1639-1647.

[8] XUE SW, LEE D, BERRY DC. Thermogenic adipose tissue in energy regulation and metabolic health[J]. Frontiers in Endocrinology, 2023, 14: 1150059.

[9] VLAVCHESKI F, TSAKIRIDIS N, GIACCA A, TSIANI E. 1507-P: carnosic acid-induced browning in

3T3-L1 adipocytes is dependent on AMPK activation[J]. Diabetes, 2023, 72(supplement_1): 1507-P.

[10] NICHOLLS DG, BRAND MD. A critical assessment of the role of creatine in brown adipose tissue thermogenesis[J]. Nature Metabolism, 2023, 5(1): 21-28.

[11] JIA M, XU TC, XU YJ, LIU YF. Dietary fatty acids activate or deactivate brown and beige fat[J]. Life Sciences, 2023, 330: 121978.

[12] 罗肖. Wnt/β-catenin信号通路在猪脂肪组织发育过程中的调控作用[D]. 杨凌: 西北农林科技大学硕士学位论文, 2008.
LUO X. Regulation of Wnt/β-catenin signaling pathway in the development of porcine adipose tissue[D]. Yangling: Master's Thesis of Northwest A&F University, 2008 (in Chinese).

[13] SHIN MC, JUNG YH, JEONG Y, OH AR, LEE SB, KIM K. Kctd17-mediated chop degradation promotes adipogenic differentiation[J]. Biochemical and Biophysical Research Communications, 2023, 653: 126-132.

[14] XING K, LIU HT, ZHANG FX, LIU YB, SHI Y, DING XD, WANG CD. Identification of key genes affecting porcine fat deposition based on co-expression network analysis of weighted genes[J]. Journal of Animal Science and Biotechnology, 2021, 12(1): 100.

[15] 孙金梅, 路兴中, 杨公社, 唐文花. 不同经济类型猪种脂肪细胞的发育及其脂肪合成能力的比较研究[J]. 畜牧兽医学报, 2000, 31(2): 131-136.
SUN JM, LU XZ, YANG GS, TANG WH. The comparison research on the development of adipocyte and its lipid synthesis from different economical pigs[J]. Acta Veterinaria et Zootechnica Sinica, 2000, 31(2): 131-136 (in Chinese).

[16] 杨公社, 邱怀, 路兴中. 猪体脂肪形成的细胞学和形态学研究[J]. 西北农业大学学报, 1997(1): 8-14.
YANG GS, QIU H, LU XZ. Cytological and morphological studies on adipose development in swine[J]. Acta Universitatis Agriculturae Boreali-Occidentalis, 1997(1): 8-14 (in Chinese).

[17] 杨公社, 邱怀, 路兴中. 关中黑猪与长白猪脂肪形成的细胞学和组织化学比较研究[J]. 畜牧兽医学报, 1996, 27(1): 25-31.
YANG GS, QIU H, LU XZ. Cellula and histochemical comparative siudies for development of adipose tissue between Guanzhong black and Landrace pigs[J]. Acta Veterinaria et Zootechnica Sinica, 1996, 27(1): 25-31 (in Chinese).

[18] LEE EO, JOO HK, LEE YR, KIM S, LEE KH, LEE SD, JEON BH. APE1/ref-1 inhibits adipogenic transcription factors during adipocyte differentiation in 3T3-L1 cells[J]. International Journal of Molecular Sciences, 2023, 24(4): 3251.

[19] LI A, LI YY, WANG YL, WANG Y, LI X, QUBI WQ, XIONG Y, ZHU JJ, LIU W, LIN YQ. ACADL promotes the differentiation of goat intramuscular adipocytes[J]. Animals, 2023, 13(2): 281.

[20] NAKANO T, SASAKI Y, NORIKURA T, HOSOKAWA Y, KASANO M, MATSUI-YUASA I, HUANG XD, KOBAYASHI Y, KOJIMA-YUASA A. The suppression of the differentiation of adipocytes with *Mallotus furetianus* is regulated through the posttranslational modifications of C/EBPβ[J]. Food Science & Nutrition, 2023: FSN3-2023.

