

Article

Monochromatic Light Orchestrates Integrated Transcriptomic and Metabolic Reprogramming to Alleviate Phosphorus Starvation in Banana (*Musa spp.*)

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Highlights

What are the main findings?

- Far-red (FR) light alleviates phosphorus (Pi) starvation by promoting shoot elongation and enhancing the accumulation of phosphorus, iron, and calcium, whereas blue (B) and ultraviolet (UV-A) light aggravate growth inhibition and oxidative damage.
- B and UV-A trigger massive transcriptomic reprogramming of stress-related genes and secondary metabolism, while FR specifically enriches photosynthesis and cell wall biogenesis pathways.
- Antioxidant systems are activated in a spectrum-specific manner: B light upregulates SOD, CAT, and POD, whereas UV-A light specifically enhances GSH-Px activity, revealing tailored ROS-scavenging strategies.

What are the implications of the main findings?

- This study provides a mechanistic framework for using LED-based light-quality management to improve phosphorus-use efficiency and stress tolerance in banana and other horticultural crops.
- Our findings offer practical strategies for optimizing controlled-environment lighting to enhance crop resilience and nutritional quality under Pi-limited conditions.

Abstract

Phosphorus (Pi) deficiency limits plant productivity. Light quality modulates growth and stress responses, but its interaction with Pi starvation in banana is unclear. We investigated physiological, transcriptomic, and metabolomic responses of banana seedlings to low Pi under white (WL), red (R), far-red (FR), blue (B), and ultraviolet (UV-A) light. FR light promoted shoot elongation and increased phosphorus, iron, and calcium accumulation, whereas B and UV-A exacerbated growth inhibition and oxidative stress (higher H₂O₂, MDA, and proline). Transcriptomics revealed that B and UV-A enriched cell cycle and stress pathways, while FR enriched photosynthesis and cell wall biogenesis. Expression of phosphate transporters and starvation-responsive genes was spectrum-specific. Metabolomics showed B and UV-A triggered massive accumulation of ABA, flavonoids, and secondary



Academic Editor: Anoop Kumar Srivastava

Received: 1 July 2026

Revised: 21 July 2026

Accepted: 22 July 2026

Published: 23 July 2026

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metabolites, indicating strong stress defense. Antioxidant enzyme activities were differentially activated: B upregulated SOD, CAT, and POD; UV specifically enhanced GSH-Px. Integrated correlation networks revealed distinct regulatory hubs: blue light centered on ROS scavenging, red light on phosphate transport. Our findings demonstrate that FR light acts as a positive regulator, while B and UV-A act as additional stressors under Pi deficiency, providing a mechanistic framework for using light spectra to improve crop resilience in Pi-limited conditions.

Keywords: banana; phosphorus deficiency; light quality; transcriptomics; metabolomics

1. Introduction

Phosphorus (Pi) is an essential macronutrient and a structural component of nucleic acids, phospholipids, and ATP, playing a pivotal role in plant metabolism, energy transfer, and signal transduction [1]. However, its bioavailability in agricultural soils is often limited due to its fixation into insoluble organic and inorganic complexes, posing a severe threat to crop productivity worldwide [2,3]. To cope with Pi deficiency, plants have evolved a suite of adaptive strategies, including the modulation of root architecture, secretion of organic acids and phosphatases, and the establishment of symbiotic associations with mycorrhizal fungi [4,5]. At the molecular level, the phosphate starvation response (PSR) is centrally governed by the PHR1 transcription factor, which orchestrates the expression of a large set of genes involved in Pi uptake, translocation, and remobilization [6,7]. Despite these adaptations, prolonged Pi deficiency leads to severe growth retardation, metabolic imbalance, and oxidative stress due to the impairment of photosynthetic electron transport and cellular redox homeostasis [8,9].

Light is not only the primary energy source for photosynthesis but also a critical environmental cue that regulates a myriad of plant physiological and developmental processes through complex signaling networks [10,11]. Plant photoreceptors, including phytochromes (sensing R/FR), cryptochromes, and phototropins (sensing UV-A/blue), and UVR8 (sensing UV-B), perceive specific light wavelengths and transduce signals to modulate gene expression, ultimately shaping plant morphology, phenology, and stress tolerance [12,13]. The interplay between light and nutrient signaling is emerging as a key regulatory axis for optimizing plant growth and resource allocation. For instance, it has been demonstrated that light intensity and quality can influence the expression of Pi transporters and the overall PSR [14,15]. *Arabidopsis thaliana* PHR1 has been shown to mediate the interaction between Pi starvation and light signaling through its integration of hormonal pathways, such as jasmonic acid (JA) and abscisic acid (ABA) [16,17]. Furthermore, other abiotic stresses like salt, drought, and heavy metal toxicity are also known to interact with light signaling pathways, often at the level of shared downstream components like reactive oxygen species (ROS) and hormonal crosstalk [18,19].

In agricultural practices, the manipulation of light spectra using advanced lighting technologies, such as light-emitting diodes (LEDs), has gained significant traction as a means to enhance crop yield, quality, and stress resilience in controlled-environment agriculture [20,21]. Monochromatic or composite light treatments have been shown to improve the nutritional quality of vegetables, stimulate the accumulation of beneficial secondary metabolites, and even mitigate the effects of pathogen attack [22–25]. However, the application of specific light wavelengths to alleviate the specific effects of nutrient stress, particularly Pi deficiency, and the underlying molecular mechanisms remain largely unexplored in major fruit crops like banana.

Banana (*Musa* spp.) is a staple food crop and a major source of nutrition and income in tropical and subtropical regions. However, its productivity is severely constrained by low soil Pi availability, especially in acid soils where it is predominantly cultivated [26]. Previous transcriptomic studies in banana have identified several Pi-starvation responsive genes [27,28], but the potential of using specific light spectra to mitigate this stress has not been explored.

The objective of this study was to systematically investigate the effects of different monochromatic light qualities (R, FR, B, and UV-A) on the physiological, transcriptomic, and metabolomic responses of Pi-deficient banana seedlings. We hypothesized that (1) FR light would alleviate Pi deficiency by enhancing photosynthetic efficiency and nutrient uptake; (2) B and UV-A would exacerbate stress through increased ROS production and metabolic reprogramming; and (3) each spectrum would induce distinct transcriptional and metabolic signatures reflecting tailored adaptive strategies. Our findings provide a comprehensive framework for understanding the complex light-Pi crosstalk and offer potential strategies for optimizing light environments to improve banana cultivation under Pi-limiting conditions.

2. Materials and Methods

2.1. Plant Material and Growth Conditions

Banana (*Musa* spp., Cavendish) plantlets obtained from tissue culture were acclimatized and grown in a controlled-environment growth chamber. The conditions were set at 25/20 °C (day/night), 70% relative humidity, and a 12 h/12 h photoperiod with white light (WL; 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) as the control.

