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Special issue: Manipulation/regulation of secondary metabolites in medicinal plants

ABSTRACT

Medicinal plants, rich sources of valuable natural products with therapeutic potential, play a pivotal role in both traditional and modern medicine. The urgency for mass production and optimized utilization of plant secondary metabolites has intensified, particularly in response to the emergence of diseases following the COVID-19 pandemic. Groundbreaking advancements in genomics and biotechnologies have ushered in a new era of research, transforming our understanding of the biosynthesis, regulation, and manipulation of bioactive molecules in medicinal plants. This special issue serves as a convergence point for a diverse array of original research articles and reviews, collectively aiming to unveil the intricate regulatory mechanisms that govern the biosynthesis of secondary metabolites in medicinal plants. The issue delves into the exploration of the impact of both abiotic and biotic factors on the regulation of plant secondary metabolites. Furthermore, it extends its focus to innovative approaches, such as molecular breeding and synthetic biology, which provide valuable insights into modifying or enhancing the production of secondary metabolites. The special issue leverages cutting-edge techniques, including genomics, metabolomics, and microbiome characterization, to facilitate understanding the multifaceted aspects of specialized metabolism in medicinal plants. As we navigate through this scientific journey, the contributions within this special issue collectively enhance our knowledge and offer potential avenues for optimizing the production of natural products in medicinal plants.

1. Regulation at transcription level

The studies from original research articles featured in this issue delve into the intricate realm of transcriptional regulation in medicinal plants, unraveling the complex networks of genes and transcription factors. Mi et al. (2023) unraveled the regulatory network of rutin, a therapeutic flavonol in Tartary buckwheat, pinpointing FtMYB102 and FtbHLH4 as key transcription factors forming a complex that directly induced chalcone isomerase expression, thereby enhancing rutin production (Mi et al., 2023). Similarly, Han et al. (2023a) examined gene expression and metabolites in sumac pericarp, correlating it with increased flavonoid content, improving understanding on the biosynthetic pathways of flavonoid glycosides and bioflavonoids, besides their distribution in *Toxicodendron vernicifluum* fruits (Han et al., 2023a). Mishra et al. (2023) examined the role of the R2R3-MYB transcription repressor HlMYB7 in hop (*Humulus lupulus*), highlighting its role in the secondary metabolite biosynthesis, plant development, and disease susceptibility (Mishra et al., 2023).

The exploration extended to novel aspects, with Wei et al. (2023) uncovering the involvement of polyphenol oxidases from *Nicotiana tabacum* in pollen development by affecting flavonoid homeostasis and the reactive oxygen species signal pathway (Wei et al., 2023). Additionally, Li et al. (2023a) provided a comprehensive overview of tea germplasm, emphasizing molecular markers' pivotal roles in studying tea plant origin, evolution, germplasm preservation, identification, and breeding (Li et al., 2023a).

Further studies investigated triterpenoid variation in *Cyclocarya paliurus* and offered practical insights into the medicinal industry (Wang et al., 2023a), as well as phenylpropanoid glucosides biosynthesis in *Artemisia annua* (Yin et al., 2023a), and *O*-methyltransferases in *Angelica decursiva* (He et al., 2023). The metabolic flux of the flavonoid pathway in *Polygonatum cyrtonema* Hua was characterized by Han et al. (2023b), while Tian et al. (2023) expanded our understanding of diterpenoid alkaloid biosynthesis in the *Aconitum* genus. Finally, Fan et al. (2023a) linked the transcription of monoterpene synthases to volatile terpenoid production in *Zanthoxylum ailanthoides* (Fan et al., 2023a).

Collectively, these studies provide an important synthesis of the transcription regulatory mechanisms, offering insights into the biosynthesis, regulation, and manipulation of bioactive molecules in medicinal plants.

