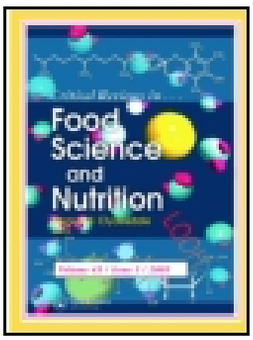

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The regulatory role of dietary factors in skeletal muscle development, regeneration and function

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REVIEW

The regulatory role of dietary factors in skeletal muscle development, regeneration and function

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ABSTRACT

Skeletal muscle plays a crucial role in motor function, respiration, and whole-body energy homeostasis. How to regulate the development and function of skeletal muscle has become a hot research topic for improving lifestyle and extending life span. Numerous transcription factors and nutritional factors have been clarified are closely associated with the regulation of skeletal muscle development, regeneration and function. In this article, the roles of different dietary factors including green tea, quercetin, curcumin (CUR), eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and resveratrol (RES) in regulating skeletal muscle development, muscle mass, muscle function, and muscle recovery have been summarized and discussed. We also reviewed the potential regulatory molecular mechanism of these factors. Based on the current findings, dietary factors may be used as a potential therapeutic agent to treat skeletal muscle dysfunction as well as its related diseases.

KEYWORDS

Dietary factor; curcumin; DHA; EGCG; EPA; quercetin; regeneration; resveratrol; skeletal muscle; disease

Introduction

Skeletal muscle is the largest motor organ in human body, which accounts for about 40% of body mass (Janssen et al. 2000). Skeletal muscle plays a key role in physical activities of human life, such as motor function, energy homeostasis, and respiration (Iizuka, Machida, and Hirafuji 2014). Besides, skeletal muscle also has the ability to secrete a number of myokines as a paracrine and endocrine organ (Giudice and Taylor 2017), such as the interleukin 6 (IL-6) (Steensberg et al. 2000), IL-8, IL-15 (Pedersen 2009), brain-derived neurotrophic factor (BDNF) (Pedersen et al. 2009), leukemia inhibitory factor (LIF) (Broholm et al. 2008) and Irisin (Bostrom et al. 2012). Thus, the development and function of skeletal muscle play essential roles in maintaining normal life activity and metabolism.

Skeletal muscle is composed of multinucleated myofibers that are formed through activation and fusion of muscle stem cells also called satellite cells (SCs). During myogenesis, SCs undergo proliferation, differentiation and fusion (Bentzinger, Wang, and Rudnicki 2012). After muscle injury, skeletal muscle has a strong capacity to regenerate and repair the damaged muscle. During regeneration, quiescent SCs are activated to repair the injured muscle and maintain muscle stem cells pool. Thus, muscle SCs are responsible for the postnatal skeletal muscle growth and maintenance. The development and regeneration of skeletal muscle, as well as the cell fates and functions of muscle SCs, have been found to be regulated by a number of signaling molecules (Yue et al. 2017) and various myogenic transcription factors, such as paired box 7 (Pax7) (Olguin et al. 2007), myogenic differentiation (MyoD) (Buckingham and Rigby 2014), myogenin (MyoG) (Comai and Tajbakhsh 2014), myostatin (MSTN) (Pedersen and Febbraio 2012), myomaker (Millay et al. 2013) and myomixer (also called myomerger or minion) (Bi et al. 2017; Chen et al. 2020).

Many studies have demonstrated that diets and/or nutrients can regulate the cell fates of SCs and modulate muscle development and recovery (Dort et al. 2012; Farup et al. 2014; Owens et al. 2015). Dietary factors (also known as nutritional factors) are taken from the external environment and extracted from foods, drinks and plants which are beneficial for maintaining the growth, development and survival of life activities and processes. In this article, we mainly review and discuss recent research progress and the current discoveries of dietary factors, including foods, chemicals and plant extracts and their effects on skeletal muscle development, regeneration, and function, as well as their molecular mechanism. Our review provides some available information for regulating skeletal muscle development, regeneration and dysfunction, as well as the treatment of muscle-related diseases by nutritional measures.

Regulatory role of dietary factors in skeletal muscle

Green tea

Green tea is one of the most popular drinks in Asian countries. It contains a class of polyphenolic flavonoids known as catechins, which consists of four major epicatechin

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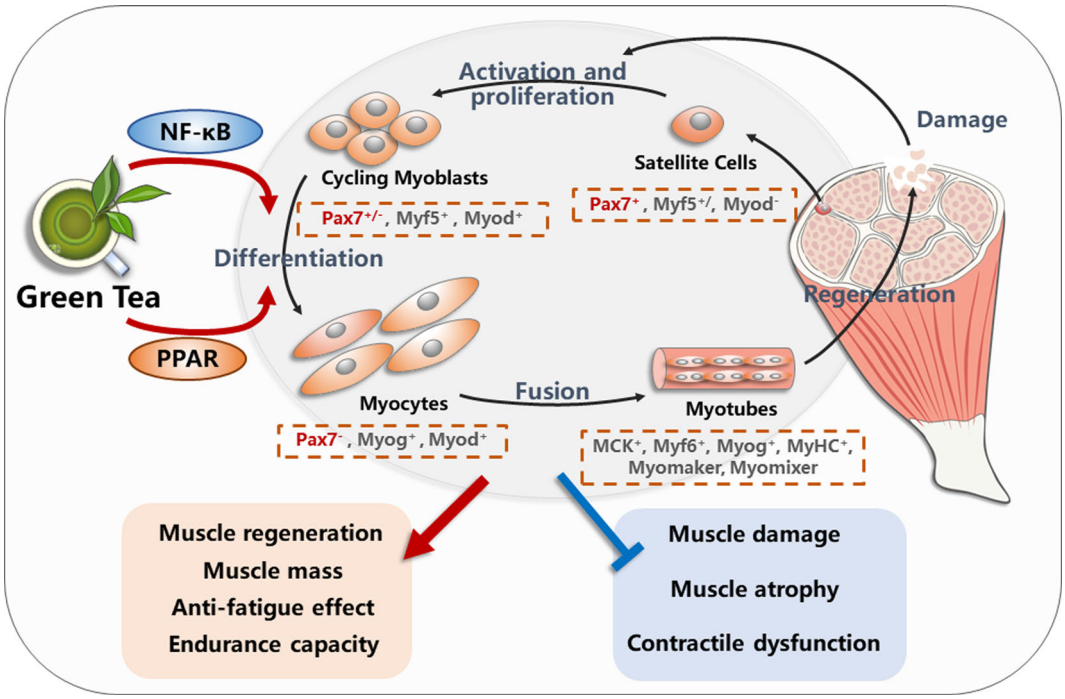

Figure 1. The role and regulatory mechanism of green tea in skeletal muscle development, regeneration and function. NF-κB, nuclear factor-κB; PPAR, peroxisome proliferator-activated differentiation; Pax 7, paired box 7; MyoD, myogenic differentiation; MyoG, myogenin; MCK, muscle creatine kinase; MyhC, myosin heavy chain.

derivatives: (−)-epicatechin (EC), (−)-epicatechin gallate (ECG), (−)-epigallocatechin (EGC), and (−)-epigallocatechin-3- gallate (EGCG). Green tea has many beneficial properties such as antioxidant, anti-cancer, anti-mutagenic, anti-diabetic, anti-inflammatory, and anti-obesity (Cabrera, Artacho, and Gimenez 2006; Kafeshani et al. 2017; Mozaffari-Khosravi, Ahadi, and Barzegar 2013; Ueda-Wakagi et al. 2019; Zhong et al. 2011). Recently, it is reported that green tea extracts (GTEs) can affect myogenesis, skeletal muscle function and regeneration (Figure 1).