2.2. Experimental Design and Light Treatments

After acclimatization, uniform three-leaf-stage seedlings (height ~15 cm) were transferred to a hydroponic system containing a modified Hoagland solution. The full nutrient solution contained (mM): 2.0 $\text{Ca}(\text{NO}_3)_2$, 2.5 KNO_3 , 1.0 MgSO_4 , 0.5 $(\text{NH}_4)_2\text{SO}_4$, and micronutrients (μM): 20 Fe-EDTA, 10 MnSO_4 , 1.0 ZnSO_4 , 0.5 CuSO_4 , 0.5 Na_2MoO_4 , and 50 H_3BO_3 . For the low-Pi treatment, KH_2PO_4 was reduced to 5 μM , while the control (+Pi) received 200 μM . K^+ concentration was balanced by adding KCl.

After one week of hydroponic adaptation, the seedlings were subjected to various light quality treatments for three weeks. The treatments included: (1) WL + P (control, Pi-sufficient under WL), (2) WL (Pi-deficient under WL), (3) R (Pi-deficient under red light, 660 nm), (4) FR (Pi-deficient under far-red light, 730 nm), (5) B (Pi-deficient under blue light, 450 nm), and (6) UV-A (Pi-deficient under UV-A light, 380 nm). The selected intensities were determined through preliminary dose–response experiments, in which seedlings were exposed to three different PPFD levels for each wavelength: 30, 50, and 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for R, FR, and B; and 10, 30, and 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for UV-A. Based on growth performance (plant height and biomass) and visual assessment of leaf damage (chlorosis and necrosis), 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was chosen for R, FR, and B as it induced clear spectral responses without causing severe photoinhibition, while 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was selected for UV-A to avoid acute photodamage while still eliciting stress-related responses [24]. Light was provided by LED modules (P50, CSNJ, Shenzhen, China) with spectral peaks confirmed by a spectroradiometer (LI-180, LI-COR). Each treatment was replicated in three independent biological replicates, each consisting of six plants.

2.3. Phenotypic and Physiological Measurements

After three weeks of treatment, plant height was measured. Leaf samples from the second fully expanded leaf were collected, immediately frozen in liquid nitrogen, and

stored at -80°C for subsequent analyses. Total phosphorus content was determined colorimetrically using the vanadomolybdo-phosphoric acid method after digestion with $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$. For mineral element analysis (Fe, Ca), leaf tissues were digested with HNO_3 and analyzed using inductively coupled plasma optical emission spectrometry (ICP-OES) (Agilent 5110, Santa Clara, CA, USA).

2.4. Determination of Oxidative Stress Markers and Enzyme Activities

H_2O_2 content was assayed using a commercial kit (Solarbio, Beijing, China; cat. no. BC3595) according to the manufacturer's instructions. The activities of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione peroxidase (GSH-Px) were also measured using corresponding assay kits (Solarbio; cat. nos. BC0175, BC0205, BC0095, BC0225, BC1395). Proline (Pro) and malondialdehyde (MDA) levels were determined using standard spectrophotometric methods. Phenylalanine ammonia-lyase (PAL) activity was assayed by measuring the production of cinnamic acid at 290 nm. All measurements were performed at Genepioneer Co., Ltd. (Nanjing, China) and in triplicate for each biological sample.

2.5. RNA Extraction, Library Construction, and RNA-Seq

Total RNA was extracted from leaf samples using the RNeasy Pure Plant Kit (Qiagen, Beijing, China). RNA integrity and concentration were assessed using an Agilent 2100 Bioanalyzer (Santa Clara, CA, USA). Stranded RNA-seq libraries were constructed using the NEBNext Ultra Directional RNA Library Prep Kit (Ipswich, MA, USA). The libraries were sequenced on the Illumina NovaSeq 6000 (San Diego, CA, USA). Clean reads were trimmed for adapter sequences and low-quality bases and then aligned to the *Musa acuminata* reference genome (v. 2) using HISAT2 (v2.2.1). Gene expression levels were quantified as FPKM (Fragments Per Kilobase of transcript per Million fragments mapped) using StringTie (v2.1.5). DEGs were identified by DESeq2 (v1.38.3) with $|\log_2\text{FC}| \geq 1$ and an adjusted p -value < 0.05 considered as differentially expressed genes (DEGs).

2.6. RT-qPCR Validation

To validate the RNA-seq data, twelve key genes were selected for RT-qPCR analysis. First-strand cDNA was synthesized from 1 μg of total RNA using a PrimeScript RT reagent Kit (TaKaRa) (Dalian, Liaoning, China). RT-qPCR was performed on a CFX96 real-time PCR system (Hercules, CA, USA) using TB Green Premix Ex Taq II (Takara Bio Inc., Dalian, Liaoning, China). The relative expression of each gene was calculated using the $2^{-\Delta\Delta\text{Ct}}$ method with MaActin as an internal control. The primers used in this study are listed in Table S1.

2.7. Non-Targeted Metabolomics Analysis

Metabolites were extracted from 50 mg of frozen leaf powder using a methanol/ acetonitrile/water (2:2:1, $v/v/v$) solution. After vortexing and centrifugation, the supernatant was analyzed by UHPLC (Ultimate 3000, Thermo Fisher, Waltham, MA, USA) coupled to Q-Exactive Orbitrap MS. Separation used a Waters ACQUITY UPLC HSS T3 column (1.8 μm , 2.1 mm $\times$ 100 mm) at 40°C . Mobile phases: A = water + 0.1% formic acid, B = acetonitrile + 0.1% formic acid. Gradient: 0–2 min, 5–25% B; 2–4 min, 25–99% B; 4–5.5 min, 99% B; 5.5–6.0 min, 99–5% B; 6.0–7.0 min, 5% B. Flow rate 0.4 mL/min, injection 4 μL . MS operated in ESI+ and ESI− modes (mass range 50–1250 Da) with data-dependent MS/MS. QC samples (pooled extracts) were injected every 10 runs. Metabolites were identified by matching MS/MS spectra to in-house and public databases (HMDB, Metlin) with mass tolerance ≤ 10 ppm and retention time alignment. Features with VIP > 1 (OPLS-DA) and $|\log_2\text{FC}| \geq 1.2$ were considered DAMs.

2.8. Bioinformatics Analysis

GO and KEGG enrichment analyses were performed using clusterProfiler (v4.6.0) in R (v4.2.1). GSEA was run with pre-ranked $\log_2\text{FC}$ values. For multi-omics integration, Spearman correlation coefficients between DEGs and DAMs were calculated using the psych package; networks ($|\rho| > 0.7$, $p < 0.05$) were visualized in Cytoscape (v3.9.1). Figures were generated with ggplot2 (v3.3.6) and ComplexHeatmap (v2.14.0).

