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Agronomic Practices and Secondary Metabolite Accumulation in *Salvia miltiorrhiza*

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Abstract *Salvia miltiorrhiza*, known as Danshen, is an important medicinal herb, whose main secondary metabolites including tanshinones and salvianolic acids are considered responsible for antioxidant activity, cardiovascular protection, among other pharmacological effects. The agronomic practices of light exposure, temperature, water management, soil nutrient fertilization, planting density, pruning, cultivation patterns, and plant hormone regulation can affect the accumulation of such secondary metabolites. Using multi-omics techniques such as transcriptomics, proteomics, and metabolomics, regulatory networks related to secondary metabolite biosynthesis have been unveiled, as well as signaling pathways. Those studies provided a theoretical basis for optimization in agronomic practices. Taking into consideration different environmental factors and control methods of cultivation management that would affect the accumulation of secondary metabolites of Danshen, this study systematically summarizes the results, explains the key regulatory factors and potential synergistic interactions, and then discusses strategies for integrating the best agronomic practices with corresponding molecular studies to promote high-yield, high-quality, sustainable production. Through a synthesis of the current research achievements, the study lays a theoretical foundation for standard cultivation and industrial utilization of the active ingredients of Danshen.

Keywords *Salvia miltiorrhiza*; Secondary metabolites; Agronomic practices; Biosynthetic regulation; Standardized cultivation

1 Introduction

Salvia miltiorrhiza Bunge, most commonly known as Danshen, is one of the most commonly used traditional medicinal herbs in East Asia. Most therapeutic applications, especially in cardiovascular and cerebrovascular disorders, are attributed to its rich array of secondary metabolites. Compounds in tanshinones and salvianolic acids are claimed to show potent bioactivities such as antioxidant, anti-inflammatory, and vasodilatory effects and hence are critical determinants of the medicinal value of the herb (Chen et al., 2021).

The pharmacological efficacy of *S. miltiorrhiza* is closely related to the composition and concentration of its secondary metabolites. Tanshinones are major diterpenoid compounds with cardioprotective and anticancer activities, while salvianolic acids are water-soluble phenolic compounds that serve as the main contributors to their antioxidant and anti-inflammatory activities. Apart from its applications in medicine, these metabolites also underpin applications in functional foods, nutraceuticals, and quality control of herbal products (Wang et al., 2025).

Not only genetic factors but also environmental conditions and cultivation practices importantly influence the accumulation of secondary metabolites in *S. miltiorrhiza*. Agronomical factors, including light, temperature, soil nutrient management, irrigation, planting density, fertilization regimes, pruning, and plant hormone treatments, can modulate biosynthetic pathways and improve metabolite content. Knowledge of such regulatory effects provides the basis for developing methods to optimize plant cultivation strategies for yield and quality of bioactive compounds (Hou et al., 2024).

A systematic investigation into the agronomic influence on the accumulation of secondary metabolites will shed light on the physiological and molecular mechanism of metabolite biosynthesis in *S. miltiorrhiza*. In this study, we combine current studies conducted on cultivation variables with their respective biosynthetic and regulatory

networks, providing a theoretical guide for high-quality, sustainable, and industrially feasible cultivation of Danshen.

2 Major Secondary Metabolites of *Salvia miltiorrhiza* and Their Bioactivities

2.1 Tanshinones: types, chemical structures, and pharmacological effects

Tanshinones include lipophilic diterpenoid quinones, the principal types being tanshinone I, tanshinone IIA, cryptotanshinone, and dihydrotanshinone I. It displays potent antioxidant, anti-inflammatory, antitumor, and cardiovascular protective activities. Among them, tanshinone IIA is commonly used in clinical treatment against cardiovascular diseases and serves as the principal marker for quality control in medicinal preparations (Jiang et al., 2019; Ren et al., 2019). Tanshinones have also demonstrated neuroprotection and immunomodulation activities (Bonaccini et al., 2015; Tang and Zhao, 2024).