[21] 吴小敏, 张双翔, 朱二鹏, 许厚强, 赵佳福, 程振涛, 代兴红, 陈秀华, 袁超. LncRNA NONSUST004358.1在猪脂肪细胞分化中的作用研究[J]. 中国畜牧杂志, 2022, 58(9): 172-178.
WU XM, ZHANG SX, ZHU EP, XU HQ, ZHAO JF, CHENG ZT, DAI XH, CHEN XH, YUAN C. Study on the role of LncRNA NONSUST004358.1 in the differentiation of porcine adipocytes[J]. Chinese Journal of Animal Science, 2022, 58(9): 172-178 (in Chinese).

[22] WANG ZL, LI YL, WU LL, GUO Y, YANG GS, LI X, SHI XE. Rosiglitazone-induced PPARγ activation promotes intramuscular adipocyte adipogenesis of pig[J]. Animal Biotechnology, 2023: 1-10.

[23] CAO YQ, CHEN YY, MIAO K, ZHANG SY, DENG FC, ZHU M, WANG C, GU W, HUANG YX, SHAO ZJ, DONG XY, GONG YF, PENG H, YANG H, WAN Y, JIA XD, TANG S. PPARγ as a potential target for adipogenesis induced by fine particulate matter in 3T3-L1 preadipocytes[J]. Environmental Science & Technology, 2023, 57(20): 7684-7697.

[24] YAN H, LI Q, LI MY, ZOU XQ, BAI NN, YU ZC, ZHANG J, ZHANG D, ZHANG Q, WANG JM, JIA H, WU YJ, HOU ZY. Ajuba functions as a co-activator of C/EBPβ to induce expression of PPARγ and C/EBPα during adipogenesis[J]. Molecular and Cellular Endocrinology, 2022, 539: 111485.

[25] GHABEN AL, SCHERER PE. Adipogenesis and metabolic health[J]. Nature Reviews Molecular Cell Biology, 2019, 20(4): 242-258.

