



EDITORIAL

Plant Secondary Metabolism and Functional Biology

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1 Plant Secondary Metabolism and Functional Biology Progress

Plants have long been recognized as biochemical powerhouses, producing a vast array of compounds through their secondary metabolic pathways [1]. Although historically referred to as 'secondary' due to their perceived non-essential role in basic plant survival, it is now understood that these metabolites are integral to plant growth, development and adaptation to environmental challenges. Secondary metabolites, such as alkaloids, terpenoids, phenolics and flavonoids, serve as critical mediators of plant-environment interactions, conferring resistance to biotic and abiotic stressors [2]. Beyond their ecological functions, these compounds are invaluable to humans, supporting industries ranging from pharmaceuticals and nutrition to agrochemicals and chemical additives.

The biosynthesis of secondary metabolites in plants is a complex, highly regulated process involving intricate metabolic pathways and molecular machinery. Secondary metabolites are derived from primary metabolic precursors, such as amino acids, sugars, and fatty acids, through specialized enzymatic pathways [3]. These pathways are often compartmentalized within specific tissues or organelles, reflecting their spatiotemporal regulation [4]. Advances in understanding these regulatory networks have revealed that secondary metabolite production is not a static process but a dynamic response to internal and external stimuli, enabling plants to adapt to changing environments [5]. These discoveries provide a foundation for manipulating biosynthetic pathways to enhance the production of valuable secondary metabolites.

By integrating data from multiple biological layers, researchers can construct comprehensive models of metabolic networks, identify key regulatory nodes, and uncover novel biosynthetic genes. Genomics has been instrumental in identifying gene clusters responsible for secondary metabolite biosynthesis [6]. Transcriptomics has enabled the identification of differentially expressed genes under various environmental conditions [7]. Proteomics complements transcriptomics by giving us information about the functional proteins involved in secondary metabolism. Mass spectrometry-based proteomics has enabled the identification of enzymes and regulatory proteins that are post-translationally modified, offering a deeper understanding of pathway dynamics [8]. The integration of multi-omics data, facilitated by bioinformatics tools and machine learning, has enabled the construction of predictive models for secondary metabolism. Systems biology approaches, such as network analysis, have identified key regulatory hubs that control metabolic flux, paving the way for targeted metabolic engineering [9,10].



Synthetic biology has emerged as a powerful tool for reconstructing and optimizing metabolic pathways, enabling the large-scale production of valuable secondary metabolites. In plants, metabolic engineering strategies often involve the overexpression or silencing of key biosynthetic genes [11]. Heterologous expression systems, such as bacteria, yeast, or plant cell cultures, offer an alternative approach for producing secondary metabolites [12]. Synthetic biology has also enabled the creation of novel metabolic pathways by combining enzymes from different species, leading to the production of non-natural analogs with enhanced bioactivity. CRISPR/Cas9-based gene editing has further revolutionized metabolic engineering by enabling precise modifications to biosynthetic genes [13,14].

The physiological regulation of secondary metabolism is tightly linked to stress response pathways, allowing plants to dynamically adjust their metabolic output. Biotic stressors, such as herbivory and pathogen attack, trigger the production of defense-related secondary metabolites, such as glucosinolates, terpenoids, and phytoalexins [15]. Abiotic stressors, such as drought, salinity, and temperature extremes, induce the accumulation of secondary metabolites with protective functions [16]. The physiological regulation of secondary metabolism involves complex signaling networks, including phytohormones like jasmonic acid, salicylic acid, and abscisic acid [17]. These hormones act as master regulators, coordinating the expression of biosynthetic genes in response to stress. These hormones act as master regulators, coordinating the expression of biosynthetic genes in response to stress [18]. Recent studies have also revealed the role of secondary metabolites in plant growth and development, challenging their “secondary” classification [19,20].

Despite their significance, the low natural abundance of many secondary metabolites poses a challenge for large-scale production, limiting their commercial and therapeutic potential. Recent advances in plant biology, particularly in understanding the biosynthesis, regulation, and functional roles of these compounds, have provided fresh prospects for overcoming these limitations. This editorial investigates the various facets of plant secondary metabolism, focusing on biosynthesis and molecular control, multi-omics approaches, metabolic engineering through synthetic biology, and the role of secondary metabolites in stress tolerance and physiological regulation. By probing these areas, we aim to highlight the transformative potential of secondary metabolites in both plant biology and human applications.