2.2 Salvianolic acids: major components and biological activities

Salvianolic acids are water-soluble phenolic acids, among which salvianolic acid A, salvianolic acid B, and rosmarinic acid are the most abundant. All these acids have shown strong activities related to antioxidant effects, anti-inflammatory, anti-atherosclerotic, and endothelium-protective properties, making them important in treating cardiovascular and cerebrovascular diseases (Ren et al., 2019; Tang and Zhao, 2024). Salvianolic acid B has been particularly recognized for its vascular protection and anti-thrombotic properties (Wei et al., 2023).

2.3 Other important secondary metabolites and their pharmacological potential

Other secondary metabolites comprise polysaccharides and flavonoids. The polysaccharides in *S. miltiorrhiza* demonstrated antioxidative, anti-tumor, hepatoprotective, anti-inflammatory, immune-regulative, and cardioprotective effects, thus widening the therapeutic uses of the plant (Luo et al., 2023). Flavonoids, along with other phenolic acids, have contributed to the pharmacological range of the plant activity (Wei et al., 2023).

Tanshinones mainly accumulate in the roots, especially the periderm, while salvianolic acids are present in both roots and leaves; some phenolic acids are more abundant in leaves. The content and composition of these metabolites vary with tissue type and developmental stage and are influenced by environmental and genetic factor (He et al., 2023; Li et al., 2025).

3 Effects of Light, Temperature, and Water Management on Secondary Metabolites in *Salvia miltiorrhiza*

3.1 Regulation of secondary metabolism by light intensity, quality, and photoperiod

Light is one of the most important environmental signals that regulate the biosynthesis of secondary metabolites. In *S. miltiorrhiza*, combined blue and red LED light-especially with a 3:7 blue:red ratio-conspicuously improves both plant growth and the accumulation of phenolic acids, such as rosmarinic acid and salvianolic acid B, by upregulating major biosynthetic genes (*SmPAL1*, *Sm4CL1*) (Zhang et al., 2020). On the contrary, however, blue light can decrease the tanshinone IIA constituent in hairy roots due to the downregulation of tanshinone biosynthetic genes (Chen et al., 2018). Different light qualities and intensities affect metabolic pathways due to photoreceptor-mediated signaling and circadian clock regulation; thus, light affects not just the quantity but also the composition of secondary metabolites in plants (Wu et al., 2025).

3.2 Effects of temperature (high and low) on metabolite accumulation

Of the influential climatic factors, temperature is paramount in these herbs. Temperature may bring about optimal photosynthetic efficiency and levels of major constituents, such as salvianolic acid B and tanshinones, at about 20 °C (Seo et al., 2015). Low temperature and increased UV-B radiation are able to increase the levels of rosmarinic acid and salvianolic acid B, possibly by turning on the key transcription factors and metabolic gene clusters (Yu et al., 2025). High temperatures may cause an imbalance in metabolism, leading to poor overall yield and quality.

3.3 Influence of water management and irrigation strategies

Water availability directly influences the growth and synthesis of secondary metabolites. The moderate drought stress could induce the expression of biosynthetic genes of phenolic acids and the ABA-dependent signaling pathways, hence promoting their accumulation (Zhang et al., 2024; Zhang et al., 2025). Severe drought and excess moisture stress suppress plant growth, photosynthetic capacity, and the content of both salvianolic acid B and tanshinones. In *S. miltiorrhiza*, the optimal soil relative water content is in the range of 55%-65%, balancing yield and metabolite quality (Li et al., 2025).

3.4 Integrated effects of light, temperature, and water on metabolic networks

Light, temperature, and water interact in determining the metabolic landscape of *S. miltiorrhiza*. The climatic variables of air temperature, precipitation, and duration of sunshine interact with each other to control the content and composition of bioactive ingredients, which gives rise to specific regional metabolite profiles. The environmental cues orchestrate complex gene expression networks, including key transcription factors such as WRKY and MYB, which integrate multiple signals into the fine-tuning of secondary metabolism. Examples include Yu et al. (2025) and Wu et al. (2025). Understanding such interacting effects is a basic requirement for an optimization of agronomic practices with the aim of improving medicinal product quality.