2.9. Statistical Analysis

All physiological data are presented as mean $\pm$ SD. Comparisons among treatments were performed by one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) post hoc test, using R software (v4.2.1). A p -value < 0.05 was considered statistically significant. For differential gene expression analysis, raw read counts were analyzed using DESeq2 (v1.38.3) with the Wald test and Benjamini–Hochberg correction for multiple testing; genes with $|\log_2(\text{FC})| \geq 1$ and adjusted $p < 0.05$ were considered differentially expressed. For metabolomics data, OPLS-DA was performed using the MetaboAnalystR package (v1.0.1) in R, and VIP scores were calculated to identify discriminating metabolites. GO and KEGG enrichment analyses were carried out using clusterProfiler (v4.6.0), and figures were generated using ggplot2 (v3.3.6) and ComplexHeatmap (v2.14.0) in R.

3. Results

3.1. Monochromatic Light Qualities Differentially Govern Phenotype, Growth, and Phosphorus Utilization of Pi-Starved Banana Seedlings

After a three-week exposure to Pi-deficient conditions, a pronounced growth inhibition was observed in banana seedlings under white light (WL), characterized by severe stunting compared to the Pi-sufficient controls (WL + P). However, the application of specific monochromatic light qualities elicited markedly divergent morphological outcomes (Figure 1A). Notably, far-red (FR) light most effectively promoted shoot elongation, followed by red (R) light, whereas both blue (B) and ultraviolet (UV-A) light significantly exacerbated the growth suppression relative to the WL treatment (Figure 1B). Consistent with these phenotypic observations, total phosphorus content in the leaves of FR-treated seedlings was significantly higher than that of the WL group, and a similar trend, though less pronounced, was observed under UV-A light (Figure 1C). This suggests that specific wavelengths may help sustain phosphate homeostasis, possibly by modulating the expression and activity of phosphate transporters. Moreover, mineral element analysis (Figure S1) revealed that FR light significantly enhanced the accumulation of iron (Fe) and calcium (Ca), while B light tended to suppress their uptake. These findings indicate a complex interplay between light quality signaling and the assimilation of essential mineral nutrients beyond phosphorus.

3.2. Light Qualities Exert Spectrum-Specific Control over the Expression of Core Phosphorus Starvation-Responsive Genes

To validate the transcriptomic data and pinpoint key regulatory nodes within the phosphate starvation signaling network, we performed RT-qPCR to quantify the expression of twelve central genes, including members of the *MaPHR1* family, *MaPHO1A*, and various *MaPAP* genes. The quantitative results demonstrated a high degree of concordance with the FPKM values obtained from the RNA-seq analysis (Figure 2). More importantly, the expression patterns of these P-starvation-responsive genes were drastically influenced by the specific light environment. For instance, the transcript abundance of the phosphate transporter *MaPHO1A* was sharply upregulated under B and R light, while *MaPAP28*, an

acid phosphatase-encoding gene, was strongly induced by UV light. These results imply that monochromatic light does not simply act additively with low-Pi signals; rather, it imposes precise, pathway-specific transcriptional controls through synergistic or antagonistic interactions with core transcriptional regulators such as PHR1.

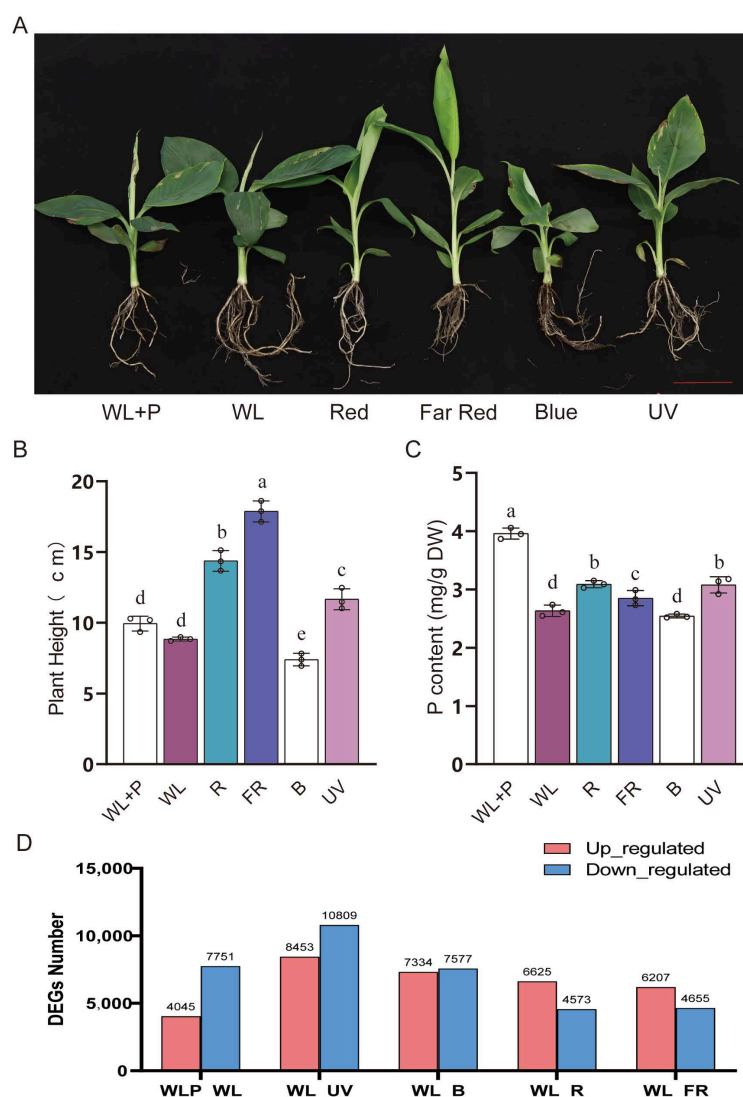


Figure 1. Phenotypic, physiological, and global transcriptomic responses of banana seedlings to different light qualities under low phosphorus stress. **(A)** Morphological phenotypes of banana seedlings under different light conditions (WL + P, WL, Red, Far Red, Blue, UV-A) after 3 weeks of treatment. Scale bar = 10 cm. **(B)** Plant height of seedlings under various treatments. **(C)** Total phosphorus content in leaves. **(D)** Number of differentially expressed genes (DEGs) identified in pairwise comparisons between WL-P and other light treatments. Data in **(B,C)** are presented as mean $\pm$ SD. Different lowercase letters indicate significant differences ($p < 0.05$) according to one-way ANOVA followed by Tukey's test.