It has been shown that ECG and EGCG could activate satellite cells by the induction of Myf5 transcription factors, ECG also promotes myogenic differentiation through the activation of myogenic markers such as MyoG and muscle creatine kinase (MCK) in satellite and C2C12 myoblast cells, and EGCG significantly increases muscle fiber size for regeneration (Kim, Kim, Byun, Hwang, Park, Oh, Kim, Kim, Byun, Hwang, Park, Oh, Jeong, et al. 2017). Tea catechins supplementation combined with exercise have a beneficial effect on walking ability, muscle mass and muscle strength in elderly Japanese sarcopenic women (Kim, Suzuki, et al. 2013). Besides, ingestion of tea catechins can significantly inhibit contractile dysfunction in skeletal muscle and muscle atrophy (loss of skeletal muscle mass) in unloaded murine soleus muscle (Ota et al. 2011). And GTEs can improve endurance capacity via increasing oxidation capacity, metabolic capacity and utilization of fatty acid during exercise in mice (Murase et al. 2005; Murase et al. 2006; Tsai et al. 2017). GTEs can ameliorate high-fat diet-induced muscle atrophy in senescence-accelerated prone-8 mice, which is related to insulin resistance and is accompanied by a change in serum leukocyte cell-derived chemotaxin 2 (LECT2) (Onishi et al. 2018). Similarly, a study has reported that EGCG could prolong exhaustive swimming time and has an anti-fatigue effect including decreasing the levels of blood lactic acid, serum urea nitrogen, serum creatine kinase and malondialdehyde (Teng and Wu 2017). In addition, green tea extract supplementation has positive effects on skeletal muscle recovery after exercise, ameliorating muscle damage and promoting regeneration. GTEs supplementation can reduce the marker of muscle damage after strenuous exercise (da Silva et al. 2018), promote cell survival and against citrinin- induced skeletal myotube damage in C2C12 cells (Sharath Babu et al. 2017). However, Hadi et al. found that GTEs had no effect on muscle damage in athletes (Hadi et al. 2017). Moreover, catechins can enhance skeletal muscle performance, including regulating mitochondria biogenesis, glucose level, and lipids metabolism in muscle cells (Li et al. 2020). A 3-day EGCG- supplementation could decrease postprandial plasma glycerol and interstitial lactate concentration in skeletal muscle (Most et al. 2015). However, Pence et al. found that long-term supplementation with EGCG and β-alanine decreased mortality but did not have an effect on muscle function in aged mice (Pence et al. 2017).

Mechanically, EGCG can stimulate myogenic differentiation through activating TAZ, a transcriptional co-activator with a PDZ-binding motif (Kim, Kim, Byun, Hwang, Park, Oh, Jeong, et al. 2017). EC supplementation can attenuate skeletal muscle deterioration in aged mice through activating peroxisome proliferator-activated receptor (PPAR) pathway (Figure 1). And a diet containing EGCG can regulate gene expression including PPAR-γ coactivator-1α (PGC-1α) and silent information regulator of transcription 1 (sirtuin1, *Sirt1*), insulin-like growth factor 1 (*Igf1*), and macrophage marker CD11b (*Itgam*) in the gastrocnemius of skeletal

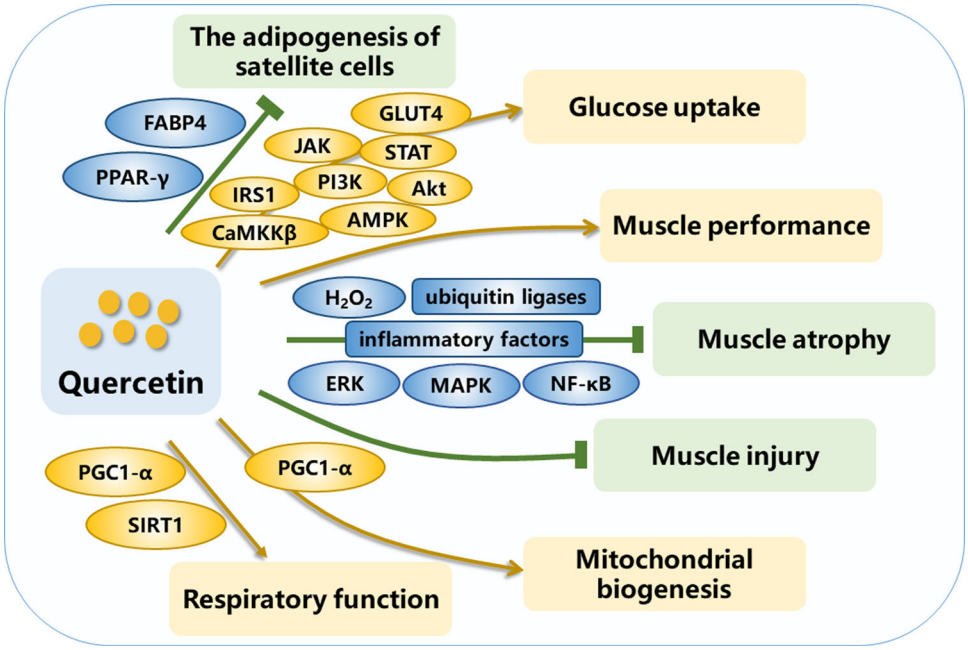

Figure 2. The regulatory role of quercetin in skeletal muscle. FABP4, fatty acid binding protein 4; CaMKKβ, Ca^{2+}/calmodulin- dependent kinase kinaseβ; AMPK, adenosine monophosphate-activated protein kinase; IRS1, insulin receptor substrate 1; PI3K, phosphoinositide 3-kinase; Akt, protein kinase B; JAK, Janus kinase; STAT, signal transducers and transcriptional activators; GLUT4, glucose transporter type 4; H2O2, hydrogen peroxide; ERK, extracellular signal-regulated kinase; MAPK, p38 mitogen-activated protein kinase; PGC-1α, PPAR-γ coactivator-1α; SIRT1, silent information regulator of transcription 1.

muscle in aged mice (Pence et al. 2016). Furthermore, GTEs supplementation can decrease dystrophic muscle pathology potentially via regulating the nuclear factor-κB (NF-κB) pathway in regenerating muscle fibers (Evans et al. 2010) (Figure 1). Similarly, long-term intake of catechins can reduce the muscle damage caused by downhill running and accelerate the physical recovery of mice by inhibiting the oxidative stress and inflammatory response of muscles (Haramizu et al. 2013). These findings suggest that GTEs can not only affect muscle development and function but also prevent, mitigate and even treat muscle-related disorders caused by aging and diseases.

Quercetin

Quercetin (3,3′,4′,5,7-pentahydroxy flavone) is an abundant polyphenolic flavonoid ubiquitously present in fruits and vegetables, such as onions, garlic, cabbages, leeks, blueberries, apples, tea, and red wine (Manach et al. 2004). Quercetin has been considered as a potential therapeutic agent for various diseases because of its bioactive effects, such as antioxidant, anti-inflammatory, anti-cancer and anti-obesity properties (Arias et al. 2017; Boots et al. 2011; Harwood et al. 2007; Liu et al. 2017). Importantly, recent studies have discovered that quercetin has prominent effects on skeletal muscle, including affecting the adipogenesis of muscle satellite cells, muscle mass, muscle atrophy, muscle injury and mitochondrial function (Figure 2).