2 Key Advances and Contributions

2.1 *Ginseng PgZFP Gene in Response to Methyl Jasmonate (Jiang et al.)*

Jiang et al. conducted a correlation analysis to examine the relationship between *PgZFP* gene expression and ginsenoside content. *PgZFPs* belong to the C₂H₂-type zinc finger protein family. The researchers also conducted a genome-wide association study of *PgZFPs* and a co-expression analysis linking *PgZFPs* with validated key enzyme genes. Through this research, they identified five candidate genes involved in ginsenoside biosynthesis. *In vitro* experiments using methyl jasmonate induction confirmed the roles of *PgZFP27* and *PgZFP59* in ginsenoside biosynthesis [21].

2.2 *Comparative Transcriptomic Analysis of Two Tomato Cultivars (Amin et al.)*

Amin et al. screened two tomato cultivars, Riogrand and Salar F1, from a total of 19 cultivars that varied in shelf life. Riogrand exhibited greater firmness and less weight loss than SalarF1. During post-harvest storage, SalarF1 produced notably more ethylene than Riogrand. Transcriptomic analysis revealed that differentially expressed genes (DEGs) were enriched in pathways associated with ethylene biosynthesis and response, as well as with cell wall structure. Forty days post-harvest (DPH), ERF2 and ERF4 were highly expressed in SalarF1, which has a shorter shelf life. The ethylene biosynthetic genes ACO1, ACO4, ACS6, and ACS2 were significantly upregulated in SalarF1 [22].

2.3 Transcriptome and Phenolic Compounds Profile of Soursop (Palomino-Hermosillo et al.)

Palomino-Hermosillo et al. conducted a thorough analysis of the soursop transcriptome and phenolic compound profiles during ripening. Their integration analysis revealed that genes and phenolic compounds primarily participate in starch and sucrose metabolism pathways during soursop ripening. The phenolic compounds and genes were found to be correlated and differentially accumulated and expressed: kaempferol 3-O-galactoside, procyanidin C1, procyanidin trimer C1, m-coumaric acid, ubiquitin-like protein 5, ATP-dependent zinc metalloprotease FtsH8, zinc transporter 4, thioredoxin-like 3-1, mitogen-activated protein kinase, 26S protease regulatory subunit 6A homolog, CYP72A13, CYP84A1, and homoserine O-transacetylase [23].

2.4 Petal Color Transition in *Hibiscus mutabilis* Flowers (Shi et al.)

Shi et al. investigated the mechanisms behind the production of primary active compounds in *Hibiscus mutabilis* using metabolomics and transcriptomics analyses. The white and pink flowers have different flavonoid metabolism, with pink flowers having a higher flavonoid content. The transition from white to pink in cotton rose flowers may be associated with the formation of pelargonidin-3-O-glucoside. Expression analysis of genes associated with flavonoid structure revealed that pink flowers had more genes that were upregulated than white flowers. This resulted in increased flavonoid accumulation in pink flowers, highlighting the potential applications and developmental value of cotton rose flowers [24].

2.5 MYB Gene in Fatty Acid Biosynthesis of Walnut (Su et al.)

Su et al. investigated *JrMYB* genes through whole-genome and transcriptomic analyses to identify *MYB* genes potentially associated with fatty acid metabolism. 126 *MYB* genes were identified in the walnut genome, characterized by hydrophilic proteins with lengths ranging from 78 to 1890. The cis-acting elements in the promoter regions of these genes are associated with cellular development, environmental stress, and phytohormones. The transcriptomic profile indicated heterogeneous expression patterns of fatty acid-related genes across various tissues, exhibiting differing expression levels and patterns. Ten genes potentially implicated in the regulation of fatty acid synthesis were identified through the integration of the phylogenetic tree and expression level correlations [25].

2.6 Functional Analysis of *CsABCC11* in *Camellia sinensis* (Luo et al.)

Luo et al. identified 25 *CsABCC* genes in the tea plant genome and conducted analyses of the phylogenetic tree, gene structure, targeted miRNA, and other bioinformatics aspects. Expression patterns of *CsABCCs* in eight different tissues and under abiotic stress suggest their potential involvement in regulating tea's growth, development, and defense mechanisms. Correlation analysis revealed a close association between the expression of the *CsABCC11* gene and EGCG content in the buds of the 108 Kingbird strains. Furthermore, subcellular localization experiments in tobacco revealed that the *CsABCC11* is located on the plasma membrane. A virus-induced gene silencing experiment in tea plants further confirmed *CsABCC11*'s role in EGCG accumulation [26].

