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Effect of far-red light on the production and diversity of ginsenosides in leaves of *Panax ginseng* Meyer

Padmanaban Mohanan¹, Tae-Jin Yang^{1,2,3*} and Young Hun Song^{1,3,4*}

Abstract

Ginsenosides are the most valuable and pharmacologically active triterpenoid saponins found in *Panax ginseng*. Although light quality affects ginsenoside content, little is known about the underlying genetic and regulatory mechanisms. Additionally, the correlation between the adaptability of ginseng to shade and ginsenoside biosynthesis remains poorly understood. In the present study, transcriptome analysis of ginseng seedlings using RNA sequencing revealed that the expression of ginsenoside biosynthesis genes, including *PgHMGR*, *PgFPS*, *PgSS*, and *PgUGT*, was enhanced in shade conditions but downregulated by red light, indicating that far-red light might play an essential role in ginsenoside production. Further, gene expression analysis in adventitious roots and 2-year-old plants using qRT-PCR showed that the light quality-mediated expression patterns of ginsenoside genes varied with tissue and age. However, unlike the transcriptome, there was no difference in the total ginsenoside content in seedlings among various light conditions. Nevertheless, the amount of major protopanaxadiol-type ginsenosides increased under shade and red light conditions. Unlike seedlings and adventitious roots, there was a decrease in the expression of *PgHMGR*, *PgFPS*, *PgSS*, and *PgDDS* in 2-year-old plants, along with an increase in the ginsenoside content, under far-red light. Taken together, our findings suggest that far-red light is an important environmental factor for ginsenoside biosynthesis and diversification and provide information that can improve the quality of ginseng produced for medicinal purposes.

Keywords Ginseng, Far-red light, Ginsenosides, Secondary metabolites

Introduction

Plants depend on light for various processes during their growth and development, such as germination, photomorphogenesis, photosynthesis, and other metabolic processes [1, 2]. In addition to orchestrating the biosynthesis of primary metabolites (PMs), light also affects the biosynthesis and accumulation of secondary metabolites (SMs) [2, 3]. While PMs are crucial for growth and development, SMs play a vital role in plant fitness under diverse environmental conditions [2, 4, 5]. The biosynthesis of SMs is greatly influenced by environmental factors that include several biotic and abiotic stresses as well as variations in light [6–9]. Transcriptomic analysis of plants, such as Arabidopsis and rice (*Oryza sativa*), has shown that light determines morphogenesis and

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functional metabolite production through changes in gene expression patterns [10–12]. In addition, appropriate quality and intensity of light are crucial for the accumulation of secondary metabolites [2, 5, 13–17]. Specific wavelengths in the light spectrum are responsible for the induction of SM biosynthesis along with their composition and content [18]. In the visible light spectrum, blue light (BL; 400–500 nm) and red light (RL; 600–700 nm) affect the accumulation of SMs in medicinal plants [16].

Panax ginseng is a perennial herbaceous plant of the *Araliaceae* family widely used in traditional medicine. The pharmacological benefits of ginseng mainly depend on the triterpenoid saponins called ginsenosides [19–24], which are mainly produced in the leaves and stored in the roots [25–28]. They are classified into dammarane-type and oleanolic acid-type ginsenosides. Ginseng mainly consists of the dammarane-type ginsenosides [26, 28, 29], which are further grouped into the protopanaxadiol (PPD) and protopanaxatriol (PPT) types based on the sugar moieties attached to their aglycone structure [29]. The biosynthesis of ginsenosides begins with isoprenoid metabolic pathways involving the cytosolic mevalonate (MVA) pathway and plastid 2-C-Methyl-D-erythritol 4-phosphate (MEP) pathway [27, 30]. Both contribute to ginsenoside biosynthesis by synthesizing isopentenyl diphosphate (IPP) [27, 30, 31]. The backbone for ginsenoside biosynthesis is produced through several condensation and cyclization reactions involving the enzymes farnesyl pyrophosphate synthase (PgFPPS), squalene synthase (PgSS), and squalene epoxidase (PgSE). The first step in ginsenoside biosynthesis is catalyzed by dammarenyliol synthase (PgDDS), which converts 2,3-oxidosqualene into a dammarenyliol backbone [32, 33]. This backbone is further converted into diverse ginsenosides present in ginseng through numerous cytochrome P450 enzymes and UDP-glucuronosyltransferases (PgUGTs) [34–36].

Recent studies have shown that changes in light quality lead to differences in ginsenoside content [37–39]. However, studies on gene expression and ginsenoside biosynthesis in ginseng, which is a shade-adapted plant, have not been actively conducted under far-red (FR) enriched shade conditions to date. Therefore, in the present study, we performed transcriptome and ginsenoside analyses on ginseng seedlings exposed to various light conditions, including white light (WL), BL, RL, and shade (R:FR ratio = 0.2). We further analyzed the expression of genes involved in ginsenoside biosynthesis and ginsenoside content in adventitious roots and 2-year-old plants using quantitative real-time PCR (qRT-PCR) and ultra-performance liquid chromatography (UPLC), respectively, to determine whether light quality-mediated

ginsenoside production depends on the types of tissue or the age of the ginseng plant.