It has been shown that quercetin can inhibit the adipogenesis of muscle satellite cells in vitro (Funakoshi et al. 2018) and increase insulin action in L6 myotubes (Anhe et al. 2012). The acute ingestion of quercetin may enhance muscle performance during and after a resistance training session (Patrizio et al. 2018). However, Casuso et al found that quercetin supplementations during exercise decreased mitochondrial DNA (mtDNA) content and citrate synthase (CS) activity and had a negative effect on exercise-induced muscle adaptations (Casuso et al. 2014). Quercetin can limit the loss of muscle mass (Francaux and Deldicque 2018) and prevent trichostatin A (TSA)-induced muscle wasting in tumor-bearing mice (Chan et al. 2018). In addition, long-term quercetin dietary enrichment may decrease disease-related muscle injury in *mdx* mice and protect skeletal muscle from damage (Hollinger et al. 2015; Spaulding, Ballmann, Quindry, and Selsby et al. 2016). Similarly, quercetin supplementation can mitigate eccentric exercise-induced muscle damage including myofibrillar disruption and sarcolemmal action potential propagation impairment (Bazzucchi et al. 2019) and protect rat skeletal muscle from ischemia reperfusion injury (Ekinci Akdemir et al. 2016). Besides, quercetin could promote mitochondrial biogenesis, protect respiratory function and activate Ca^{2+} release channel (CRC) of sarcoplasmic reticulum in skeletal muscle (Islam, Hood, and Gurd 2020; Lee, Meissner, and Kim 2002; Selsby et al. 2016).

At the molecular level, quercetin inhibits the adipogenesis of muscle satellite cells via suppressing the transcription of adipogenic markers, such as PPAR-γ and fatty acid binding protein 4 (FABP4) (Funakoshi et al. 2018). Quercetin can promote glucose uptake and via increasing glucose transporter type 4 (GLUT4) translocation by activating different signaling pathways, including Ca^{2+}/calmodulin-dependent kinase kinase β (CaMKKβ)/adenosine monophosphate-activated protein kinase (AMPK), insulin receptor substrate 1 (IRS1)/phosphoinositide 3-kinase (PI3K)/protein kinase B (Akt) and Janus kinase (JAK)/signal transducers and transcriptional activators (STAT) pathway (H. Jiang, Yamashita,

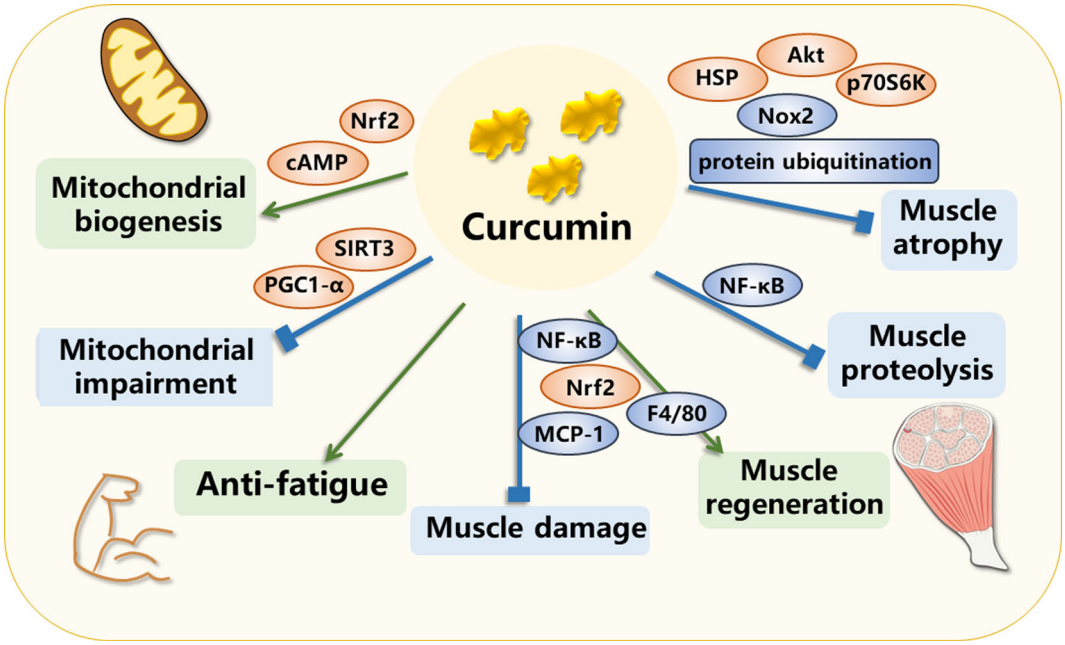

Figure 3. The regulatory role of curcumin in skeletal muscle. Nrf2, nuclear factor (erythroid-derived 2)-like 2; HSP, heat shock proteins; Nox2, NADPH oxidase-2; MCP-1, monocyte chemoattractant protein-1.

et al. 2019) (Figure 2). Several studies demonstrated that quercetin could prevent muscle atrophy through protecting mitochondria from decreasing biogenesis and reducing mitochondrial hydrogen peroxide (H_2O_2) release, attenuating the expression of ubiquitin ligases and inhibiting inflammatory receptors and their signaling pathway such as extracellular signal-regulated kinase (ERK), p38 mitogen-activated protein kinase (MAPK), and NF-κB in denervated mice (Mukai et al. 2016), as well as in tail-suspension mice (Mukai et al. 2010) and obesity-induced skeletal muscle (Le et al. 2014) (Figure 2). Similarly, quercetin can increase mitochondrial DNA and messenger RNA levels and promote skeletal muscle mitochondrial biogenesis through PGC-1α pathway (Islam, Hood, and Gurd 2020; Nieman et al. 2010). And Selsby et al. found that in dystrophin-deficient mice, oral quercetin administration transiently protected respiratory function by sustaining elevated SIRT1 activity and downstream PGC-1α signaling (Selsby et al. 2016). These studies clarify that quercetin plays an important role in skeletal muscle development and may mediate muscle damage protection.

Curcumin

Curcumin (CUR) is a natural phenolic compound extracted from the herb turmeric (*Curcuma longa* L.). CUR has been widely used to treat numerous diseases due to its various biological activities, such as anti-inflammatory (Kondamudi et al. 2015; Kong, Sudirman, Lin, and Chen 2019; Shahid et al. 2019), antioxidant (Al-Rubaei, Mohammad, and Ali 2014; Khan et al. 2019; Takahashi et al. 2014), antimicrobial (Guran et al. 2019; Moghadamtousi et al. 2014; Mun et al. 2013), anti-cancer (Devassy, Nwachukwu, and Jones 2015; Kasi et al. 2016; Koroth et al. 2019) and anti-diabetes (Javidi et al. 2019; Pivari et al. 2019; Soetikno et al. 2013) properties. In addition, more and more studies have found that CUR has various beneficial effects on skeletal muscle (Figure 3).

A study reported that consumption of CUR coupled with reduced food intake could ameliorate skeletal muscle biochemical and functional responses in aged male rats (Receno et al. 2019). It also has shown that CUR is able to alleviate skeletal muscle atrophy and ameliorate the NF-κB-dependent skeletal muscle proteolysis in rat (He, Xie, and Wu 2016). Meanwhile, CUR supplementation may improve exercise performance and prevent fatigue in mice (W. C. Huang et al. 2015). And multiple studies have shown that the supplement or ingestion of CUR before and after exercise could attenuate muscle damage, facilitate faster recovery and muscle regeneration (Delecroix et al. 2017; Tanabe et al. 2019; Tanabe et al. 2015). In addition, CUR could promote mitochondrial biogenesis and reduce mitochondrial impairment in skeletal muscle (Ray Hamidie et al. 2015; Zhang et al. 2017).