3.3. Transcriptomic Reprogramming by Distinct Light Qualities Reveals Divergent Stress and Adaptive Pathways

Global transcriptional profiling under the various light regimes, coupled with GO enrichment analysis, revealed that each light quality governs a distinct set of biological processes (Figure 3). B and UV-A light treatments strongly enriched pathways associated with the cell cycle, DNA replication, and oxidative stress responses, suggesting that high-energy, short-wavelength lights impose severe cumulative stress on Pi-deprived seedlings. Conversely, FR light specifically enriched GO terms related to cell wall biogenesis and

photosynthesis, which aligns with its ability to sustain photosynthetic stability and promote growth under phosphorus-deficient conditions. While Pi deficiency itself triggered substantial transcriptional responses involving secondary metabolism and carbon fixation (Figure S2A,B), the addition of specific monochromatic lights, particularly B and UV-A, intensified and redirected these responses. Notably, UV-A and B light induced a significantly greater number of differentially expressed genes (DEGs) than R or FR light (Figure S2C–F).

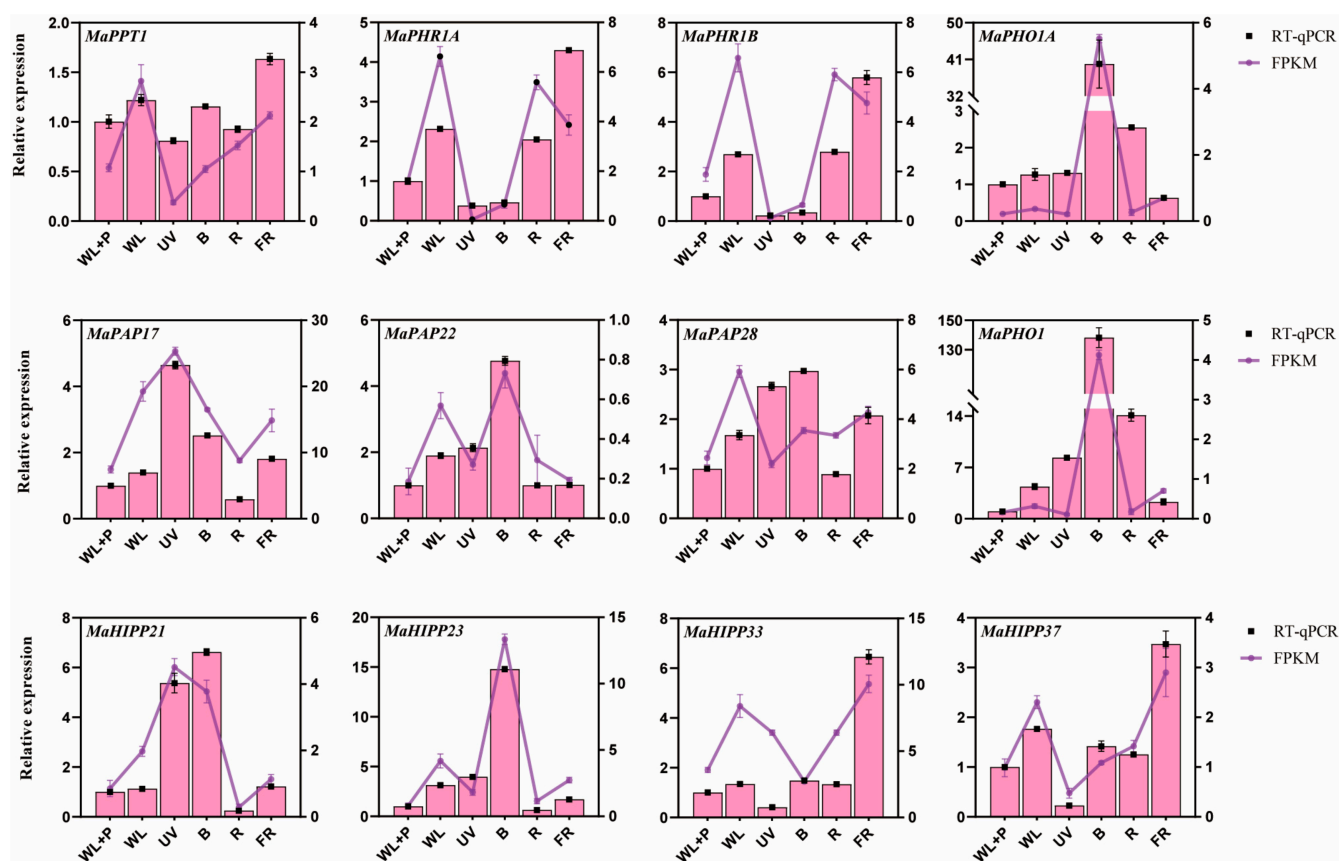


Figure 2. Validation of RNA-sequencing data by RT-qPCR. Expression profiles of selected genes (*MaPPT1*, *MaPHR1A*, *MaPHR1B*, *MaPHO1A*, *MaPAP17*, *MaPAP22*, *MaPAP28*, *MaPHO1*, *MaHIPP21*, *MaHIPP23*, *MaHIPP33*, *MaHIPP37*) under different light qualities. The left y-axis indicates the relative expression levels determined by RT-qPCR (histograms), while the right y-axis shows the FPKM values derived from RNA-seq data (line charts). The data demonstrate a high consistency between the two methods.

3.4. Light Quality Coordinates Glutathione Metabolism and Antioxidant Enzymes to Maintain Cellular Redox Homeostasis

Low phosphorus stress can disrupt cellular redox balance, leading to the accumulation of reactive oxygen species (ROS). Our results show that H_2O_2 content peaked under B light treatment, indicating this condition induced the most severe oxidative damage (Figure 4E). To counteract this ROS burst, the plant's antioxidant defense system was precisely activated in a spectrum-specific manner. Transcriptomic mapping of the glutathione (GSH) metabolism pathway revealed a reprogramming of gene expression, with UV light significantly upregulating multiple GGT and GPX family members (Figure 4A–D). Corroborating this transcriptional data, enzymatic activity assays (Figure 4F–J) demonstrated that B light triggered the strongest activation of Superoxide Dismutase (SOD), Catalase (CAT), and Peroxidase (POD), whereas UV-A light particularly enhanced Glutathione Peroxidase (GSH-Px) activity.