4 Soil Conditions and Fertilization Management in *Salvia miltiorrhiza* Cultivation

4.1 Effects of soil nutrient levels (N, P, K, and trace elements) on metabolite content

Both N and P are critical to the growth of and secondary metabolite biosynthesis in *S. miltiorrhiza*. The optimum N fertilization, 6-8 g/plant, increases root biomass, tanshinones, and salvianolic acid B, while excess N may decrease photosynthetic efficiency (Xing et al., 2023). Phosphorus exerts a "peaked" effect with an optimal value of 0.625 mmol/L inducing maximum biomass and metabolite accumulation, while deficiency/excess suppresses the growth and biosynthesis of bioactive compounds (Zuo et al., 2025). Potassium availability has been reported to be negatively correlated with salvianolic acid B but positively correlated with tanshinone IIA, indicating a metabolic trade-off. Trace elements including copper and cadmium also regulate metabolite content; copper positively affects tanshinone IIA, and cadmium enhances salvianolic acid B in *S. miltiorrhiza* (Hou et al., 2024) (Figure 1).

4.2 Influence of organic and inorganic fertilizers on metabolic pathways

Organic fertilizers, especially traditional Chinese medicine residues, greatly enhanced plant growth and accumulation of both phenolic acids and salvianolic acid B, and they improved soil microbial diversity and health. Inorganic fertilization with NPK resulted in increased biomass and the levels of some metabolites, though high dosages of chemical fertilizer have been found to lower the tanshinone content and have a negative impact on soil health. The use of biofertilizers like Bacillus and microalgae had positive results in improving root biomass and bioactive compound contents due to the enrichment of beneficial microbes in the soil and reduction of heavy metal uptake (Wu et al., 2021; Wei et al., 2022).

4.3 Effects of soil physicochemical properties (pH, texture, organic matter)

Hence, soil pH and organic matter content along with soil texture become the critical determinants of metabolite accumulation. The contents of Salvianolic acid B and tanshinone IIA increased with the increase in pH and OM of the soil (Hou et al., 2024). Better root development, indicative of superior structural and organic conditions of the soil, attained frequently by organic amendments, contributes to good secondary metabolism (Wang et al., 2024). Certain soil amendments help in the reduction of heavy metal contamination, especially Cd and Pb, thus improving metabolite accumulation and plant health (Wu et al., 2023).

4.4 Optimization strategies combining fertilization and irrigation

Balanced fertilization, integrated with optimized irrigation at the soil relative water content of 55-65%, ensures the maximization of yield with regard to metabolite quality (Li et al., 2023; 2025). Site-specific fertilization based on soil testing and predictive modeling resulted in a well-matched nutrient supply and optimal use of resources (Liu et al., 2022). Organic/inorganic fertilizers, combined in proper irrigation and soil amendments such as

biofertilizers or mycorrhizae, enhance plant health, secondary metabolite content, and sustainability (Wu et al., 2021; Wei et al., 2022).