Materials and methods

Plant materials

The *P. ginseng* cultivar Yunpoong was used in all the experiments. Stratified seeds were obtained from the Department of Herbal Crop Research, National Institute of Horticultural and Herbal Science, Republic of Korea, and 2-year-old sprouts were obtained from Korea Ginseng Corporation. Adventitious roots derived from the Yunpoong cultivar were divided, transferred into three bioreactors for generating biological replicates, and collected 4 weeks later for light quality studies.

Light treatment and growth conditions

The seeds and 2-year-old sprouts were cultivated in a growth room maintained at 23 °C for 1 month in long-day (16-h light/ 8-h dark) conditions until fully expanded leaves were obtained. For light quality studies, plants were transferred to growth incubators with white light (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$), blue light (30 $\mu\text{mol m}^{-2} \text{s}^{-1}$), red light (30 $\mu\text{mol m}^{-2} \text{s}^{-1}$), far-red light (FRL; 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$), or shade (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:FR ratio = 0.2) conditions. Blue, red, and far-red light was generated using blue LEDs (450 nm), red LEDs (660 nm), and far-red LEDs (730 nm), respectively. Light intensity was measured using UPRtek spectral PAR meter (PG200N; UPRtek Corp., Taiwan).

Total RNA extraction, cDNA synthesis, and real-time PCR

The light-treated plants and adventitious roots were harvested in the dark and immediately frozen in liquid nitrogen. For total RNA extraction, TRIzol – RNAeasy hybrid method was followed to avoid contamination with sugars and other secondary metabolites. Frozen ginseng materials were homogenized to a fine powder using a mortar and pestle in the presence of liquid nitrogen, and an appropriate volume of TRI reagent (TRI18, Molecular Research Center Inc., Cincinnati, OH, USA) was added according to the manufacturer's instructions. After mixing and centrifuging, the resulting aqueous phase was transferred to a new tube. Total RNA was precipitated with 70% ethanol and collected using the Qiagen RNAeasy Mini Kit (Qiagen Inc, Hilden, Germany). For cDNA synthesis, 1 μg of total RNA was used as a template in the reverse transcription reactions along with 5X PrimeScript™ RT Master Mix (Takara Bio Inc., Shiga, Japan). Quantitative real-time PCR (qRT-PCR) was performed to analyze the expression of genes involved in ginsenoside biosynthesis using the primers listed in Additional file 1: Table S1. *Cyclophilin* (PgCYP) or *glyceraldehyde*

3-phosphate dehydrogenase (GAPDH) expression [40] was used as an internal control to normalize cDNA levels.

RNA-Seq analysis

Library construction was performed by the National Instrumentation Center and Environmental Management (NICEM), South Korea and sequencing was performed by PHYZEN, South Korea. Paired-end reads with an average length of 101 base pairs (bp) were generated using the Illumina HiSeq2000 platform. Sequencing quality was examined using FastQC (v0.11.3) before further analysis. Poor-quality reads were removed and clean reads were combined and assembled using the Trinity transcriptome assembler (version r20140717). Nine GB of clean data was generated on average per sample. The final assembly of the light-treated samples contained 59,352 unigenes. Functional annotation revealed 56,968, 50,293, 46,399, 38,819, and 24,905 unigenes with alignments to NR (non-redundant protein database), Protein domains (InterProScan), Gene Ontology (BLAST2GO), and KEGG (Kyoto encyclopedia of genes and genomes) databases, respectively. The selected unigenes were validated according to the *P. ginseng* draft genome from the Ginseng Genome Database [34]. Differences in the transcript levels of each gene under various light treatments were analyzed using DeSeq2. Differentially expressed genes were defined based on a 2-fold change difference ($p < 0.05$) in the transcription level of genes between plants treated with white light and plants treated with other light wavelengths, such as blue, red, and shade. A heat map was drawn based on FPKM values using the online program heat mapper [41].

Total ginsenoside extraction and HPLC analysis

Total ginsenoside content was analyzed in frozen and powdered ginseng samples for qualitative and quantitative analyses. Each sample (0.1 mg) was ground and mixed with methanol (80%; 1:10 wt/vol) used as an extraction solvent. The mixture was sonicated in an ultrasonic bath at 25 kHz for 30 min at 25 °C (Branson ultrasonic cleaner, Emerson Electric, Brookfield, CT, USA) and centrifuged at 3000 rpm for 20 min. The supernatant was sonicated and centrifuged twice. The resultant supernatant was filtered through a 0.2 µm syringe filter and analyzed using UPLC (Shimadzu LCMS-8050 system; Shimadzu Corp., Kyoto, Japan). The sample (1.0 µL) was separated using Cortecs UPLC T3 1.6 µm 2.1 × 150 mm column (Waters Corp., Milford, MA, USA), and the temperature of the column was maintained at 35 °C. Distilled water containing 0.1% formic acid (A) and methanol/acetonitrile (9/1, v/v, 0.1% formic acid, B) was used as the mobile phase with a gradient of 35% A to 95% B for

20 min and a flow rate of 0.45 mL/min. To detect ginsenosides, negative ionization mode of ESI-mass spectrometry (MS)/MS was used.