CUR can increase the abundance of heat shock proteins (e.g., HSP70) and anabolic signaling pathway (Akt phosphorylation, p70S6K phosphorylation), while decrease NADPH oxidase-2 (Nox2) (Lawler et al. 2019) and inhibit proteins ubiquitination following prevent skeletal muscle atrophy (Ono et al. 2015) (Figure 3). A previous study suggested that after traumatic injury, CUR could regulate myogenesis, modulate NF-κB activity and stimulate skeletal muscle regeneration (Thaloor et al. 1999). In an in vivo model, CUR has the potential to prevent muscle damage through activating the NF-κB and nuclear factor (erythroid-derived 2)-like 2 (Nrf2) pathways (Sahin et al. 2016) (Figure 3). However, CUR treatment ameliorates hindlimb injury following ischemic surgery via inhibiting the NF-κB pathways, which implies that CUR could be used for peripheral arterial disease (PAD) treatment (Y. Liu et al. 2016) (Figure

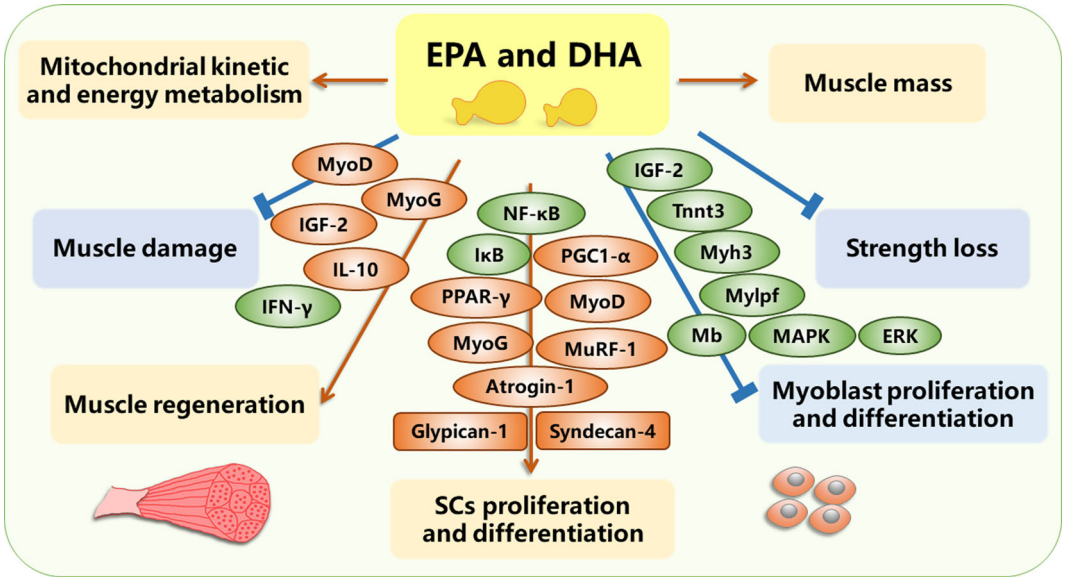

Figure 4. EPA and DHA regulate SCs fates and skeletal muscle regeneration and function. IGF-2, insulin-like growth factor-2; IL-10, interleukin-10; IFN-γ, interferon-γ; IκB, inhibitor-κB; MuRF-1, muscle RING-finger protein-1; Tnnt3, troponin T3; Myh3, myosin heavy polypeptide 3; Mylpf, myosin light chain phosphorylatable fast skeletal muscle; Mb, myoglobin.

3). Furthermore, Kawanishi et al demonstrated that CUR significantly attenuated monocyte chemoattractant protein-1 (MCP)-1 and F4/80 mRNA expression levels and reduced oxidative stress following downhill running-induced muscle damage (Kawanishi et al. 2013) (Figure 3). Besides, the combination of CUR treatment and endurance training can accelerate mitochondrial biogenesis in skeletal muscle via increasing cAMP levels (Ray Hamidie et al. 2015). In a high-fat-diet mouse model, CUR effectively ameliorates oxidative stress and attenuates mitochondrial fraction in skeletal muscle by activating Nrf2 function which is a novel mechanism for its effect on enhancing glucose intolerance (He et al. 2012). Additionally, Zhang et al. discovered that CUR attenuated skeletal muscle mitochondrial impairment in chronic obstructive pulmonary disease (COPD) rats by up-regulating the PGC-1α/SIRT3 signaling pathway (Zhang et al. 2017) (Figure 3). The above-mentioned results elucidate that CUR can affect mitochondrial function, muscle atrophy, muscle wasting, muscle damage and regeneration in skeletal muscle and it may be used as a medicine to treat muscle-derived diseases.

Eicosapentaenoic acid and docosahexaenoic acid

Eicosapentaenoic acid (EPA; 20:5 n-3) and docosahexaenoic acid (DHA; 22:6 n-3) belong to omega-3 polyunsaturated fatty acids (n-3 PUFAs), which are mainly contained in fish oil supplements. Previous studies have shown that n-3 PUFAs have plenty of biological activities, such as anti-inflammatory, improving cardiac function and blood, anti-cancer, anti-diabetes, improving depression and cognitive, and so on (Brown et al. 2019; Calder 2003, 2015; F et al. 2019; Flachs, Rossmeisl, and Kopecky 2014; Group et al. 2018; Johnson et al. 2008; Manson et al. 2019; Natto et al. 2019; Tomdio, Ritchie, and Miller 2019; Yang et al. 2019). Recently, many researchers have investigated that EPA and DHA are effective in skeletal muscle growth and regeneration (Figure 4).

There are numerous studies confirmed that EDA and DHA could affect SCs and myoblast proliferation and differentiation (Bhullar, Putman, and Mazurak 2016; Peng et al. 2012; J. Zhang, Xu, et al. 2019). Besides, EDA and DHA can increase muscle strength and mass under wasting condition (Ochi and Tsuchiya 2018) and attenuate strength loss after exercise (Tachtsis, Camera, and Lacham-Kaplan 2018; Tsuchiya et al. 2016). Meanwhile, several studies have reported that EDA can improve the regenerative capacity of skeletal muscle and prevent skeletal muscle from damage (Carvalho et al. 2013; Saini et al. 2017). Furthermore, EPA and DHA supplements can increase the capacity for mitochondrial reactive oxygen species emission and alter respiration kinetics in human skeletal muscle (Herbst et al. 2014). A study found that incubation of human myotubes with EPA increased processes of fatty acid turnover and oxidation in human skeletal muscle, which implied EPA may activate futile substrate cycling of fatty acids and influence body energy metabolism (Lovsletten et al. 2018).

It has shown that both EPA and DHA can regulate SCs proliferation and differentiation in skeletal muscle, including affecting inflammatory pathways (NF-κB, inhibitor-κB (IκB) phosphorylation, PPAR-γ and PGC-1α), affecting glucocorticoid-induced muscle degradation (MyoD, myogenin, atrogin-1, and muscle RING-finger protein-1 (MuRF-1)) and affecting proteoglycans needed for myogenesis (syndecan-4 and glypican-1) (Bhullar, Putman, and Mazurak 2016) (Figure 4). Besides, EPA and DHA down-regulate the expression of muscle-related genes such as IGF-2, troponin T3 (Tnnt3), myoglobin (Mb), myosin light chain phosphorylatable fast skeletal muscle (Mylpf), myosin heavy polypeptide 3 (Myh3) (Zhang, Xu, et al. 2019) and MAPK/ERK pathway (Peng et al. 2012) accordingly exert an inhibitory effect on myoblast proliferation and differentiation (Figure

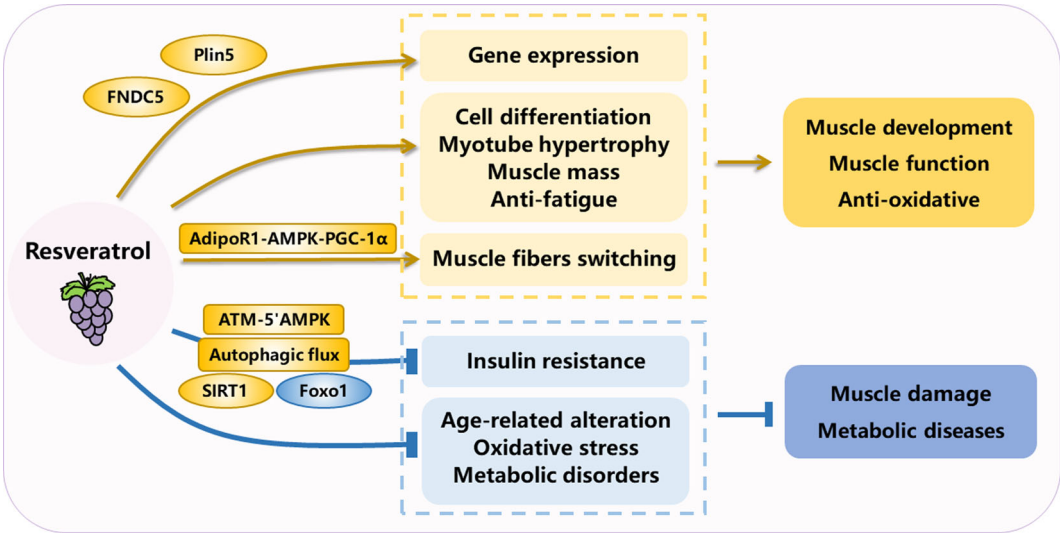

Figure 5. The role of resveratrol in regulating skeletal muscle development and metabolism. ROS, reactive oxygen species; ATM, ataxia telangiectasia mutated; AdipoR1, adiponectin receptor1; Plin5, Perilipin 5; FNDC5, fibronectin type III domain containing-5.