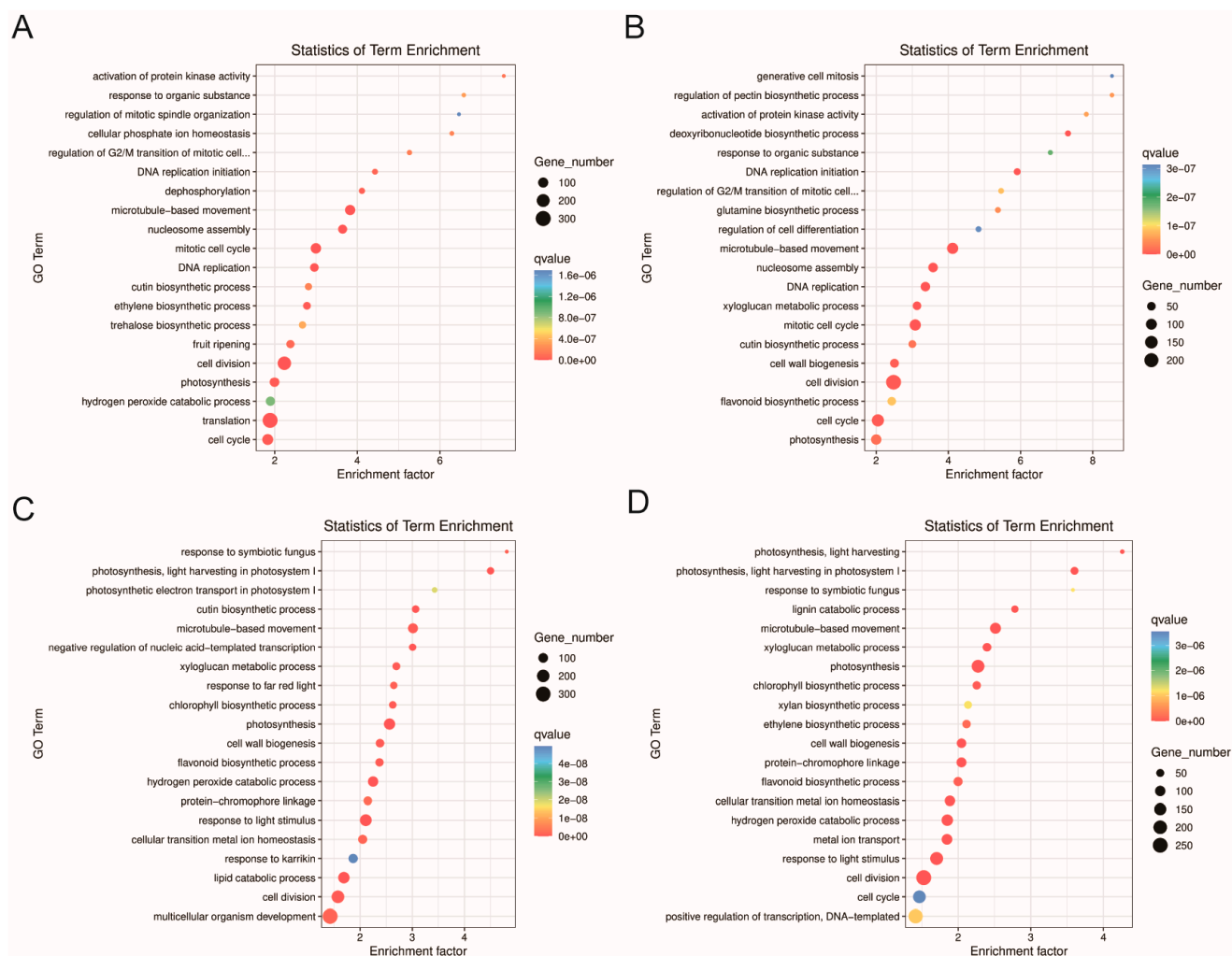


Figure 3. GO enrichment analysis of DEGs under different light qualities compared to WL. (A–D) Bubble charts showing significantly enriched Gene Ontology (GO) terms for the specific comparisons of WL_UV (A), WL_B (B), WL_R (C), and WL_FR (D). The size of the bubble represents the number of genes, and the color gradient represents the q-value (adjusted p -value). GO terms related to photosynthesis, cellular homeostasis, cell cycle, and secondary metabolism are prominently highlighted, indicating distinct physiological adaptations to different light spectra.

3.5. Metabolomic Profiling and Multi-Omics Integration Uncover Distinct Regulatory Networks Under Altered Light Qualities

To further explore the metabolic underpinnings of light-regulated responses under Pi deficiency, we performed non-targeted metabolomic analysis. The results showed that B and UV-A treatments caused the most profound changes in metabolic accumulation, with a greater number of differentially accumulated metabolites (DAMs) identified compared to R and FR treatments (Figure 5A). KEGG pathway enrichment (Figure 5B–F) and Gene Set Enrichment Analysis (GSEA) (Figure S3A) consistently pointed to amino acid biosynthesis, ABC transporters, and the biosynthesis of secondary metabolites (e.g., flavonoids) as the central metabolic hubs responding to light-imposed stress. Metabolite screening by VIP (Variable Importance in Projection) scores (Figure S3B) further highlighted the significant accumulation of abscisic acid (ABA) and its derivatives, especially under B and UV-A conditions.