2. Regulatory mechanisms revealed by comparing closely-related species or cultivars

Several studies within this issue contribute valuable insights into the regulatory mechanisms governing the biosynthesis of natural products by dissecting metabolic and transcriptomic differences among cultivars or closely-related species. For example, Liu et al. (2023a) focused on two rose cultivars, Yellow Island and its bud mutant Past Feeling, to unravel genes and transcription factors associated with differentially accumulated metabolites. This exploration enabled the generation of models for biosynthetic pathways of shikimate, terpenoid, carotenoid, and green leaf volatile metabolites (Liu et al., 2023a). Schmiderer et al. (2023) investigated monoterpene synthases (TPS) in some *Salvia* species, revealing a noteworthy correlation between the expression levels of different TPS genes and the resulting composition of essential oils within these species (Schmiderer et al., 2023). Their finding suggested that gene duplication or triplication may significantly influence TPS expression in *Salvia* species. Fan et al. (2023b) studied flavonoid biosynthesis in *Citrus grandis* 'Tomentosa' in two varieties, Zheng-Mao

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and Guang-Qing, identifying 25 genes related to flavonoid biosynthesis and 16 differentially expressed transcriptional regulators (MYBs, bHLHs, WD40) between these two varieties (Fan et al., 2023b).

Zhang et al. (2023) explored differences between cultivated and wild *Atractylodes lancea* rhizomes (Zhang et al., 2023), revealing numerous differentially accumulated metabolites and expressed unigenes post-cultivation. The study showed a strong correlation between cultivation-altered volatile organic compounds and genes involved in sesquiterpenoid biosynthesis, resulting in a decrease of bioactive sesquiterpenoid concentration. In their exploration of two *Houttuynia cordata* accessions with distinct flavonoid content, Liu et al. (2023b) identified flavonoids as the most abundant metabolites with over a hundred differentially expressed genes related to flavonoid metabolism, highlighting eight candidate genes likely key to flavonoid synthesis and accumulation (Liu et al., 2023b).

Lim et al. (2023) investigated the molecular mechanisms underlying anthocyanin composition in radish roots of different colors, finding that variations in *RsF3′H* expression led to differences in anthocyanin types. Notably, RsMYB1 and RsTT8 were abundant in pigmented roots but scarce in white roots (Lim et al., 2023).

Collectively, these studies enrich our understanding of the regulatory mechanisms associated with transcriptional differences between closely related cultivars and species, shedding light on the synthesis and diversity of bioactive compounds in medicinal plants.

3. Regulation associated with biotic factors (bacteria, viruses and fungi)

The impact of biotic factors, encompassing bacteria, viruses, and fungi, on the regulation of secondary metabolites in medicinal plants is a dynamic and multifaceted aspect. Fan et al. (2023c) examined the intricate relationship between the phenotype of *Codonopsis pilosula*, secondary metabolites, antioxidant capacity, and rhizosphere soil nutrients across different regions and seasons. Their study revealed significant variations in rhizosphere soil properties and bacterial diversity, influencing root phenotype, stress resistance, and polysaccharide accumulation (Fan et al., 2023c).

Considering species from Cucurbitaceae family, Almeida et al. (2023) explored ways to enhance cucurbitacin production and uncovered that *Rhizobium rhizogenes* transformation reduced cucurbitacin level. This reduction was effectively compensated by overexpressing the cucurbitacin-inducing bHLH transcription factor 1 (*CpCUCbH1*) gene, resulting in substantial changes in the metabolic profile and transcriptome of hairy roots compared to wild-type roots (Almeida et al., 2023).

In Yunnan, China, *Panax notoginseng* plants exhibiting virus-induced leaf abnormalities were investigated by Chen et al. (2023), which identified ten viruses causing down-regulated saponin biosynthesis genes, reduced saponin content and photosynthesis-related enzyme activities. In response, antioxidant gene expression and enzyme activities increased, along with the up-regulation of resistance-related genes in *P. notoginseng* (Chen et al., 2023).