[26] LEE JE, SCHMIDT H, LAI BB, GE K. Transcriptional

and epigenomic regulation of adipogenesis[J]. Molecular and Cellular Biology, 2019, 39(11): e00601-e00618.
[27] REN DL, COLLINGWOOD TN, REBAR EJ, WOLFFE AP, CAMP HS. PPARγ knockdown by engineered transcription factors: exogenous PPARγ2 but not PPARγ1 reactivates adipogenesis[J]. Genes & Development, 2002, 16(1): 27-32.
[28] MORENO-QUIROGA G, ALBA-JIMÉNEZ JE, AQUINO-BOLAÑOS EN, CHÁVEZ-SERVIA JL. Phenolic compounds and antioxidant activity in *Cucurbita ficifolia* fruits, an underrated fruit[J]. Frontiers in Nutrition, 2023, 9: 1029826.
[29] SILVA A, SILVA V, IGREJAS G, AIRES A, FALCO V, VALENTÃO P, POETA P. Phenolic compounds classification and their distribution in winemaking by-products[J]. European Food Research and Technology, 2023, 249(2): 207-239.
[30] NACZK M, SHAHIDI F. Phenolics in cereals, fruits and vegetables: occurrence, extraction and analysis[J]. Journal of Pharmaceutical and Biomedical Analysis, 2006, 41(5): 1523-1542.
[31] YANG XQ, WANG WB, JIANG Q, XIE SD, ZHAO P, LIU Z, ZHU GL, XU JM, WANG JY, LI YH. Subcritical water extraction of phenolic compounds from *Vaccinium dunalianum* wight leaves and their antioxidant and tyrosinase inhibitory activities *in vitro*[J]. Chemistry & Biodiversity, 2023, 20(5): e202201099.
[32] YANG J, SIDDIQUI MK, HUSSAIN M, MANZOOR S, HUSSAIN N, SADDIQUE Z. QSPR analysis of some phenolic compounds present in *Moringa oleifera*[J]. Polycyclic Aromatic Compounds, 2023: 1-18.
[33] FERREIRA AR, de SOUSA DP. Chemistry and antifungal activity of homoisoflavonoids[J]. Journal of Chemistry, 2023, 2023: 1-7.
[34] CHEN YF, XIA GB, WANG CF, WU HW, XU XG, MAO GX, WU J, ZHAO ZL. Impact of dietary plant flavonoids on 7,8-dihydroxyflavone transepithelial transport in human intestinal Caco-2 cells[J]. Food Science & Nutrition, 2023: FSN3-2023.
[35] SEUNG-HONG L, SUNG-MYUNG K, SEOK-CHUN K, MIN-CHEOLl K, YOU-JIN J. Octaphlorethol A, a novel phenolic compound isolated from *Ishige foliacea*, protects against streptozotocin-induced pancreatic β cell damage by reducing oxidative stress and apoptosis[J]. Food and Chemical Toxicology, 2013, 59: 643-649.
[36] CHI-HAO W, CHI-TAI Y, GOW-CHIN Y. Epigallocatechin gallate (EGCG) binds to low-density lipoproteins (LDL) and protects them from oxidation and glycation under high-glucose conditions mimicking diabetes[J]. Food Chemistry, 2010, 121(3): 639-644.
[37] MARCELA A VAZQUEZ-PRIETO, AHMED B, FAWAZ GH, CESAR GF, PATRICIA IO. (−)-epicatechin prevents TNFα-induced activation of signaling cascades involved in inflammation and insulin sensitivity in 3T3-L1 adipocytes[J]. Archives of Biochemistry and Biophysics, 2012, 527(2): 113-118.
[38] LU A, YUAN SM, XIAO H, YANG DS, AI ZQ, LI QY, ZHAO Y, CHEN ZZ, WU XM. QSAR study of phenolic compounds and their anti-DPPH radical activity by discriminant analysis[J]. Scientific Reports, 2022, 12: 7860.
[39] SADEGHI M, MIROLIAEI M, KAMYABIAMINEH A, TASLIMI P, GHANADIAN M. The impact of AGEs on human health and the development of their inhibitors based on natural compounds[J]. Arabian Journal of Chemistry, 2023, 16(10): 105143.
[40] DUDYLINA AL, IVANOVA MV, SHUMAEV KB, RUUGE EK. Superoxide formation in cardiac mitochondria and effect of phenolic antioxidants[J]. Cell Biochemistry and Biophysics, 2019, 77(1): 99-107.
[41] OYENIHI AB, SMITH C. Are polyphenol antioxidants at the root of medicinal plant anti-cancer success?[J]. Journal of Ethnopharmacology, 2019, 229: 54-72.
[42] DAI J, MUMPER RJ. Plant phenolics: extraction, analysis and their antioxidant and anticancer properties[J]. Molecules (Basel, Switzerland), 2010, 15(10): 7313-7352.
[43] YAMAGATA K, YAMORI Y. Potential effects of soy isoflavones on the prevention of metabolic syndrome[J]. Molecules (Basel, Switzerland), 2021, 26(19): 5863.
[44] HUANG BQ, ZHANG ZG, DING NS, WANG BL, ZHANG GG, FEI P. Investigation of the pectin grafting with gallic acid and propyl gallate and their antioxidant activities, antibacterial activities and fresh keeping performance[J]. International Journal of Biological Macromolecules, 2021, 190: 343-350.
[45] ISLAM A, ISLAM MS, RAHMAN MK, UDDIN MN, AKANDA MR. The pharmacological and biological roles of eriodictyol[J]. Archives of Pharmacal Research,

2020, 43(6): 582-592.

[46] MÉNDEZ-DEL VILLAR M, GONZÁLEZ-ORTIZ M, MARTÍNEZ-ABUNDIS E, PÉREZ-RUBIO KG, LIZÁRRAGA-VALDEZ R. Effect of resveratrol administration on metabolic syndrome, insulin sensitivity, and insulin secretion[J]. Metabolic Syndrome and Related Disorders, 2014, 12(10): 497-501.

[47] RAUF A, IMRAN M, ABU-IZNEID T, IAHTISHAM-UL-HAQ, PATEL S, PAN XD, NAZ S, SILVA AS, SAEED F, SULERIA HAR. Proanthocyanidins: a comprehensive review[J]. Biomedicine & Pharmacotherapy, 2019, 116: 108999.

[48] SAMINI M, FARKHONDEH T, AZIMI-NEZHAD M, SAMARGHANDIAN S. Chrysin's impact on oxidative and inflammation damages in the liver of aged male rats[J]. Endocrine, Metabolic & Immune Disorders-Drug Targets, 2021, 21(4): 743-748.