4). Similarly, Magee et al. discovered that EPA has a protective action against the damaging effects of tumor necrosis factor-α (TNF-α) during murine skeletal muscle cell differentiation (Magee, Pearson, and Allen 2008). EPA supplements can increase gene expression of myogenic factors like MyoD, MyoG and IGF-2 and enhance myotube formation thereby partially rescue mouse skeletal muscle cell differentiation under lipotoxic plus cytotoxic conditions (Saini et al. 2017). Moreover, de Carvalho et al. found that EPA could increase IL-10, reduce interferon-γ (IFN-γ) expression and promote a shift from the M1 to M2 macrophage phenotype following protect against muscle damage in the *mdx* mouse model of Duchenne muscular dystrophy (DMD) (Carvalho et al. 2013). These data highlight the active effects of EDA and DHA on maintaining and improving the skeletal muscle growth and regenerative capacity.

Resveratrol

Resveratrol (3, 5, 4′-trihydroxystilbene, RES), is a natural polyphenol and extracted from grape seed, polygonum cuspidatum, peanut and other plants. Previous studies have shown that RES has multiple therapeutic effects on several diseases, including cancer (Aggarwal et al. 2004; Han et al. 2015; Rauf et al. 2018), cardiovascular diseases (Hung et al. 2000; Penumathsa and Maulik 2009; Xia et al. 2017), neurological diseases (Jardim et al. 2018; Wang et al. 2002; Zhang et al. 2010), diabetes (Ozturk et al. 2017; Yazgan et al. 2015), and so on. It has been reported that RES plays a vital role in the regulation of skeletal muscle development and regeneration (Figure 5).

Recent researches have elucidated that RES can affect skeletal muscle development, such as influencing cell differentiation, myotube hypertrophy and ameliorating impaired myotube growth during glucose restriction (Dugdale et al. 2018). A combination of astaxanthin, β-carotene, and RES can elevate protein synthesis during muscle hypertrophy in mice (Kawamura et al. 2020). Besides, numerous researches have reported that RES has positive effects on muscle function (Gordon et al. 2014; Zhou et al. 2019), the recovery of muscle mass (Bennett, Mohamed, and Alway 2013) and anti-fatigue (Toniolo et al. 2018) in aged rats, it implicated that RES is beneficial for reducing age-related alterations in skeletal muscle. RES can prevent exercise-induced muscle damage (Malaguti, Angeloni, and Hrelia 2013) and liposome microbubbles loading RES (LMLR) can ameliorate muscle injury in rats (Feng et al. 2019). Additionally, RES has a strong ability to anti-oxidative and attenuate skeletal muscle oxidative stress (Bosutti and Degens 2015; Sin et al. 2013; Wilson et al. 2015). RES could ameliorate metabolic disorders and regulate insulin resistance in skeletal muscle (Gong, Guo, and Zou 2020; Kang and Chiang 2019), thus it may be used as a medicine for the treatment of metabolic diseases.

RES could affect muscle- and adipose-derived gene expression, including increasing expression of perilipin 5 (Plin5) in skeletal muscle (Mehdi et al. 2018) and up-regulating fibronectin type III domain containing-5 (FNDC5) gene expression in C2C12 cells (Abedi-Taleb et al. 2019) (Figure 5). Jiang et al. also found that RES regulated skeletal muscle fibers switching via the adiponectin receptor1 (AdipoR1)-AMPK- PGC-1α pathway (Jiang, Yamashita, et al. 2019) (Figure 5). Moreover, many studies have found that RES can protect against reactive oxygen species (ROS) by improving Sirt1 levels in myoblasts (Haramizu et al. 2017). RES regulates insulin resistance by altering intracellular redox homeostasis (Quan et al. 2020), activating the ataxia telangiectasia mutated (ATM)-5'AMPK axis (Zhang, Xu, et al. 2019), ameliorating autophagic flux (Chang et al. 2018) and modulating SIRT1-Foxo1 signaling axis (Sin, Yung, and Siu 2015) (Figure 5). In summary, these results show that RES has significant effects on anti-oxidative, maintaining insulin resistance and gene expression in skeletal muscle and it can serve as a potentially useful agent for the treatment of many muscle-derived diseases.

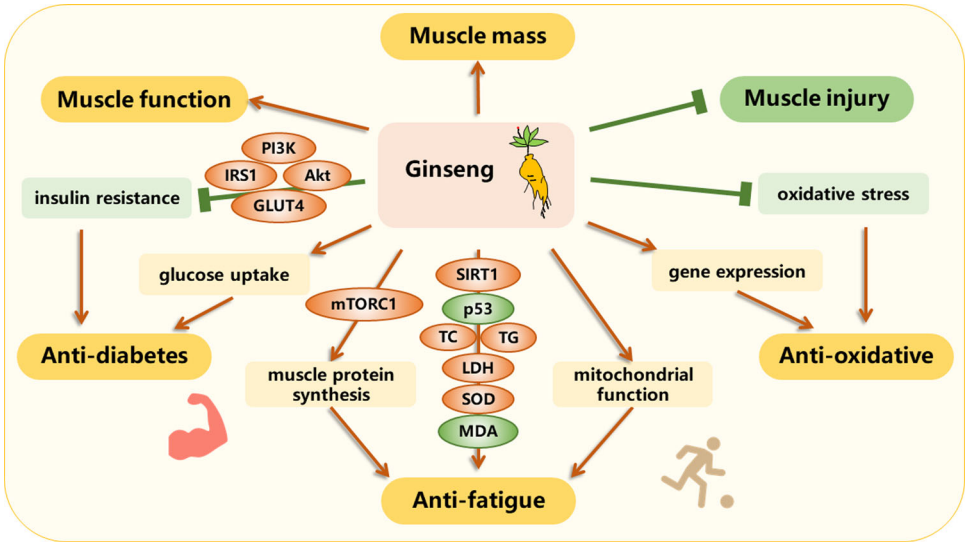

Figure 6. Proposed regulatory mechanism of *ginseng* on skeletal muscle development and regeneration. TC, total cholesterol; TG, serum triglyceride; LDH, lactate dehydrogenase; SOD, superoxide dismutase; MDA, malondialdehyde; mTORC1, mammalian target of rapamycin complex 1; p53, protein 53.

Ginseng

Panax ginseng, the root of the Araliaceous plant, is widely used as a traditional and medicinal herb that has many biological activities. Previous researches have reported that *Panax ginseng* and its compounds have numerous pharmacological effects on cardiovascular diseases (Lee and Kim 2014), nervous system (Kim, Kim, et al. 2013), anti-inflammation (Cabral de Oliveira et al. 2001; Park et al. 2018) and diabetes (Shishtar et al. 2014). Most pharmacological functions of *Panax ginseng* are attributed to ginsenosides, which can act on a wide range of tissues. Ginsenoside Rg1 and Rg3 are one of the most abundant ginsenosides. Recently, more and more studies have demonstrated that *Panax ginseng* and Rg3 are also able to affect skeletal muscle (Figure 6).