Results

Light quality dramatically alters the expression patterns of secondary metabolite biosynthetic genes

To investigate the effect of shade and light quality on gene expression and ginsenoside production in ginseng, 1-month-old ginseng seedlings were exposed to WL, BL, RL, or shade and further grown for five days. Transcriptomic analysis revealed a striking number of differentially expressed genes (DEGs) between the light quality treatments. BL had the highest number of upregulated DEGs, whereas RL had a significantly higher number of downregulated genes (Fig. 1A). Interestingly, GO term analysis revealed a dramatic increase in the metabolic activity following BL treatment. Notably, the genes involved in alkaloid and cinnamic acid metabolic processes and sugar transporter activity were upregulated (Fig. 1B). KEGG enrichment analysis revealed that the phenylpropanoid and flavonoid biosynthesis pathway genes were enriched under BL. In contrast, genes involved in most SM pathways were significantly downregulated under RL (Fig. 1C). These genes encode hydroxymethylglutaryl-CoA reductase (HMGCR), farnesyl diphosphate farnesyltransferase and components in terpenoid, sesquiterpenoid, and isoprenoid metabolisms (Fig. 1C). Shade conditions (enriched FR) upregulated 89 DEGs, including genes involved in abiotic stress pathways, and downregulated 97 DEGs, mainly involved in photosystem, photosynthesis, and plastid development (Fig. 1D). Because ginsenoside production is influenced by abiotic stresses, these results suggest that shade conditions may increase ginsenoside content by upregulating ginsenoside biosynthesis genes.

Shade conditions upregulate genes involved in isoprenoid metabolism

Isoprenoids in plants are mainly produced by the MVA and MEP metabolic pathway end products (Fig. 2A), which serve as precursors for many secondary metabolites present in plants [42, 43]. Light has a profound effect on the isoprenoid pathway, especially the MEP pathway. Light-induced changes in isoprenoid metabolic pathways were observed in our transcriptomic analysis (Fig. 1). This led us to analyze the changes in the expression of genes involved in the MVA and MEP pathways. RL treatment tended to reduce the expression levels of MVA and MEP pathway genes compared to BL and shade conditions (Fig. 2B and C). However, the expression of isoprenoid metabolism genes in the MVA and MEP pathways was not altered by RL treatment (Fig. 2B and C). Moreover, in