Thokchom et al. (2023) studied the influence of arbuscular mycorrhiza on the leaf metabolome of *Ocimum tenuiflorum* L., revealing increased activities and expression of enzymes in terpenoid, shikimate, and phenylpropanoid pathways. This resulted in a shift towards secondary metabolism over primary metabolism, facilitated by the allocation of carbon resources (Thokchom et al., 2023). Additionally, Xie et al. (2023) discovered that arbuscular mycorrhizal symbiosis enhanced the defense response of licorice plants against drought stress, evidenced by fewer dead leaves, less biomass reduction, and consistent lignin accumulation in roots (Xie et al., 2023). Under drought conditions, mycorrhizal roots showed elevated accumulation of specialized metabolites, including phenolics and flavonoids. Collectively, these studies highlight the intricate interplays between medicinal plants and biotic factors, underlining the diverse regulatory mechanisms behind secondary metabolism.

4. Regulation associated with elicitors/compounds

A series of studies investigate the regulatory impact of elicitors and compounds such as chitosan, β-cyclodextrin, methyl jasmonate, and ethephon on the synthesis of bioactive compounds in diverse medicinal plants. Sivanandhan et al. (2023) explored the effects of chitosan and β-cyclodextrin on Chinese cabbage shoots under controlled *in vitro* conditions. The study revealed that chitosan induced maximum glucosinolate synthesis but concurrently inhibited shoot growth, while β-cyclodextrin enhanced glucosinolate without compromising or even enhancing shoot growth (Sivanandhan et al., 2023). In the study by Sagharyan et al. (2023), the impact of methyl jasmonate (MeJA) on lignan accumulation in *Linum album* was investigated. MeJA influenced H_2O_2, NO, and lipid peroxidation levels, increasing antioxidant enzyme activity by redirecting free sugars and amino acids towards phenolic compound production (Sagharyan et al., 2023).

Yin et al. (2023b) employed MeJA to enhance resveratrol accumulation in peanut sprouts, and when combined with calcium chloride ($CaCl_2$), this elicitor increased resveratrol biosynthesis. The study elucidated the influence of MeJA on key enzyme activities and gene expression related to resveratrol biosynthesis, along with antioxidant capacities, sprout growth, and stress tolerance in peanut sprouts (Yin et al., 2023b). Karami et al. (2024) investigated biotechnological strategies for enhancing withanolide synthesis in *Withania somnifera* plants. Their study revealed that plant genotype, explant type, and *Agrobacterium* strain exerted significant influence on hairy root induction. Notably, the G3/ATCC/LEAF (genotype/*Rhizobium* strain/explant) culture combination demonstrated the highest efficacy, especially when subjected to β-cyclodextrin and MeJA treatments. These conditions led to substantial enhancements in withaferin A production, potentially attributed to the upregulation of *SMT-1*.

In another study, Yin et al. (2023c) optimized germination conditions for soybean to enhance isoflavone accumulation using exogenous application of ethephon (Yin et al., 2023c). Although ethephon treatment inhibited sprout growth, it concurrently increased antioxidant enzyme activities and ethylene synthesis, ultimately elevating the total flavonoid content in soybean sprouts during germination. Collectively, these investigations contribute to understand the intricate regulatory mechanisms associated with elicitors and compounds, offering insights into the manipulation of bioactive compound synthesis in medicinal plants for potential applications in various fields.

5. Regulation associated with abiotic stress/environmental and ecological conditions

Several articles within this issue delve into the intricate relationship between medicinal plants and their environment, exploring the impact of abiotic stress, as well as environmental and ecological conditions, on secondary metabolite production. These studies provide a comprehensive understanding of the holistic interplay between medicinal plants and their surroundings.

Mehravi et al. (2023) conducted a comprehensive assessment of the impact of water deficit stress on anise seeds. The study revealed that severe stress significantly reduced seed yield and various seed-related components, affecting physiological functions, fatty acid content, and essential oil composition (Mehravi et al., 2023). However, moderate drought stress increased essential oil content, altering bioactive compound production and thereby influencing the industrial and nutritional values of anise seeds.

In the study by Burton et al. (2023), the antibacterial activity of wild garlic was explored in hundreds of leaves across diverse ecological conditions (Burton et al., 2023). Allicin emerged as the sole metabolite positively correlated with antibacterial activity in wild garlic, exhibiting consistency across different ecological conditions. This finding suggests the independence of allicin production from growing conditions, reinforcing its significance as a key contributor to antibacterial properties in wild garlic.