2.7 Metabolomic Analysis of the Anthocyanins of *Cymbidium goeringii* (Wu et al.)

Flower color is a significant feature of *C. goeringii* and contributes to its high economic value. To elucidate the molecular mechanisms, Wu et al. used the LC/MS method to perform metabolomics targeting anthocyanins on seven varieties of *C. goeringii*. A total of 64 anthocyanins were identified. Analysis of the differentially expressed metabolites revealed that peonidin-3-O-(6-O-malonyl- β -D-glucoside) is the

key metabolite responsible for the color variations among the varieties. Procyanidin B2, pelargonidin-3-O-galactoside, and naringenin may also play a role in the color formation of different varieties [27].

2.8 Formation Mechanism of Anthocyanins in *Chrysanthemum* (Liu et al.)

Liu et al. demonstrated that anthocyanin accumulation is highly dependent on light in the '2021135' genotype of chrysanthemum. Through phenotypic analysis of 44 F generations, the authors discovered that light independence is a dominant trait that can be stably inherited by progeny. Transcriptome data were collected from ray florets of both the '2021135' and '2001402' genotypes under light and bagging treatments. Using weighted gene co-expression network analysis (WGCNA), the authors identified 16 genes highly correlated with anthocyanin content. The result revealed that blue light significantly impacts anthocyanin accumulation in ray florets under various light conditions. Additionally, CmBIC1.1 and CmBIC1.2 directly regulate the anthocyanin-related gene *CmCHS2* [28].

2.9 *SQE08-01* Gene in Ginsenoside Biosynthesis in *Panax ginseng* (Zhu et al.)

Zhu et al. employed bioinformatics methods to systematically analyze the genes encoding squalene epoxidase (SQE) in ginseng. They selected six *PgSQE* candidates that are closely involved in ginsenoside biosynthesis and identified *PgSQE08-01* as being highly associated with this process. Subsequently, we constructed the overexpression vector pCambia3301-*PgSQE08-01* and the RNAi vector pART27-*PgSQE08-01*. We then transformed ginseng adventitious roots using *Agrobacterium rhizogenes* to obtain positive hairy root clones. The qRT-PCR and HPLC analyses were employed to analyze the expression of relevant genes and the ginsenoside content, respectively. The results demonstrated the role of the *PgSQE08-01* gene in ginsenoside biosynthesis [29].

3 Future Directions and Challenges

The study of plant secondary metabolism is at a pivotal juncture, with significant opportunities and challenges ahead. Advancements in multi-omics, synthetic biology, and gene editing have yielded sophisticated tools that facilitate the elucidation of intricate secondary metabolic pathways and the augmentation of their production. However, several challenges persist, including the scalability of metabolic engineering approaches, the ecological impact of genetically modified plants, and the ethical considerations of synthetic biology [30,31]. Future research endeavors should prioritize the integration of multi-omics data to develop predictive models of metabolic flux, thereby facilitating the design of efficient biosynthetic pathways. Furthermore, an exploration of the ecological and evolutionary roles of secondary metabolites will facilitate a more profound comprehension of their adaptive significance, thereby informing conservation and agricultural strategies. The development of sustainable production platforms, such as plant cell cultures and microbial factories, will be critical for meeting the growing demand for secondary metabolites in medicine, agriculture, and industry. Addressing public perception and regulatory frameworks surrounding genetically modified organisms and synthetic biology is imperative to ensure the safe and equitable application of these technologies [32,33]. The translation of scientific advances into practical solutions will require collaborative efforts between researchers, policymakers, and industry stakeholders.

4 List of Contributions

1. Jiang Y, Liu L, Wang K, Zhao M, Chen P, Lei J, et al. Response of the ginseng C₂H₂-type zinc finger protein family *PgZFPs* gene to methyl jasmonate regulation. *Phyton-Int J Exp Bot.* 2024;93(11):3055–71. doi:10.32604/phyton.2024.056384.

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