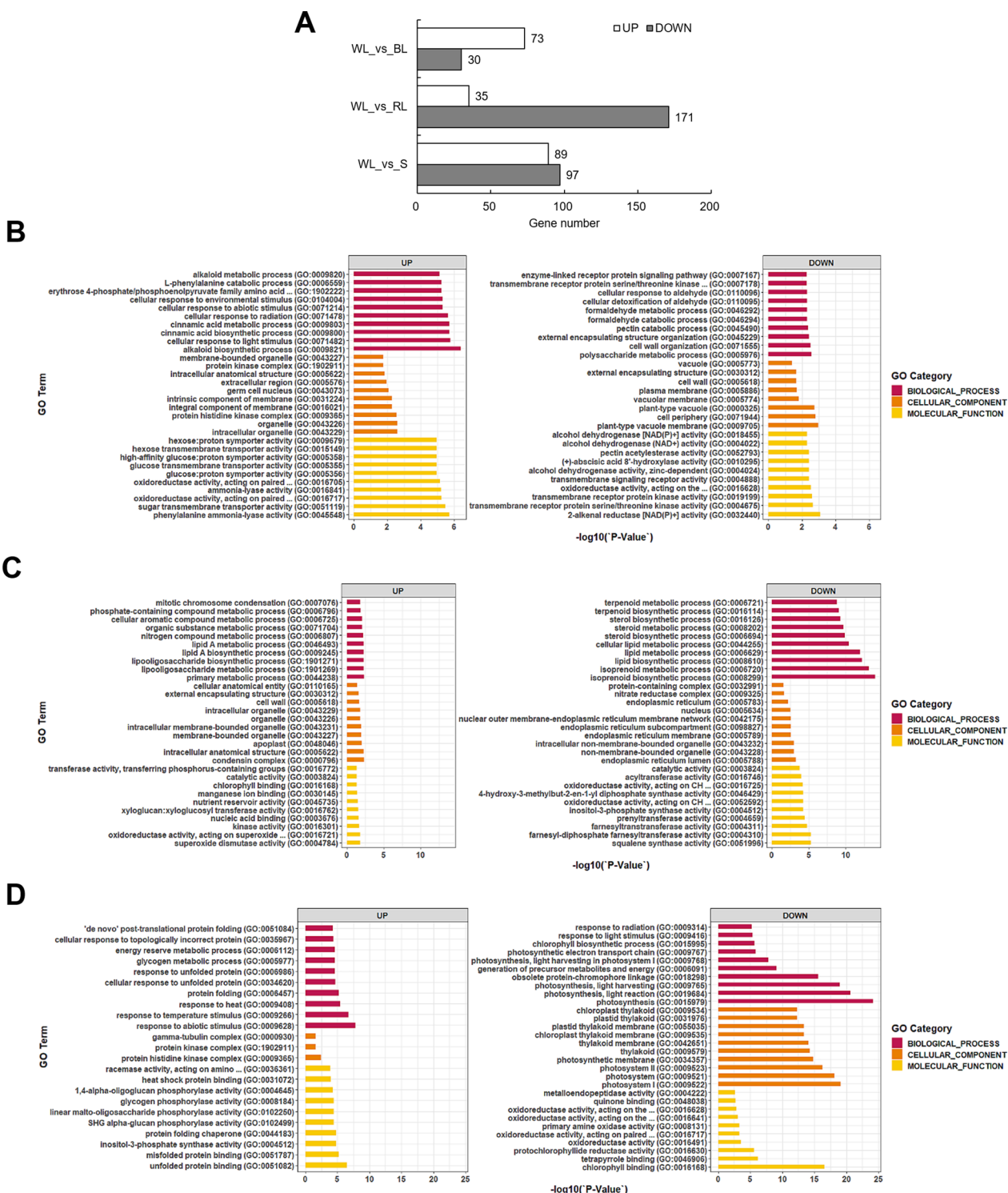


Fig. 1 Differentially expressed genes (DEGs) for GO Annotation categories. **A** Number of DEGs under light quality treatment ($\text{Log}_2(\text{FoldChange}) \geq 1$ and $\text{padj} < 0.05$). The GO analysis of genes in **B** WL vs. BL **C** WL vs. RL and **D** WL vs. Shade treatments. X-axis indicates the richness factor in \log_{10} p-value. Y-axis represents various GO terms (refer to the color category)

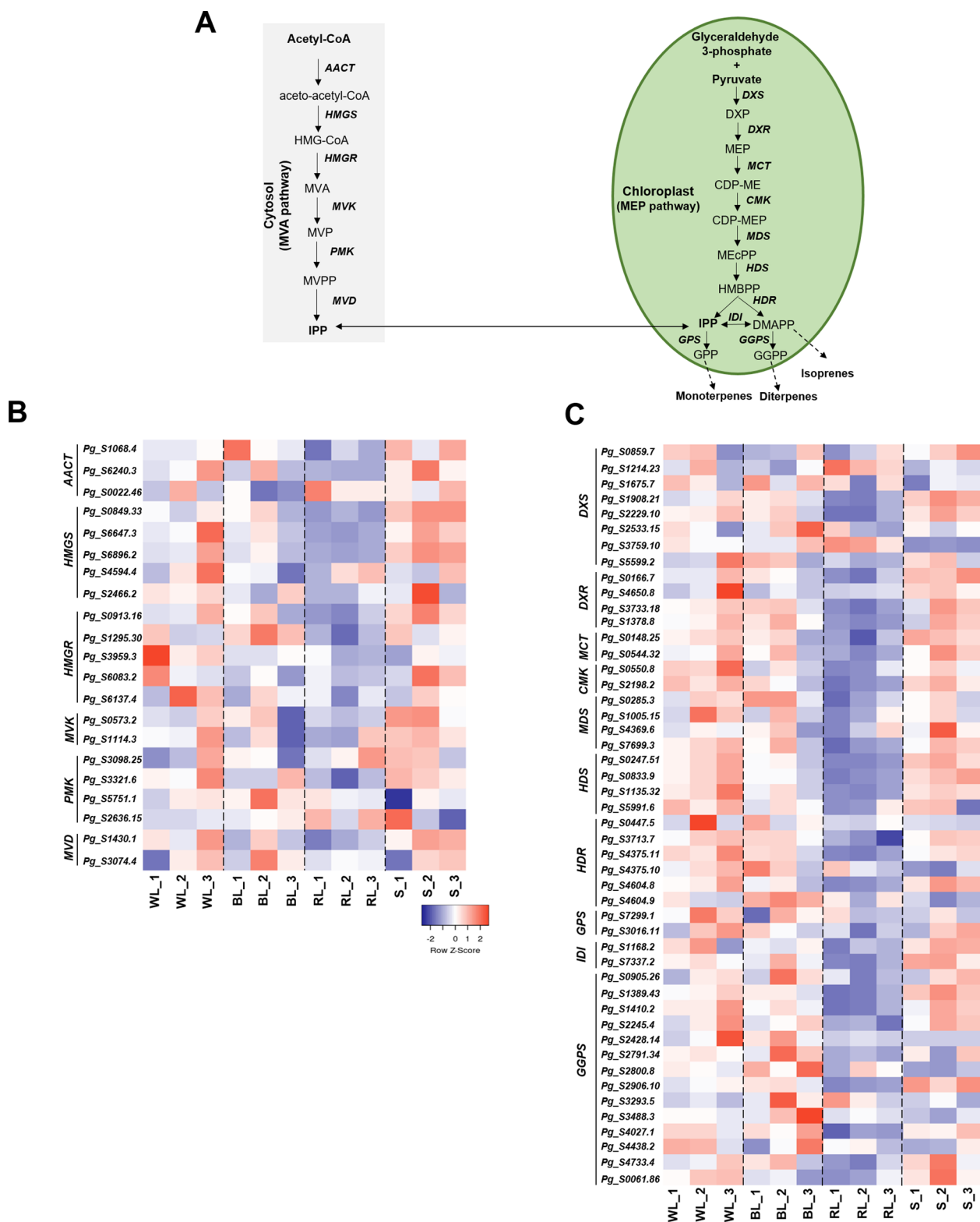


Fig. 2 Expression pattern of isoprenoid biosynthetic pathway genes in ginseng leaf tissues. **A** Mevalonic acid pathway (MVA) in the cytosol and methylerythritol 4-phosphate (MEP) pathway in the chloroplast. **B** Heat map pattern of MVA pathway in white (WL), blue (BL), red (RL), and shade (S) light conditions. **C** Heat map pattern of MEP pathway genes under various light treatments. The shift from blue to red corresponds to the increasing FPKM value