[49] EGERT S, BOSY-WESTPHAL A, SEIBERL J, KÜRBITZ C, SETTLER U, PLACHTA-DANIELZIK S, WAGNER AE, FRANK J, SCHREZENMEIR J, RIMBACH G, WOLFFRAM S, MÜLLER MJ. Quercetin reduces systolic blood pressure and plasma oxidised low-density lipoprotein concentrations in overweight subjects with a high-cardiovascular disease risk phenotype: a double-blinded, placebo-controlled cross-over study[J]. British Journal of Nutrition, 2009, 102(7): 1065-1074.

[50] SUZUKI T, PERVIN M, GOTO S, ISEMURA M, NAKAMURA Y. Beneficial effects of tea and the green tea catechin epigallocatechin-3-gallate on obesity[J]. Molecules, 2016, 21(10): 1305.

[51] MAKI KC, REEVES MS, FARMER M, YASUNAGA K, MATSUO N, KATSURAGI Y, KOMIKADO M, TOKIMITSU I, WILDER D, JONES F, BLUMBERG JB, CARTWRIGHT Y. Green tea catechin consumption enhances exercise-induced abdominal fat loss in overweight and obese adults[J]. The Journal of Nutrition, 2009, 139(2): 264-270.

[52] 崔忆馨. 姜黄素对猪和小鼠前体脂肪细胞增殖和成脂分化的作用研究[D]. 扬州: 扬州大学硕士学位论文, 2019.
CUI YX. Study on the effect of curcumin on proliferation and adipogenic differentiation of porcine and mouse precursor adipocytes[D]. Yangzhou: Master's Thesis of Yangzhou University, 2019 (in Chinese).

[53] 郑月英. 原花青素对猪前体脂肪细胞增殖与分化影响的研究[D]. 南京: 南京农业大学硕士学位论文, 2017.
ZHENG YY. Study on the effect of proanthocyanidins on the proliferation and differentiation of porcine precursor adipocytes[D]. Nanjing: Master's Thesis of Nanjing Agricultural University, 2017 (in Chinese).

[54] JIANG Q, ZHANG SB, GAO XT, HU Y, ZHANG Y, SHEN YJ, JIANG YH, HUANG YN. Resveratrol inhibits proliferation and differentiation of porcine preadipocytes by a novel LincRNA-ROFM/miR-133b/AdipoQ pathway[J]. Foods, 2022, 11(17): 2690.

[55] 刘延杰. 猪 *FoxO1* 和 *SOCS3* 基因的表达规律及白藜芦醇对其表达调控的影响[D]. 杭州: 浙江大学硕士学位论文, 2007.
LIU YJ. Expression of *FoxO1* and *SOCS3* genes in pigs and the effect of resveratrol on their expression regulation[D]. Hangzhou: Master's Thesis of Zhejiang University, 2007 (in Chinese).

[56] 吴睿帆. FTO 对猪前体脂肪细胞成脂分化的影响及调控机制研究[D]. 浙江: 浙江大学博士学位论文, 2020.
WU RF. Effect and regulatory mechanism of FTO on adipogenic differentiation of porcine precursor adipocytes[D]. Zhejiang: Doctoral Dissertation of Zhejiang University, 2020 (in Chinese).

[57] TUBA E, VICTOR W, PETER W. Isolation of dimeric, trimeric, tetrameric and pentameric procyanidins from unroasted cocoa beans (*Theobroma cacao* L.) using countercurrent chromatography[J]. Food Chemistry, 2015, 179: 278-289.

[58] WEI SJ, ZHENG YY, ZHANG MM, ZHENG H, YAN PS. Grape seed procyanidin extract inhibits adipogenesis and stimulates lipolysis of porcine adipocytes *in vitro*[J]. Journal of Animal Science, 2018, 96(7): 2753-2762.

[59] 陈玲玲. 没食子酸对猪肉品质及脂肪沉积能力的影响[D]. 杨凌: 西北农林科技大学硕士学位论文, 2021.
CHEN LL. Effects of gallic acid on pork quality and fat deposition capacity[D]. Yangling: Master's Thesis of Northwest A&F University, 2021 (in Chinese).

[60] ZHANG C, LUO JQ, YU B, CHEN JQ, CHEN DW. Effects of resveratrol on lipid metabolism in muscle and adipose tissues: a reevaluation in a pig model[J]. Journal of Functional Foods, 2015, 14: 590-595.

[61] 崔悦悦. 白藜芦醇通过脂联素信号通路调节猪脂肪沉积的机制研究[D]. 广西: 广西大学硕士学位论文, 2019.