Panaxatriol, which is derived from *Panax ginseng*, combined with aerobic exercise could alleviate skeletal muscle insulin resistance as well as maintain skeletal muscle mass in type II diabetic mice (Takamura et al. 2017). Moreover, black ginseng extract (GBG05-FF) can increase glucose uptake in C2C12 myotubes and exert an anti-diabetes effect (Seo et al. 2016). In addition, many studies have shown that both *Panax ginseng* (Cabral de Oliveira et al. 2005; Jung et al. 2011) and North American *ginseng* (Estaki and Noble 2015) could protect muscle from injury and inflammation after exercise. A recent study found that Rg1 supplementation can effectively clear senescence-associated β-galactosidase and eliminate senescent cells in exercising human skeletal muscle thereby improve high-intensity endurance performance (Wu, Saovieng, et al. 2019). Similarly, *ginseng* oligopeptides (GOP) possess the anti-fatigue effect by inhibiting oxidative stress and improving mitochondrial function in skeletal muscles (Bao et al. 2016). The administration of Ginseng extract can protect skeletal muscle from exercise-induced oxidative stress in rats (Voces et al. 2004) and Rg1 can enhance muscle gene expression and oxidative muscle metabolism thus improve muscle functionality in mice (Jeong et al. 2019). Besides, a ginseng supplement, ginseng steroids, can influence anti-oxidant status against exercise challenge in rat skeletal muscle (Hsu et al. 2017).

Deeply, *Panax notoginseng saponins* (PNS) may reduce hyperglycemia and insulin resistance by up-regulating GLUT4 expression and activating the IRS1-PI3K-AKT signaling pathway (Guo et al. 2019) (Figure 6). Besides, a herbal supplement, *Kamishimotsuto* (KST), contains extracts from 13 different herbs, including *ginseng* can increase p70S6K and pS6 phosphorylation and resistance exercise-induced muscle protein synthesis via activating mammalian target of rapamycin complex 1 (mTORC1) signaling (Kido et al. 2016) (Figure 6). Additionally, Yang et al. found that Rg3 has the ability to up-regulate the serum concentrations of total cholesterol (TC), serum triglyceride (TG), lactate dehydrogenase (LDH) and superoxide dismutase (SOD) but down-regulate malondialdehyde (MDA) release out of skeletal muscles and accordingly improve exercise performance and inhibit fatigue through activating SIRT1 activity and suppress protein 53 (p53) transcriptional activity (Yang et al. 2018) (Figure 6). These studies demonstrate that *Panax ginseng* and its derivatives play an important role in skeletal muscle including anti-oxidation, anti-diabetes, anti-fatigue and promoting muscle function and performance.

Astragalus membranaceus

Astragalus membranaceus (AM), is one of the most widely used plant-derived herbs in traditional Chinese medicine. The main ingredients of AM roots are polysaccharides, amino acids, flavonoids, saponins and trace elements (Lee et al. 2013; Ma et al. 2002). AM has multiple biological functions, such as resisting myocardial damage (Wang et al. 2019; Xu, Xia, et al. 2008; Yang et al. 2013; Zhao et al. 2013), anti-inflammatory effect (Li et al. 2016; Wang et al. 2019), modulating immune activities (Huang et al. 2012; Kuo et al. 2009; Liu et al. 2011; Wu, Saovieng, et al. 2019) and improving insulin resistance (Lv et al. 2010). *Astragalus* polysaccharide (APS) is the polysaccharide component of

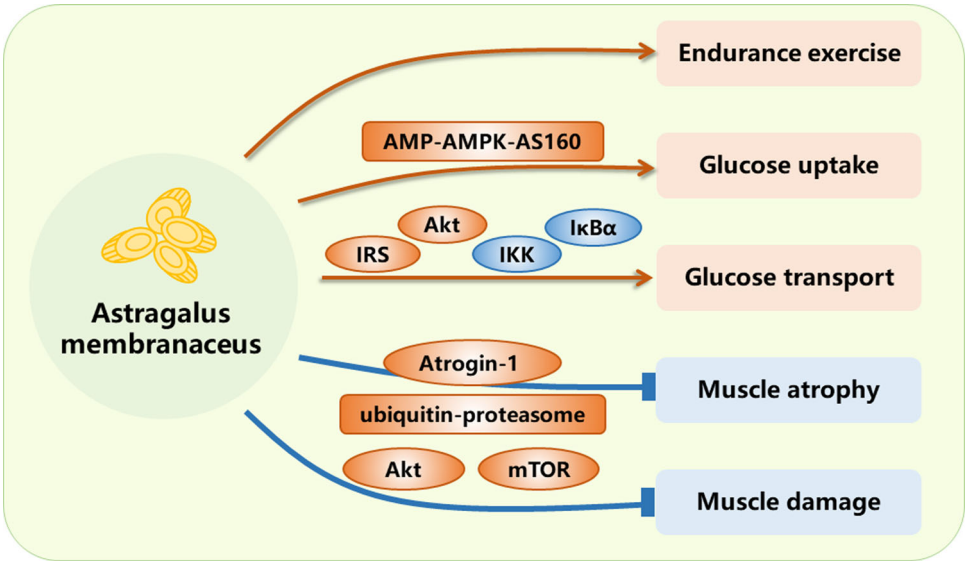

Figure 7. The regulatory role of *Astragalus membranaceus* in skeletal muscle. IKK, inhibitory κB kinase.

the water extract from *Astragalus* roots, which consists of rhamnose, arabinose and glucose (Xu, Xia, et al. 2008). Similarly, APS also has many pharmacological effects on anti-inflammatory (Jiang et al. 2010), anti-tumor (Li et al. 2008) and anti-diabetic (Zhang, Wu, and Cheng 2007). Recently, some studies found direct evidence that AM and APS have the possible anti-fatigue function and can improve exercise performance and affect muscle cell atrophy (Figure 7).

It has shown that AM supplementation can elevate endurance exercise capacity, increase hepatic and muscle glycogen content in mice after exercise training and reduce the accumulation of the byproducts blood lactate and ammonia which was induced by acute exercise (Yeh et al. 2014). Besides, APS could stimulate glucose uptake in L6 myotubes (Liu et al. 2013) and astragaloside IV, which is purified from AM, could promote glucose transport in C2C12 myotubes (Zhu et al. 2016). Additionally, APS may inhibit muscle cell atrophy associated with cachexia in an in vivo and in vitro rat model of chronic renal failure (CRF) (Geng et al. 2017) and protect C2C12 skeletal muscle myotubes and myoblasts from damage (Lu et al. 2013).

At the molecular level, APS stimulates glucose uptake in L6 myotubes via the AMP-AMPK-AS160 pathway (Liu et al. 2013) (Figure 7). Similarly, astragaloside IV facilitates the glucose transport through the IRS/AKT pathway, and suppressing the palmitate-induced activation of the inhibitory κB kinase (IKK)/IκBα pathway in C2C12 myotubes (Zhu et al. 2016) (Figure 7). Geng et al. found that APS inhibited muscle atrophy by activating atrogin-1 and the ubiquitin-proteasome pathway (Geng et al. 2017). Similarly, Lu et al also reported that APS protected C2C12 skeletal muscle from damage and inhibit dexamethasone- and peroxide-induced muscle atrophy through mitochondrial pathway and death receptor pathway (Akt/mTOR signaling pathway) (Lu et al. 2013) (Figure 7). In conclusion, these findings suggest that AM and its derivatives have beneficial effects on skeletal muscle and can serve as a protective and therapeutic agent in the management of muscle wasting.