the MVA pathway, the upstream genes encoding acetyl-CoA C-acetyltransferase (PgAACT), hydroxymethylglutaryl-CoA synthase (PgHMGS), and (PgHMGR) were reduced by RL treatment compared to BL and shade conditions (Fig. 2B). Similarly, we observed that most MEP genes were downregulated under RL conditions. Notably, genes that encode 1-deoxy-D-xylulose-5-phosphate synthase (PgDXS) and 1-deoxy-D-xylulose-5-phosphate reductase (PgDXR) synthesizing MEP were downregulated by RL treatment (Fig. 2A and C), resulting in reduced expression of all downstream genes including *isopentenyl-diphosphate Delta-isomerase* (PgIDI), which its gene product produces a terpenoid precursor, isopentenyl-diphosphate (IPP) (Fig. 2A and C). In contrast, we observed the upregulation of MVA and MEP pathway genes under BL and shade conditions (Fig. 2B and C). These results suggested that light quality is important for the regulation of isoprenoid metabolic processes in ginseng and may influence ginsenoside biosynthesis.

Far-red light affects the expression of ginsenoside biosynthetic genes differently according to tissue and age

Ginsenosides, which are ginseng saponins, are derived from the IPP precursor produced by the MVA and MEP pathways and are reportedly synthesized in the leaves [44]. Next, we analyzed the expression profiles of ginsenoside-synthesizing genes in the leaves and found characteristic changes according to light quality. The transcript abundance of ginsenoside biosynthesis genes was the highest under shade conditions (Fig. 3A and B). In particular, *PgFPPS* (*Pg_S8325.1*, *Pg_S0304.36*), *PgSS* (*Pg_S0992.8*, *Pg_S1678.33*, *Pg_S2014.27*, *Pg_S1637.7*), *PgSE* (*Pg_S3064.5*, *Pg_S0129.28*, *Pg_S1693.31*, *Pg_S2606.7*, *Pg_S2606.8*, *Pg_S2840.6*, *Pg_S6308.10*, *Pg_S4651.2*), and *PgDDS* (*Pg_S3318.3*) genes were highly induced under shade as well as BL conditions (Fig. 3A). All paralogs of these genes were upregulated under shade and BL conditions compared to RL, except *PgDDS*. Among *PgDDS* paralogs, only *Pg_S3318.3* was expressed in our study (Fig. 3A). These results suggest that ginsenoside biosynthesis is dependent on light quality. Similar to the isoprenoid pathway, the expression of most ginsenoside genes was downregulated under RL conditions, except for one paralog, *PgSQE* (*Pg_S4651.2*). Moreover, *protopanaxadiol synthase* (*PgPPDS*, *Pg_S4733.5*, *Pg_S3293.6*) and one paralog of *protopanaxatriol synthase* (*PgPPTS1*, *Pg_S1770.12*) showed the highest expression under shaded conditions (Fig. 3A), indicating that dammarane-type ginsenosides may accumulate under these conditions. β -amyrin synthase (BAS) catalyzes the cyclization of 2,3-oxidosqualene to produce β -amyrin, which serves as a precursor for the production of oleanolic acid-type ginsenosides (mainly Ro) and plant sterols. Seven *PgBAS*

genes among eight paralogs were expressed in our conditions, and their expression was unaltered by light quality changes (Fig. 3A).

To date, more than 150 ginsenosides have been identified in *Panax* species, and this diversity is due to many UDP-glycosyltransferases (UGTs) that catalyze glycosylation reactions in the final ginsenoside biosynthesis [45]. We further analyzed whether the expression of *UGT* genes was dependent on light quality. Among the 12 *PgUGTs* in our analysis, eight genes were the most enriched under shade conditions (Fig. 3B). In contrast, the expression of *Pg_S2390.5* belonging to the UGT74 clade under shade conditions was lower than that under WL and RL conditions (Fig. 3B). Similar to the ginsenoside biosynthesis genes, the expression of all *PgUGT* genes analyzed was decreased by RL treatment compared to WL conditions (Fig. 3B). These results suggest that light quality may affect the levels of specific ginsenosides.

The level of ginsenoside production varies with tissues and developmental ages [26–28]. To examine whether the effect of light quality on the expression of ginsenoside biosynthesis genes was preserved in other tissues and developmental stages, ginseng adventitious roots and 2-year-old plants were grown under WL, BL, RL, and FRL conditions. We used monochromatic FRL instead of shade conditions in order to eliminate the effect of other wavelengths on gene expression. Quantitative real-time PCR analysis showed FRL-specific enrichment in the expression of *PgHMGR* and *PgSS* genes in adventitious roots (Fig. 3C). Conversely, RL-specific enrichment of *PgHMGR*, *PgSS*, and *PgDDS* was observed in the leaves of 2-year-old plants (Fig. 3D). These results indicate that light quality may have different effects on ginsenoside production depending on the tissue and age of the ginseng.