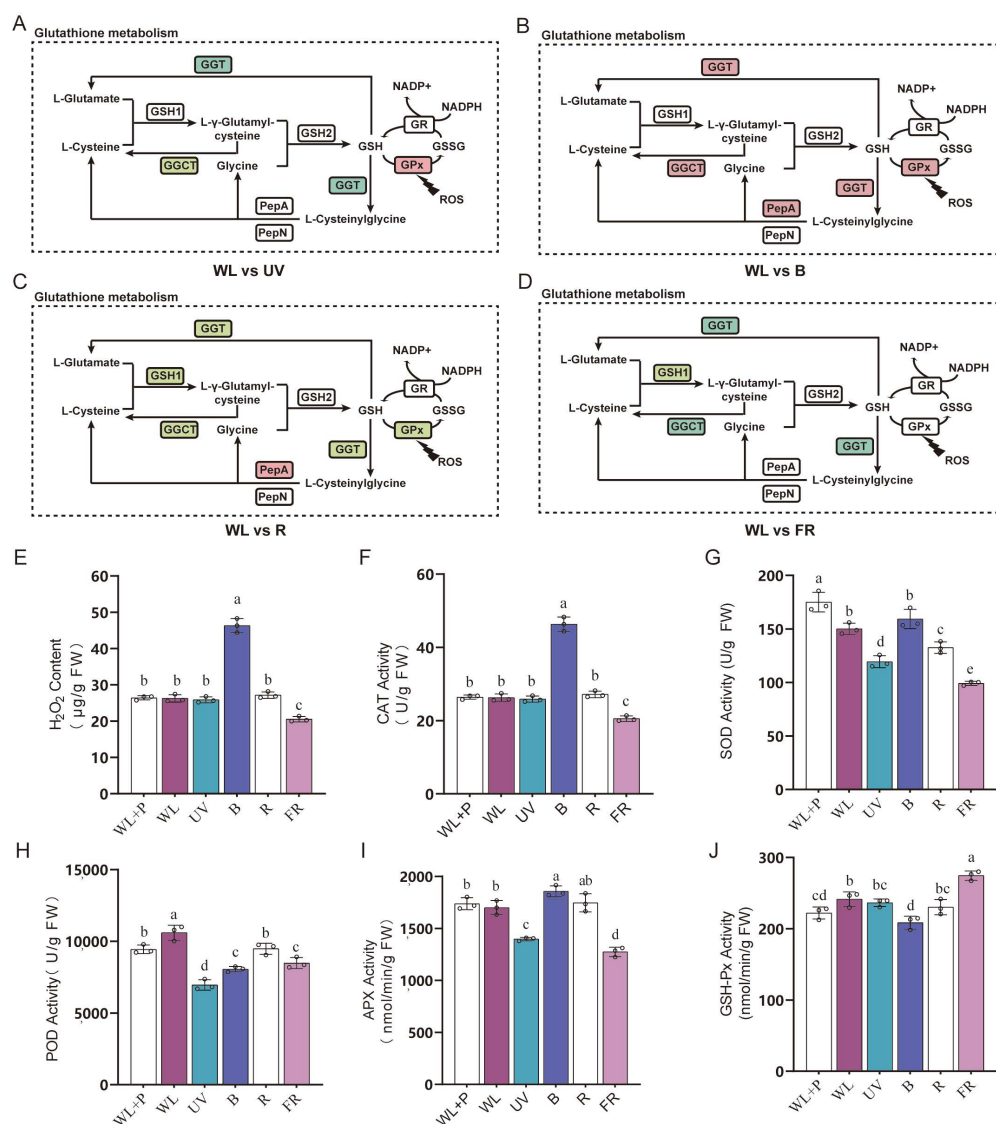


Figure 4. Light quality modulates glutathione metabolism and the antioxidant enzyme system under Pi deficiency. (A–D) Schematic representation of the glutathione metabolism pathways, with differentially expressed genes indicated in red (upregulated) and green (downregulated) boxes for the comparisons WL_UV (A), WL_B (B), WL_R (C), and WL_FR (D). (E) H₂O₂ content. (F–J) Activities of antioxidant enzymes: CAT (F), SOD (G), POD (H), APX (I), and GSH-Px (J). Data are shown as mean $\pm$ SD, and statistical significance is indicated by different lowercase letters ($p < 0.05$).

Importantly, to decipher the systemic regulatory network, we integrated transcriptomic and metabolomic datasets. Spearman correlation analysis revealed a comprehensive co-regulation landscape between gene expression profiles and metabolite accumulation patterns under the basic Pi deficiency (Figure S4). Furthermore, combined KEGG enrichment analysis of the integrated transcriptomic and metabolomic data (Figure S5) revealed functional convergence across different light qualities, where plant hormone signal transduction, starch and sucrose metabolism, and flavonoid biosynthesis were synergistically enriched. Notably, specific transcriptome–metabolome interaction networks built for B and R light treatments uncovered highly divergent regulatory hubs (Figure S6): the network under blue light (WL_B) was highly centralized on ROS-scavenging enzymes and stress defense compounds, whereas the network under red light (WL_R) was dominated by phosphate transporter-related genes and primary carbon metabolism hubs.

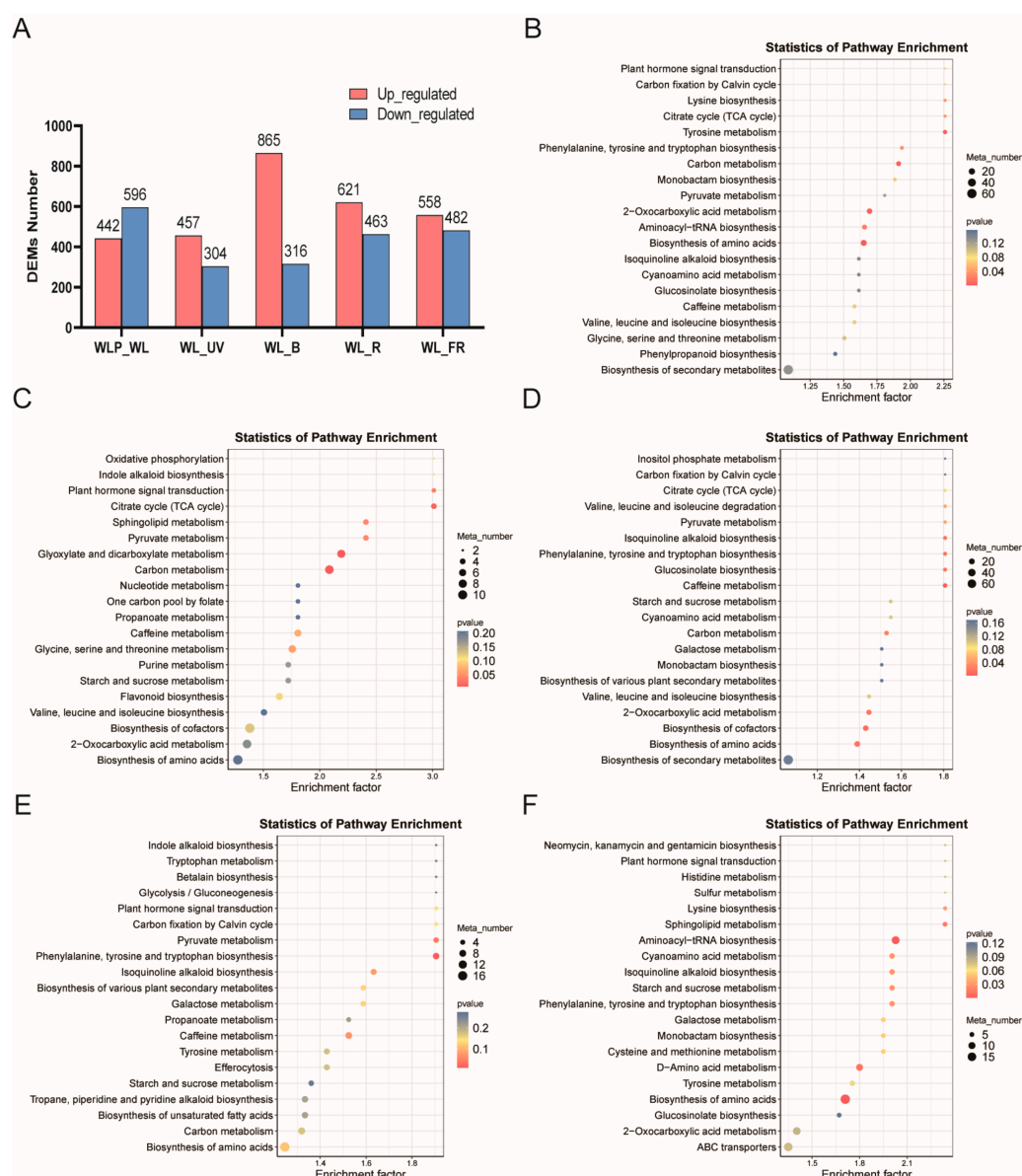


Figure 5. Metabolic profiling and pathway enrichment analysis of banana leaves under different light conditions. **(A)** The number of differentially accumulated metabolites (DAMs) in different comparison groups. **(B–F)** KEGG pathway enrichment analysis of the DAMs for the comparisons WL-P_WL **(B)**, WL_UV **(C)**, WL_B **(D)**, WL_R **(E)**, and WL_FR **(F)**. The size of the bubble represents the gene count, and color indicates the *p*-value. The results highlight that blue and UV light treatments cause massive metabolic reprogramming.