Capsaicin

Capsaicin (8-methyl-N-vanillyl-trans-6-nonenamide, CAP) is a natural and pungent component in red, chili peppers and other spicy foods, which are used as spices throughout the world (Qiu et al. 2012). Numerous studies have already shown that CAP has extensive bioactivities, such as analgesic (Derry et al. 2017), anti-inflammatory (Sancho et al. 2002), anti-cancer (Clark and Lee 2016), antioxidant (Chen et al. 2015; Materska and Perucka 2005), anti-obesity (Janssens et al. 2013; Saito, Yoneshiro, and Matsushita 2015; Sun, Xiong, and Zhu 2016) effects, and so on. CAP is known to activate the transient receptor potential vanilloid1 (TRPV1) channel (Caterina et al. 1997) to promote mitochondrial function through regulation of uncouple protein expression (Gannon, Lambalot, and Vaughan 2016; Kim et al. 2010) and to increase energy metabolism (Luo et al. 2012).

In addition, TRPV1 channels may also modulate muscular hypertrophy and ATP production in muscle which reduced by regular physical exercise or training programs (Hudson et al. 2016). Activation of the TRPV1 receptor by CAP can enhance interaction between actin-myosin filaments via promoting the release of calcium by the sarcoplasmic reticulum (SR) in skeletal muscle (Lotteau et al. 2013). And the effects of CAP differ in different types of skeletal muscle may be connected with the different degrees of activation of receptors (Zhou et al. 2018). Besides, CAP could also enhance mechanical performance, bioenergetics efficiency and oxidative phosphorylation in contracting mouse skeletal muscle (Kazuya et al. 2014). Hsu et al. found that CAP supplementation dose-dependently reduced serum lactate, ammonia, blood urea nitrogen (BUN) and creatine kinase levels, and increased glucose concentration after exercise in mice, it meant that CAP supplementation may reduce physical fatigue and modulate energy homeostasis (Hsu et al. 2016). Similarly, human experimentation also demonstrated that acute CAP supplementation can ameliorate lower-body resistance training performance in trained young men (de Freitas et al. 2019). Besides, after

ischemia–reperfusion (I/R) injury, CAP can delay regeneration of the neuromuscular junctions in rat extensor digitorum longus (EDL) muscle (Turchanyi et al. 2006). These researches clarify that CAP has a strong ability to enhance muscle performance, anti-fatigue and affect muscle regeneration in skeletal muscle.

Thymol

Thymol (2-isopropyl-5-methylphenol), a natural terpenoid extracted from thyme leaves, is found in the oils of many plants such as *Lippia gracilis Schauer* (Verbenaceae) (Mendes et al. 2010), *Origanum vulgare* L. (Lamiaceae) (Hazzit et al. 2006), and *Lippia sidoides* Cham. (Verbenaceae, rosemary pepper) (Fontenelle et al. 2007). Thymol has multiple biological functions: antimicrobial (Karpanen et al. 2008), anti-inflammatory (Fachini-Queiroz et al. 2012; Riella et al. 2012; Zhou et al. 2014), antibacterial, antifungal (Marchese et al. 2016), local anesthetic (Haeseler et al. 2002), and so on. Now thymol is widely used as preservatives and antioxidants in medical practice, agriculture, food industry and cosmetics (Szentandrassy et al. 2004). In recent years, several studies have shown that thymol may have therapeutic effects on many metabolic diseases, such as promoting the biogenesis of mitochondria, maintaining glucose homeostasis and lipid metabolism (Choi et al. 2017), reducing body weight, plasma insulin and blood glucose in type-2 diabetes (Saravanan and Pari 2015). Meanwhile, thymol also plays a significant role in ameliorating skeletal muscle development and regeneration.

A study reported that thymol could affect the ATPase activity of myosin subfragment-1 (S1) and the contractile properties of skinned skeletal muscle fibers (Tamura and Iwamoto 2004). Sarkozi et al. also found that thymol could affect skeletal type sarcoplasmic reticulum Ca^{2+}-ATPase and ryanodine receptor (Sarkozi et al. 2007). Besides, thymol was found to enhance calcium release and affect kinetic properties of Ca and K currents in rat skeletal muscle (Szentandrassy et al. 2003; Szentesi et al. 2004). A recent study has elucidated that thymol can significantly reduce the area of inflammation and increase the area of regeneration after the cardiotoxin injection, it indicated that thymol could accelerate the recovery of the skeletal muscle after mice injured with cardiotoxin (Cardoso et al. 2016).

Mechanically, Luo et al. clarified that thymol played an important role in the Ca^{2+}-calcineurin-the nuclear factor of activated T-cell (NFAT) pathway, which is significant to regulate the transformation of skeletal muscle fiber type, thus thymol may influence the myosin heavy chain isoforms and promote the oxidative metabolism and fiber type switch in skeletal muscle (Luo et al. 2019). The above discoveries reveal that thymol has significant influences on skeletal muscle, including affecting the properties of myosin, kinetic properties, muscle fiber-type switch and muscle recovery after injury.

Berberine

Berberine (BBR) is a quaternary ammonium isoquinoline alkaloid, which is found in plants such as the family *Berberidaceae*, *Papaveraceae*, *Menispermaceae*, *Ranunculaceae* and *Rutaceae*. BBR is a main active ingredient of *Coptis chinensis* and *Scutellaria baicalensis*, which has been reported as a traditional Chinese medicine to treat diabetes mellitus.

It has shown that BBR can promote muscle function, stimulate glucose uptake and circumvent insulin signaling pathways and activate insulin-independent glucose transport in skeletal muscle in a time- and dose-dependent manner(Cheng et al. 2006; Ma et al. 2010; Yu et al. 2018). Furthermore, BBR plays an important role in improving insulin resistance and regulating glucose and lipid metabolism in type 2 diabetes mellitus (T2DM) rats (Mi et al. 2019). In addition, a study has shown that tetrahydropalmatine (THP), which is a natural compound isolated from *Corydalis turtschaninovii*, has a vital influence on activating MyoD and accordingly preventing fibrosis and improving muscle regeneration as a therapeutic candidate (Lee et al. 2014).

Many studies have been conducted on its molecular basis for this action. Yu et al. found that BBR could activate the AMPK/SIRT1/PGC-1α pathway and dramatically ameliorate muscular function in skeletal muscle (Yu et al. 2018). BBR can stimulate glucose uptake in L6 myotubes by promoting the phosphorylation of AMPK and p38 MAPK (Cheng et al. 2006). Similarly, Ma et al. demonstrated that BBR has the ability to stimulate glucose transport and reduce the intracellular energy status in skeletal muscle via AMPK pathway (Ma et al. 2010). Mi et al. discovered that BBR improved insulin resistance through inhibiting the hypothalamus-pituitary-adrenal (HPA) axis and increasing skeletal muscle expression of GLUT4 proteins(Mi et al. 2019). Besides, Lee et al. suggested that THP improved skeletal muscle regeneration by enhancing the activity of p38MAPK and Akt, which is the key promyogenic kinases (Lee et al. 2014). The above-mentioned data show that BBR is able to ameliorate muscle function, prevent fibrosis and improve muscle regeneration in skeletal muscle.

Ganodorma lucidum

Ganoderma lucidum (LEYSS, ex FR., *G. lucidum*), commonly known as Lingzhi, a genus of polypore mushrooms, is a traditional Chinese herb that has numerous effects on treating assorted diseases and prolonging life (Bishop et al. 2015). In the past few years, *G. lucidum* has been regarded as a folk medicine to prevent and treat human diseases, such as hepatitis, hypertension, chronic bronchitis, bronchial asthma, cancer and others in China (Berovic et al. 2003; Boh et al. 2007). Recent researchers have discovered that *G. lucidum* extract and *G. lucidum* polysaccharides (GLPs) have positive and anti-fatigue effects on skeletal muscle.