Far-red light influences the production and diversity of ginsenosides

Because our data showed that light quality plays an important role in the regulation of ginsenoside biosynthesis gene expression, we analyzed the changes in ginsenoside content under different light regimes. We quantified the total ginsenoside content and individual ginsenosides belonging to the PPD, PPT, or oleanane types in the leaves of seedlings, adventitious roots, and leaves of 2-year-old plants under the same conditions, which the gene expression was analyzed. In seedlings, unlike the transcriptome analysis, the total ginsenoside content was similar among BL, RL, and shade conditions, despite a slight variation compared to WL (Fig. 4A). However, PPD-type ginsenosides, including Rb1, Rc, Rb2, and their malonyl forms such as malonyl-Rc (mRc), malonyl-Rb1 (mRb1), and malonyl-Rb2 (mRb2), and oleanane-type

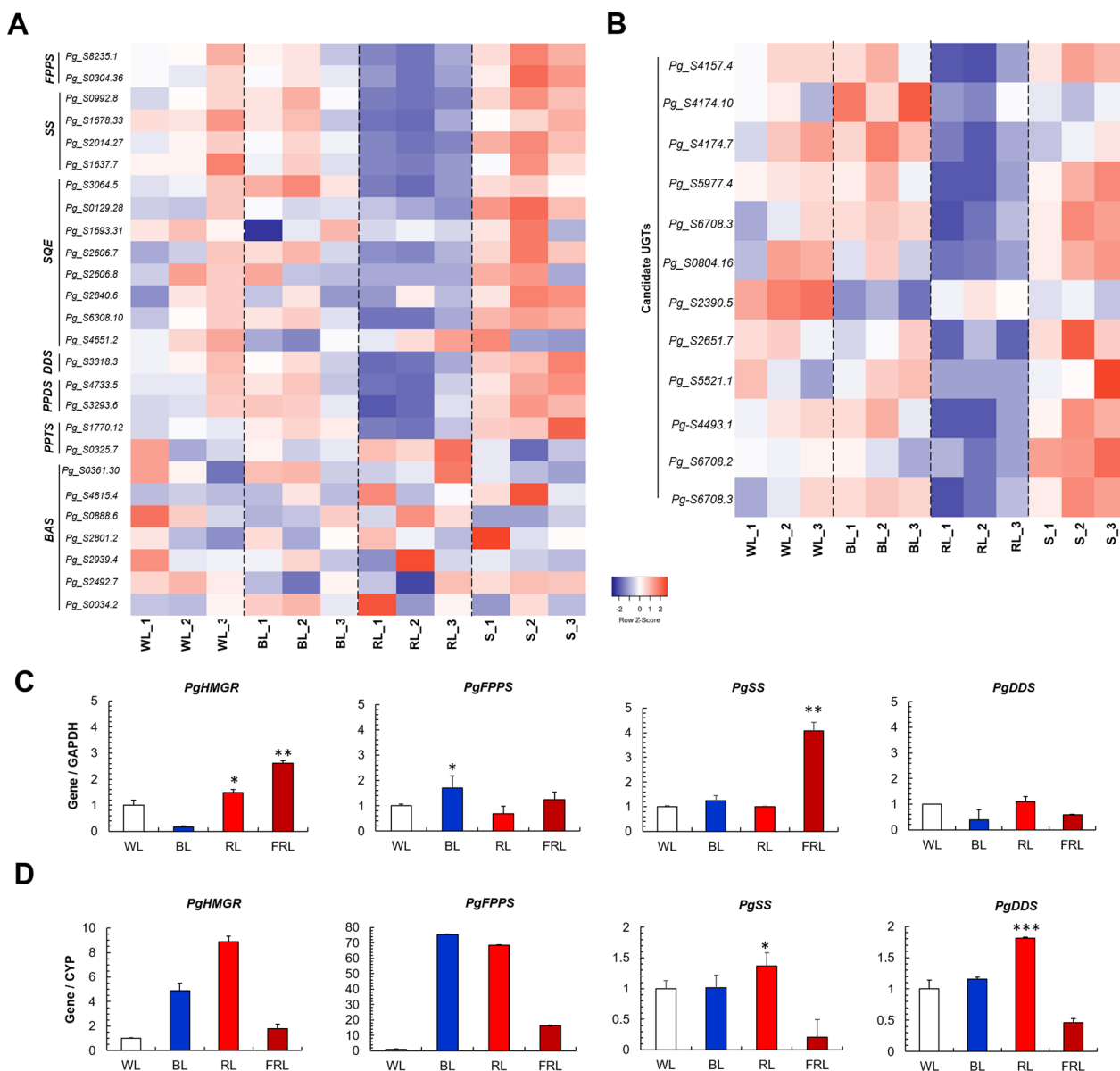


Fig. 3 Expression pattern of ginsenoside triterpenoid biosynthetic genes in ginseng leaf tissues under various light conditions. **A** Heat map showing the expression pattern of ginsenoside biosynthetic genes. **B** Expression pattern of candidate UGT genes involved in ginsenoside biosynthesis. Real-time PCR quantification of canonical ginsenoside genes encoding 3-hydroxyl-3-methylglutaryl-CoA reductase (HMGR, *Pg_S*), farnesyl diphosphate synthase (FPS), squalene synthase (SS), and dammarenediol synthase (DDS) from **C** light-quality treated ginseng adventitious roots and **D** 2-year-old plants. Values represent means \pm SE with three biological replicates ($n = 5$). Values marked with stars differ from white light significantly according to the student's t-test: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. The shift from blue to red in heat map corresponds to the increasing FPKM value. WL: white light; BL: blue light; RL: red light; FRL: far-red light