CUI YY. Study on the mechanism by which resveratrol regulates fat deposition in pigs through adiponectin signaling pathway[D]. Guangxi: Master's Thesis of Guangxi University, 2019 (in Chinese).

[62] KO SY, BAE IH, YEE ST, LEE SS, UUGANBAYAR D, OH JI, YANG CJ. Comparison of the effect of green tea by-product and green tea probiotics on the growth performance, meat quality, and immune response of finishing pigs[J]. Asian-Australasian Journal of Animal Sciences, 2008, 21(10): 1486-1494.

[63] OANH NC, THU CTT, HONG NT, GIANG NTP, HORNICK JL, DANG PK. Growth performance, meat quality, and blood characteristics of finisher crossbred pigs fed diets supplemented with different levels of green tea (*Camellia sinensis*) by-products[J]. Veterinary World, 2023: 27-34.

[64] 王桂云. 茶预混料对育肥猪生产性能及脂肪沉积的影响[D]. 安徽: 安徽农业大学硕士学位论文, 2017.
WANG GY. Effect of tea premix on production performance and fat deposition of fattening pigs[D]. Anhui: Master Thesis of Anhui Agricultural University, 2017 (in Chinese).

[65] XIE KH, SUN YX, DENG LL, YU B, LUO YH, HUANG ZQ, MAO XB, YU J, ZHENG P, YAN H, LI Y, LI H, HE J. Effects of dietary chlorogenic acid supplementation on growth performance, meat quality, and muscle flavor substances in finishing pigs[J]. Foods, 2023, 12(16): 3047.

[66] LUO Q, LI N, ZHENG Z, CHEN LL, MU SQ, CHEN L, LIU Z, YAN J, SUN C. Dietary cinnamaldehyde supplementation improves the growth performance, oxidative stability, immune function, and meat quality in finishing pigs[J]. Livestock Science, 2020, 240: 104221.

[67] 肖子通. 葡萄渣替代麦麸对育肥猪生长发育和肉品质的影响[D]. 杨凌: 西北农林科技大学硕士学位论文, 2022.
XIAO ZT. Effect of grape residue replacing wheat bran on growth and meat quality of finishing pigs[D]. Yangling: Master's Thesis of Northwest A&F University, 2022 (in Chinese).

[68] 谢宝财. Diosmetin 在脂肪沉积中的作用及机制研究[D]. 杨凌: 西北农林科技大学博士学位论文, 2021.
XIE BC. Study on the role and mechanism of diosmetin in fat deposition[D]. Yangling: Doctoral Dissertation of Northwest A&F University 2021 (in Chinese).

[69] OH HJ, KIM IH, SONG MH, KWAK WG, YUN W, LEE JH, LEE CH, OH SY, LIU SD, AN JS, KIM HB, CHO JH. Effects of microencapsulated complex of organic acids and essential oils on growth performance, nutrient retention, blood profiles, fecal microflora, and lean meat percentage in weaning to finishing pigs[J]. Canadian Journal of Animal Science, 2019, 99(1): 41-49.

[70] LIU XZ, JU Y, BAO N, LUO YL, HUANG LL, CAO NX, LIU MZ, BO JN, ZHANG S, YAN Y. Effects of polyphenol-rich *Aronia melanocarpa* pomace feeding on growth performance, biochemical profile, and meat quality in pigs at weaned and finishing stages[J]. Livestock Science, 2021, 252: 104674.

[71] FORTE C, RANUCCI D, BEGHELLI D, BRANCIARI R, ACUTI G, TODINI L, CAVALLUCCI C, TRABALZA-MARINUCCI M. Dietary integration with oregano (*Origanum vulgare* L.) essential oil improves growth rate and oxidative status in outdoor-reared, but not indoor-reared, pigs[J]. Journal of Animal Physiology and Animal Nutrition, 2017, 101(5): e352-e361.

[72] FANG JC, CAO Y, MATSUZAKI M, SUZUKI H, KIMURA H. Effects of apple pomace-mixed silage on growth performance and meat quality in finishing pigs[J]. Animal Science Journal, 2016, 87(12): 1516-1521.

[73] MAHFUZ S, SHANG QH, PIAO XS. Phenolic compounds as natural feed additives in poultry and swine diets: a review[J]. Journal of Animal Science and Biotechnology, 2021, 12(1): 1-18.

(本文责编 郝丽芳)