A study has reported that GLPs could increase antioxidant enzyme activities and decrease the MDA levels in the skeletal muscle of mice and has protective effects against

exhaustive exercise-induced oxidative stress (Zhonghui, Xiaowei, and Fang 2014). Besides, *G. lucidum* and 'essence of chicken' conjugate can markedly enhance exercise performance and promote fatigue recovery (Li et al. 2018). At a deeper level, *G. lucidum* extract can stimulate glucose uptake and maintain glucose homeostasis via both PI3K and AMPK pathway in L6 skeletal muscle cells (K. H. Jung et al. 2006). Additionally, Ouyang et al. have investigated that GLPs could ameliorate chemotherapy-related fatigue in mice by regulating inflammatory responses, oxidative stress and reducing nephrotoxicity (Ouyang et al. 2016). These results suggest that *G. lucidum* may provide a viable alternative nutritional supplement for skeletal muscle development and function.

Puerarin

Puerarin, a major active isoflavone extracted from the dried root of *Pueraria lobate* (Willd.), as a traditional food and an herbal medicine in China to treat diabetic and cardiovascular diseases (Wong et al. 2011; Wong et al. 2015; Zhang, Lam, and Zuo 2013). Several studies have discovered that puerarin could improve glucose intolerance (Zheng et al. 2015) and mitigate impairments in glucose and lipid metabolism in obese mice (Prasain et al. 2012) and streptozotocin (STZ)-induced diabetic mice (Wu et al. 2013). Recently, more and more researches have been focusing on the function of puerarin and its potential mechanisms in the skeletal muscle.

Puerarin could prevent the accumulation of intramyocellular lipids and improve insulin sensitivity in skeletal muscle (Chen, Wang, Fan, et al. 2018; Chen, Wang, Fan, et al. 2018). Moreover, a research has elucidated that Radix *Pueraria lobate* (RP) and puerarin increased mitochondrial biogenesis and myotube hypertrophy in C2C12 cells thus prevented skeletal muscle atrophy in mouse models of obesity (Jung et al. 2017). Mechanically, Chen et al. found that puerarin prevented the accumulation of intramyocellular lipids through ameliorating the performance of mitochondria in muscle and increasing the oxidation of fatty acids in diabetic rats (Chen, Wang, Fan, et al. 2018). It has been reported that puerarin improved insulin sensitivity by enhancing μ-opioid receptor expression in diabetic rats (Chen, Wang, Fan, et al. 2018). And Jung et al. clarified that puerarin alleviated skeletal muscle atrophy via activating PGC-1α and AMPK pathway and consequently energy metabolism upregulated in skeletal muscle (Jung et al. 2017). These findings conclude that puerarin has effects on antidiabetic ability and can be a potential therapeutic medicine in the treatment of diabetes in skeletal muscle.

Others

Recent studies have demonstrated that short-term proanthocyanidolic oligomer (PCO) supplementation could accelerate skeletal muscle effective regeneration and recovery by facilitating earlier recruitment of activated satellite cells (Kruger and Smith 2012; Myburgh, Kruger and Smith 2012). A research reported that an aqueous extract of *Withania somnifera* (Ashwagandha) improved body strength, body mass and had a positive effect on resistance training adaptations and recovery in recreationally active men (Ziegenfuss et al. 2018). Similarly, in STZ-induced C57BL/6 mice, the water extract of *Liuwei dihuang* (LWDH-WE) can prevent the reduction of muscle mass and muscle strength. And LWDH-WE reduced oxidative damage and regulate protein synthesis and degradation, then protected skeletal muscle in methylglyoxal (MG)-induced atrophy of C2C12 myotubes (Tseng et al. 2019). The unique polysaccharide marker of *Dendrobium officinale* (DOP) increased endurance, body weight, and food intake in BALB/c mice which meant it has a strong anti-fatigue effect (Wei et al. 2017). Besides, Juzentaihoto extract (JTT) may reverse muscle atrophy by influencing immune cells such as spleen, causing an anti-inflammatory activity and restraining excessive activation of the ubiquitin-proteasome system in STZ-induced diabetic mice (Ishida et al. 2019). Taken together, although multiple studies have demonstrated that dietary factors exert effective functions on skeletal muscle development and regeneration, its potential regulation pathways are still not completely clear.

Conclusions and remarks

Based on the above data, we conclude that various dietary factors (green tea, quercetin, CUR, EPA and DHA, RES, *ginseng*, AM, CAP, thymol, BBR, *G. lucidum*, puerarin and others) play numerous vital roles in skeletal muscle, such as activating SCs proliferation, influencing muscle differentiation, enhancing muscle mass and strength, anti-fatigue, improving resistance capacity, ameliorating muscle performance and atrophy, alleviating muscle damage and injury, promoting muscle recovery and regeneration and affecting mitochondrial kinetic and metabolism capacity. Hence, nutritional strategies seem to be a good and safe way to improve skeletal muscle function and dietary factors may be used as potential therapeutic candidates to treat muscle-related diseases. However, there are still some concerns that need to be further studied: (1) The exact effects and the regulatory mechanism of several dietary factors on skeletal muscle development and especially regeneration need to be determined, because some of the current results are controversial and the molecular mechanism is unclear. (2) Different dietary factors have different origins. Thus, it will be important to compare and investigate the regulatory efficiency of different origins. (3) Dietary factors affect skeletal muscle development in mice and humans. Whether these may work in other species such as meat production animals (e.g., pig and cattle), remains unclear. (4) Several dietary factors work in muscle-diseases mice models. Whether it may work in humans in general or specifically in patients with skeletal muscle diseases is still unknown. The potential application of dietary factors in treating muscle-derived diseases needs to be further explored. Collectively, the current findings and future studies could provide more information to reveal the regulatory and molecular mechanisms of

dietary factors during muscle development, regeneration, function, and muscle-related diseases.

Contribution statement

LW and TS designed and wrote the manuscript. TS, ZX, DL, JL, and YZW assisted interpretation and revising the article. All authors have read and approved the final manuscript.

Disclosure statement

The authors declare no conflict of interest.

Abbreviations

AdipoR1	adiponectin receptor1
AMPK	adenosine monophosphate- activated protein kinase
Akt	protein kinase B
BDNF	brain-derived neurotrophic factor
CaMKKβ	Ca^{2+}/calmodulin- dependent kinase kinase β
DHA	docosahexaenoic acid
DMD	Duchenne muscular dystrophy
EDL	extensor digitorum longus
EPA	eicosapentaenoic acid
ERK	extracellular signal-regulated kinase
FABP4	fatty acid binding protein 4
FNDC5	fibronectin type III domain containing-5
GLUT4	glucose transporter type 4
IL-6	interleukin 6
IGF1	insulin-like growth factor 1
IFN-γ	interferon-γ
IRS1	insulin receptor substrate 1
IκB	inhibitor-κB
IKK	inhibitory κB kinase
LECT2	leukocyte cell-derived chemotaxin 2
LIF	leukemia inhibitory factor
LDH	lactate dehydrogenase
MAPK	p38 mitogen-activated protein kinase
Mb	myoglobin
MCK	muscle creatine kinase
MCP-1	monocyte chemoattractant protein-1
MSTN	myostatin
mTORC1	mammalian target of rapamycin complex 1
MuRF-1	muscle RING-finger protein-1
Myh3	myosin heavy polypeptide 3
MyoD	myogenic differentiation
MyoG	myogenin
NFAT	the nuclear factor of activated T-cell
NF-κB	nuclear factor-κB
Nox2	NADPH oxidase-2
Nrf2	nuclear factor (erythroid-derived 2)-like 2
Pax7	paired box 7
PGC-1α	peroxisome proliferator- activated receptor γ coactivator-1α
PI3K	phosphoinositide 3-kinase
Plin5	perilipin 5
PUFAs	polyunsaturated fatty acids
ROS	reactive oxygen species
Sirt1	silent information regulator of transcription 1
STAT	signal transducers and transcriptional activators
SOD	superoxide dismutase
SR	sarcoplasmic reticulum
TC	total cholesterol
TG	triglyceride
TNF-α	tumor necrosis factor-α
Tnnt3	troponin T3

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