ginsenoside Ro were significantly increased under RL and shade conditions (Fig. 4A). In contrast, the PPT-type ginsenosides Re and Rg1 were enriched following BL treatment. In adventitious roots, the total ginsenoside content under FRL conditions was lower than that under WL conditions (Fig. 4B), which was inconsistent with the enriched transcripts of the canonical ginsenoside genes

PgHMGR and *PgSS* in FRL-treated adventitious roots (Fig. 3C). Moreover, the total ginsenoside content under BL and RL conditions was similar to that under WL conditions (Fig. 4B). Unlike seedlings and adventitious roots, the total amount of ginsenosides in 2-year-old plants was the highest under FRL conditions among all conditions (Fig. 4C), indicating that ginsenoside accumulation

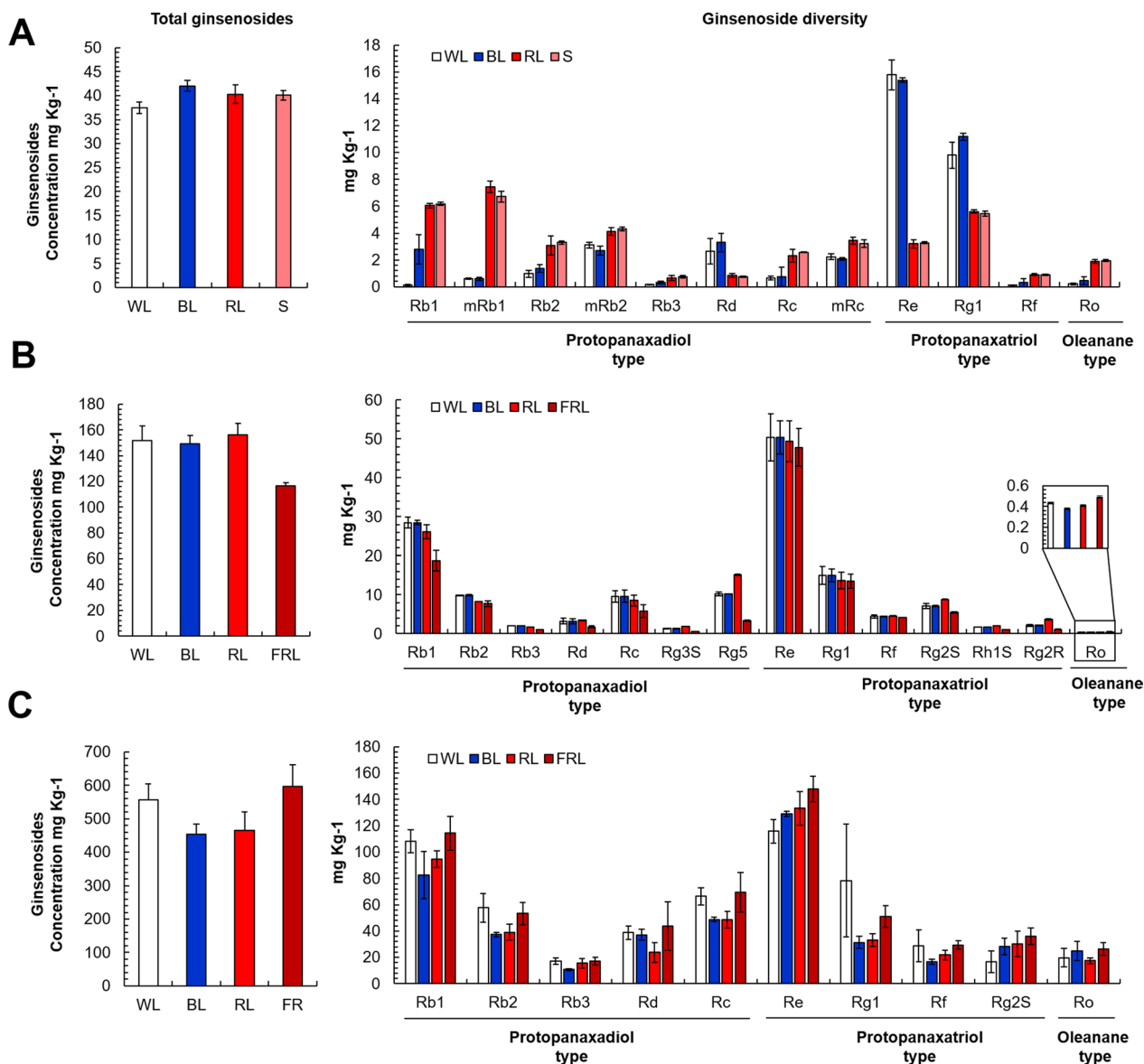


Fig. 4 UPLC quantification of ginsenoside diversity from plants exposed to various wavelengths of light. **A** One-month-old ginseng seedlings, **B** adventitious roots, and **C** 2-year-old plant after light treatment. WL: white light; BL: blue light; RL: red light; S: shade; FRL: far-red light