3.6. Light Quality Modulates a Hormonal Signal Transduction Cascade Governing Osmotic Adjustment and Stress Physiology

We next investigated the role of phytohormones in mediating the light–Pi stress interactions. KEGG pathway mapping (Figure 6A–D) revealed that, compared to WL, both UV-A and B light treatments significantly activated key genes involved in abscisic acid (ABA), jasmonic acid (JA), and ethylene (ETH) signaling pathways. This transcriptional activation was translated into distinct physiological outcomes: B and UV-A treatments led to a significant accumulation of proline (Pro) and elevated malondialdehyde (MDA) levels (Figure 6E,F), indicative of severe osmotic stress and membrane lipid peroxidation. Furthermore, phenylalanine ammonia-lyase (PAL), the rate-limiting enzyme of the phenylpropanoid pathway, showed significantly higher activity under B and FR light compared to other groups (Figure 6G).

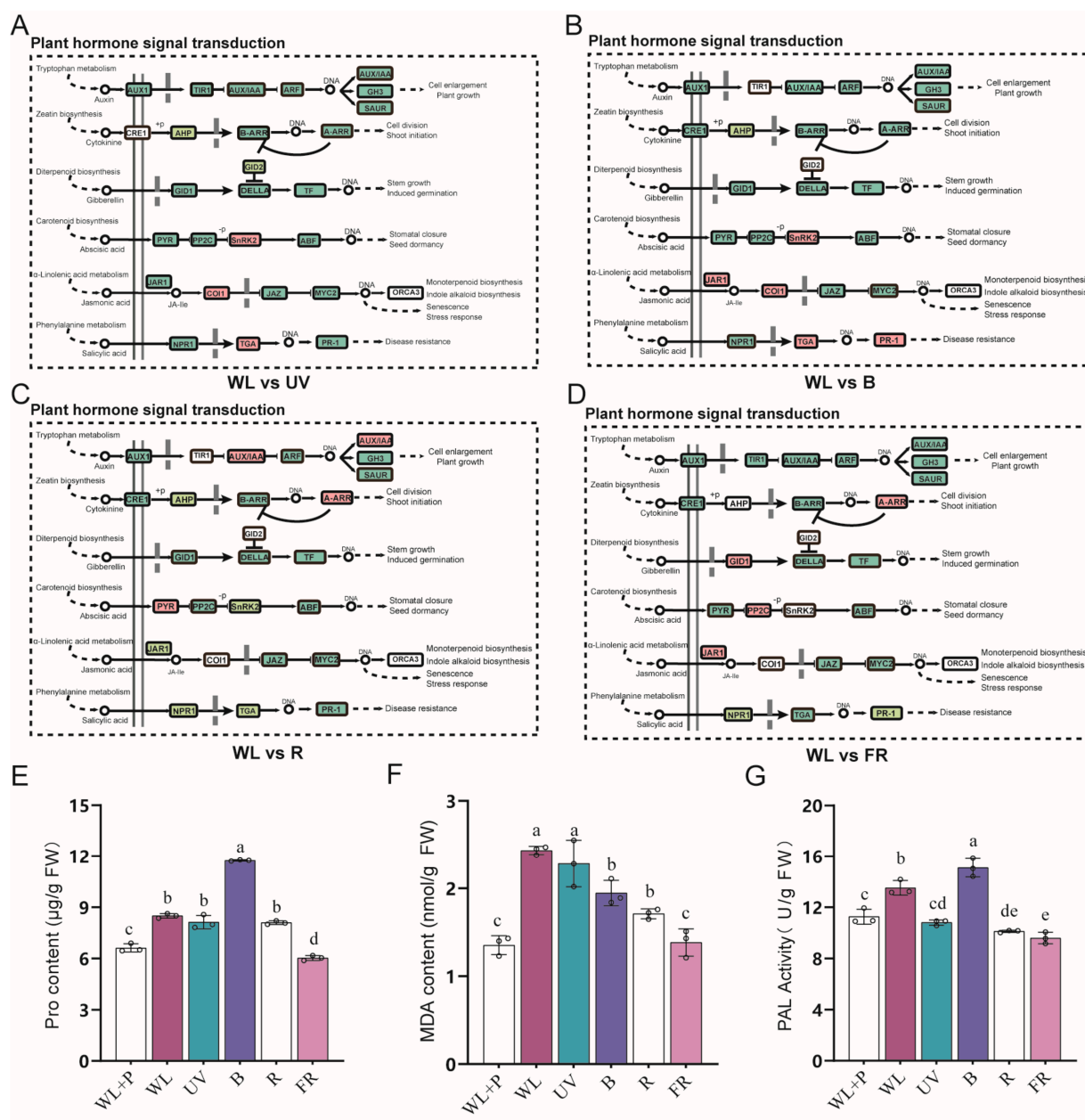


Figure 6. Plant hormone signal transduction and stress-related physiological indicators. (A–D) KEGG pathway maps illustrating the differential expression of genes involved in plant hormone signal transduction pathways across the WL_UV (A), WL_B (B), WL_R (C), and WL_FR (D) comparisons. Red and green boxes indicate up- and down-regulated genes, respectively. Arrows indicate promotion or inhibition. (E) Proline (Pro) content. (F) Malondialdehyde (MDA) content. (G) Phenylalanine ammonia-lyase (PAL) activity. Data are mean $\pm$ SD, different letters indicate significant differences at $p < 0.05$.

4. Discussion

In this study, we have provided a comprehensive integrated transcriptomic and metabolomic analysis of the interactive effects between light quality and phosphorus starvation in banana. Our findings reveal that monochromatic light spectra are not merely modulators of plant growth but are powerful determinants of the plant's physiological, transcriptomic, and metabolic adaptation to nutrient stress. The distinct effects of different wavelengths, ranging from the alleviating effects of FR to the exacerbating effects of UV and B light, highlight a complex regulatory network that integrates light signaling with the phosphate starvation response (PSR).

4.1. Light Quality Shapes Growth, Ion Homeostasis, and the Core PSR Network

One of the most striking findings of this study is that FR light, rather than R light, was the most effective in promoting shoot elongation and improving phosphorus and mineral (Fe, Ca) accumulation under Pi deficiency. This is counterintuitive, as FR light is often associated with the shade avoidance syndrome, promoting elongation at the cost of biomass, yet it appears to also confer an advantage under nutrient scarcity [29]. The enhanced Fe and Ca accumulation under FR light could be linked to increased transpiration-driven nutrient uptake or to the specific expression of metal transporters co-regulated with Pi transporters [30]. This suggests that FR light may activate a unique adaptive program that prioritizes shoot elongation and nutrient acquisition, possibly through phytochrome-mediated signaling that bypasses the typical growth-inhibitory effects of Pi starvation. Conversely, the suppressive effect of B and UV-A light on growth correlates with their strong induction of stress-related genes and metabolic pathways, indicating that these short-wavelength lights act as a secondary stressor that intensifies the negative effects of Pi deficiency.