Wang et al. (2023b) studied *Rubia cordifolia* L. for its secondary metabolites dynamics, focusing on higher concentrations of these metabolites in roots, especially purpurin. The study identified August as the optimal harvest period for *R. cordifolia*, revealing positive correlations between specific metabolites and gene expression (Wang et al., 2023b). These studies collectively contribute valuable insights into the impact of abiotic stress, environmental conditions, and ecological factors on secondary metabolite production in medicinal plants, enriching our understanding of their complex interactions with their surroundings.

6. Overview of recent advancements in the biosynthesis and regulation of secondary metabolites

This issue also features comprehensive reviews summarizing recent advancements in the biosynthesis and regulation of secondary metabolites. These reviews encompass diverse topics, ranging from the intricate molecular responses to cold stress, the application of metabolic engineering in hairy root cultures, anthocyanin synthesis in tea plants, ultraviolet (UV) stress adaptation in medicinal plants, CRISPR-based tools for plant metabolic engineering, and the commercial and biological potential of medicinal plants.

Cold stress significantly impacts plant growth and yield, prompting the activation of molecular mechanisms such as the ICE-CBF-COR (INDUCER OFCBF EXPRESSION- C-repeat binding factor- Cold regulated genes) signaling pathway (Gusain et al., 2023). Gusain et al. (2023) delve into the regulatory intricacies of this pathway, focusing on enhancing crop performance in low-temperature environments.

Hairy root cultures induced by *Rhizobium rhizogenes* offer a cost-effective and reliable alternative for metabolite production through metabolic engineering (Bagal et al., 2023). Bagal et al. (2023) underscore the potential of metabolic engineering in hairy roots to meet the increasing demands for secondary metabolites.

The review article by (Li et al., 2023b) delves into the high flavonoid content of tea plants, specifically the anthocyanin-enriched purple tea cultivars. It summarizes recent progress in understanding the anthocyanin composition, accumulation, and regulatory mechanisms, proposing a hypothetical model for leaf color transformation during growth.

Thakur et al. (2023) explore the commercial and biological potential of medicinal plants under UV stress, shedding light on their adaptation mechanisms (Thakur et al., 2023). The study emphasizes identifying key genes, transcription factors, proteins, biosynthetic pathways, and biological networks that play pivotal roles in the resilience mechanisms exhibited by high-altitude medicinal plants under UV stress. This exploration underscores the significance of understanding how these plants navigate environmental challenges, contributing to the rich array of diverse secondary metabolites that have been integral to medicine and nutraceuticals for centuries.

Shelake et al. (2023) discuss the multifactorial regulation of metabolic pathways, the application of CRISPR-based tools for plant metabolic engineering, and potential avenues for future research to enhance plant metabolic profiles (Shelake et al., 2023).

Guo et al. (2023) provide an extensive review of blue honeysuckle, a commercially valuable fruit rich in anthocyanins. The review detailed the research status, qualitative and quantitative analysis, extraction methods, and biological effects of blue honeysuckle (Guo et al., 2023).

Li et al. (2023c) address challenges and recent advancements in the development of medicinal plant resources, focusing on biosynthetic pathways, intracellular signal transduction, multi-omics applications, and gene editing technology (Li et al., 2023c). The aim is to promote the exploration and development of natural products from medicinal plants, providing valuable insights for future research and applications.

In summary, this special issue underscores the importance of comprehending the genetic, metabolomic, environmental, abiotic, and biotic factors influencing the synthesis and regulation of plant secondary metabolites. It addresses the growing demands for these metabolites in pharmaceutical industries. As we delve deeper into the intricate pathways of plant secondary metabolism, this special issue stands as a valuable reference, providing insights into the latest breakthroughs and paving the way for future innovations in medicinal plant research.

Author contributions

All authors listed have contributed to the work and approved it for publication.

Declaration of competing interest

The authors declare that they have no known competing commercial or financial interests or personal relationships that could have appeared to influence the Editorial.

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