may differ from gene expression patterns (Fig. 3D). This asynchronous relationship between gene expression and ginsenoside production may be attributed to unknown feedback and/or compensatory circuits. Additionally, major ginsenosides in the PPD and PPT types, including Rb1, Rb2, Rc, Rd, Re, and Rg1, showed FRL-specific enrichment compared to BL and RL conditions (Fig. 4C). We also found that the ginsenoside content and composition varied among all plant tissues tested (Fig. 4). Taken together, our data suggest the existence of a complicated mechanism by which light quality influences ginsenoside production and diversification of ginsenoside content

through the regulation of multiple sets of genes, likely allowing ginseng plants to optimize ginsenoside biosynthesis under a wide range of environmental conditions.

Discussion

Plants absorb, transmit, and reflect the most photosynthetically active wavelengths. The quality and intensity of light absorbed by leaves play critical roles in the development, morphogenesis, and biosynthesis of different compounds [6, 46]. Our DEG analysis showed that light treatment significantly affected the expression of genes involved in the primary and secondary metabolic

pathways. The pairwise comparison between WL- and BL-treated plants showed the upregulation of secondary metabolic pathways, such as alkaloid metabolic pathways and phenylalanine catabolic processes (Fig. 1B–D). The increase in photosynthetic gene expression observed in the BL-treated plants could contribute to active metabolic processes in ginseng. Ginseng possesses chlorophyll A/B binding proteins that are duplicated during evolution, leading to its high photosynthetic capacity [47]. We observed that genes involved in phenylpropanoid biosynthetic pathways, such as *Pg_S1239.2*, *Pg_S2256.14*, and *Pg_S3606.18*, were upregulated in the BL-treated plants in particular. Among the enriched metabolic pathways, products of the cinnamic acid and phenylpropanoid biosynthesis pathways act as precursor pools for secondary metabolites.

Red light is known to contribute to the development of photosynthetic apparatus, thereby enhancing the accumulation of starch in plants [45, 49]. Ginsenoside biosynthesis is regulated during the early growth and developmental stages of ginseng plants, which later leads to the accumulation of ginsenosides in the roots [44, 48–51]. Thus, we used young seedlings to understand light quality-mediated ginsenoside biosynthesis. Our results showed that upstream pathways, such as the MEP and MVA pathways, were significantly affected by light quality (Fig. 2). Notably, the transcripts of *PgDXS*, *PgDXR*, and *PgGGPS* in the MEP pathway and those of *PgAACT*, *PgHMGS*, *PgHMGR*, and *PgPMK* in the MVA pathway were significantly downregulated under RL conditions (Fig. 2B and C). In contrast to the plants exposed to WL, BL, and shade conditions, plants exposed to RL displayed downregulation of genes related to the terpenoid and sterol biosynthesis pathways (Fig. 1C).

We found that shade conditions enhanced the expression of genes involved in ginsenoside biosynthesis in seedlings, similar to isoprenoid metabolite pathway genes (Fig. 3A). In particular, canonical genes involved in ginsenoside biosynthesis, such as *PgDDS*, *PgPPDS*, and *PgPPTS*, were prominently expressed. Surprisingly, while the changes in the transcript levels of genes involved in ginsenoside metabolism were striking, the total ginsenoside content did not change significantly (Figs. 3A, B and 4A). However, the concentration of PPD-type ginsenosides was considerably higher under shade conditions than that of PPT-type ginsenosides (Fig. 4A); RL treatment also showed a similar trend. Unlike the seedlings, in 2-year-old plants exposed to FR light, the total ginsenoside content was increased (Fig. 4C) while the ginsenoside gene expression was downregulated (Fig. 3D). The difference in gene

expression patterns in response to FR light between seedlings and 2-year-old plants could be explained due to the difference in the duration of light treatment (5 d versus 2 wk). Alternately, it is possible that while the enzymes themselves may be activated by FR light, it might cause a feedback inhibitory effect on the expression of genes that encode key enzymes of ginsenoside biosynthesis. In addition, the post-translational modification or regulation by light quality, such as phosphorylation or stability changes, respectively, can account for discrepancies between gene expression and metabolite profiles [52]. Furthermore, the comparative analysis of transcript levels, enzyme activities, and metabolites revealed that diel changes in transcript levels were rapid, whereas diel changes in activities and metabolites were small or slow [53].

In conclusion, our transcriptome and ginsenoside analyses suggest that light quality is crucial not only for the production of ginsenosides but also for their diversity, especially highlighting the importance of shade or FR light in the promotion of ginsenoside biosynthesis in ginseng leaves via gene regulation. Our findings provide clues for improving the medicinal quality of ginseng by increasing the pharmacologically valuable PPD-based ginsenoside content in ginseng plants by using shade or FR light during their growth.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13765-023-00776-4>.

Additional file 1: Table S1. Primers used in this study.

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Not applicable.

Author contributions

PM performed the experiments and PM and YHS analyzed the data. TJY and YHS conceived of and supervised the study. PM, TJY and YHS wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed in the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests

The authors declare that they have no competing interests.

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