The spectrum-specific expression of core PSR genes provides molecular evidence for this differential regulation. The upregulation of *MaPHO1A* under B and R light suggests that these wavelengths can directly or indirectly enhance the expression of transporters for Pi uptake and translocation, even when overall growth is suppressed. This aligns with previous reports in *Arabidopsis* where light signaling components have been shown to regulate PHO1 expression [31]. Meanwhile, the UV-specific induction of *MaPAP28* indicates that UV-A light may promote the remobilization of internal phosphorus by upregulating genes encoding acid phosphatases, a crucial strategy to cope with Pi deficiency [32].

4.2. Divergent Transcriptomic and Metabolic Landscapes Orchestrated by Light Quality

The transcriptomic data clearly demonstrate that different light qualities trigger massive and divergent reprogramming of gene expression. The strong enrichment of pathways related to cell cycle and DNA replication under B and UV-A light suggests a stress-induced inhibition of cell division, which correlates with the observed growth inhibition [33]. On the other hand, the enrichment of photosynthesis-related GO terms under FR light is consistent with its role in promoting photochemical efficiency and maintaining carbon fixation under stress conditions [34].

The metabolomic analysis complemented the transcriptomic data, revealing that the most substantial metabolic shifts occurred under B and UV light, with a strong emphasis on secondary metabolism. The accumulation of flavonoids and other phenolic compounds is a classic hallmark of UV stress but is also part of a general antioxidant response [35]. The significant increase in ABA and its derivatives under short-wavelength light indicates the activation of a major stress hormone signaling pathway. This is further supported by the transcriptomic evidence of ABA, JA, and ETH pathway activation. ABA and JA are known to play positive roles in plant adaptation to a variety of stresses, including nutrient deficiency, by regulating stomatal closure, promoting ROS scavenging, and inducing the expression of defense genes [36–38]. The interplay between ABA and light signaling, particularly through the PHR1 and other transcription factors, may be a central hub for coordinating the plant's response to the combined stress of light quality and Pi deficiency [16].

4.3. Orchestration of Antioxidant Defense in a Spectrum-Specific Manner

The oxidative stress data clearly indicate that B and UV-A light treatments induced more severe oxidative damage, as evidenced by higher H₂O₂ and MDA levels. However, the plant's antioxidant systems were not activated uniformly. We observed a fascinating

pattern of specificity: B light triggered a broader activation of canonical ROS-scavenging enzymes (SOD, CAT, POD), while UV-A light specifically enhanced the glutathione-dependent pathway (GSH-Px) [39]. This suggests that the plant can distinguish between different light-induced oxidative challenges and deploy a tailored antioxidant response. This finding is novel and important, as it demonstrates the plasticity of the plant's stress response machinery. The Fenton chemistry promoted by the elevated Fe content under FR light could also contribute to ROS management, although this remains speculative.

Interestingly, despite the generally higher oxidative potential of UV-A compared to blue light, we observed the highest H₂O₂ levels under B. This may be attributed to the lower PPFD used for UV-A and the fact that blue light, through cryptochrome signaling, can directly stimulate NADPH oxidase-dependent ROS production [40], while UV-A may activate more efficient glutathione-based detoxification (as evidenced by stronger GSH-Px induction). Such spectrum-specific ROS dynamics have been observed in other species [41].

4.4. Implications for Agriculture and Future Directions

Our results have significant implications for sustainable agriculture. The manipulation of light spectra using LED technology offers an unprecedented opportunity to manage crop stress in controlled environments. The specific effects of FR light in alleviating Pi deficiency could be harnessed to improve the efficiency of Pi uptake and utilization in banana, a crucial crop often grown in Pi-poor soils. While UV-A and B light exacerbate stress, they also trigger the accumulation of health-promoting secondary metabolites like flavonoids, which could be exploited for enhancing the nutritional quality of fruits (e.g., in postharvest applications). Future research should focus on the molecular identification of the photoreceptors and downstream transcription factors mediating these responses, and on testing the effectiveness of “light-priming” strategies for enhancing crop resilience in the field.

5. Conclusions

In conclusion, this study provides the first integrated transcriptomic and metabolomic characterization of light-quality effects on Pi-starved banana seedlings. Our main findings are: (1) FR light alleviates Pi deficiency by enhancing growth and nutrient uptake; (2) B and UV-A aggravate oxidative stress but trigger distinct antioxidant responses (B: SOD/CAT/POD; UV-A: GSH-Px); and (3) integrated network analysis reveals that blue light centers on ROS scavenging while red light prioritizes phosphate transport. The originality lies in the spectrum-specific reprogramming of hormonal and metabolic pathways, which has not been previously reported in banana. These results offer a practical basis for using LED lighting to manage phosphorus nutrition in controlled-environment banana cultivation, and highlight the need for further research on photoreceptor-mediated signaling under nutrient stress.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12080908/s1>. Figure S1: Effects of different light qualities on the accumulation of mineral elements in banana leaves. Figure S2: Transcriptomic landscape of banana seedlings in response to Pi deficiency and various light spectra. Figure S3: Gene Set Enrichment Analysis (GSEA) and metabolite VIP scores. Figure S4: Spearman correlation heatmap of transcriptomes and metabolomes under phosphorus deficiency. Figure S5: Integrated KEGG pathway enrichment analysis of transcriptomes and metabolomes under distinct light qualities. Figure S6: Distinct transcriptome–metabolome interaction networks under blue and red light treatments. Table S1: Primers used in this study. Table S2: DEGs Summary. Table S3: DEMs Summary.

Author Contributions: Conceptualization, Z.Z., P.W. and J.X.; methodology, Y.H.; software, Y.C. and D.Q.; validation, J.F. and W.W.; investigation, M.Z. and D.Z.; resources, P.W., Y.W. and D.Z.; data

curation, Y.H. and Z.Z.; writing—original draft preparation, Y.H. and Z.Z.; writing—review and editing, J.X. and P.W.; project administration, J.X., Y.W. and Z.Z.; funding acquisition, Z.Z., W.W. and J.X. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the Scientific Institution Basal Research Fund for Chinese Academy of Tropical Agricultural Sciences (1630052025004), and the Youth Talent Project of State Key Laboratory of Tropical Crop Breeding (SKLTCBQN202510).

Data Availability Statement: The original contributions presented in the study are included in the article/Supplementary Materials; further inquiries can be directed to the corresponding authors.

Conflicts of Interest: The authors declare no conflicts of interest.

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