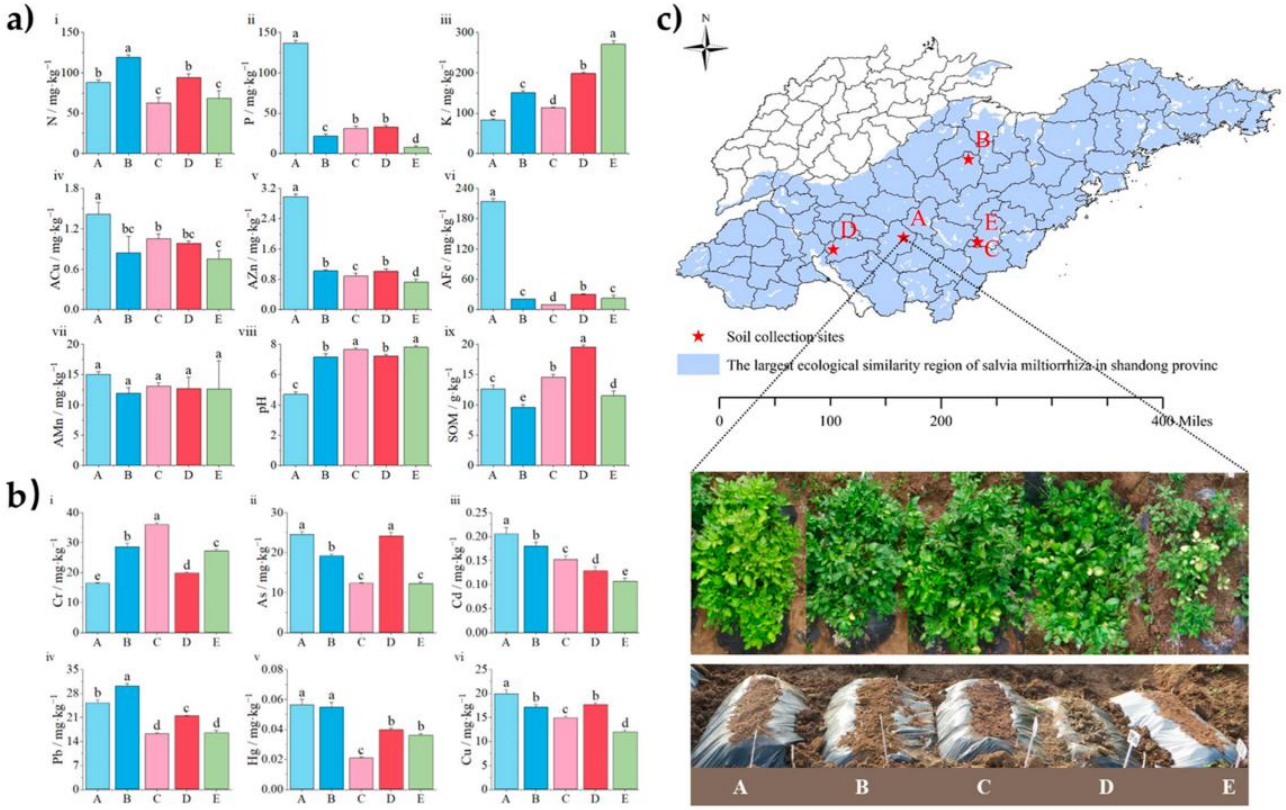


Figure 1 Samples collected from five sites (A, B, C, D, and E) in Shandong Province. (a) Physical and chemical properties of the soils. AN: alkaline nitrogen; AP: available phosphorus; AK: available potassium; ACu: available copper; AZn: available zinc; AFe: available iron; AMn: available manganese; SOM: soil organic matter. (b) Contents of soil heavy metals among different soil samples. Cd: Cadmium; Cr: Chromium; As: Arsenic; Pb: Lead; Hg: Hydrargyrum; Cu: Cuprum. Significant differences between soils were indicated by the least significant difference (LSD) test, with different lowercase letters indicating $p < 0.05$. (c) The five locations where soils were collected and the planting point in Site A where all soils were transported to (Adopted from Hou et al., 2024)

5 Planting Density, Pruning, and Cultivation Patterns in *Salvia miltiorrhiza*

5.1 Regulation of metabolite accumulation by planting density and light competition

The main effects of planting density on secondary metabolite accumulation in plants are light availability and root competition. Although there are very few specific studies with regard to the effect of density in *S. miltiorrhiza*, some evidence from related research indicates that increasing the planting density will increase the competition for light and nutrients, which may further lower root biomass and the concentration of major metabolites. On the other hand, combined blue and red LED light improves phenolic acid content and growth, and hence optimization of light conditions together with planting density may improve metabolite yields (Zhang et al., 2020).

5.2 Effects of Pruning and trimming on spatial distribution and synthesis of secondary metabolites

Although direct studies about pruning in *S. miltiorrhiza* are scanty, research on the spatial distribution of metabolites shows that different root tissues accumulate different metabolites; hence, cultivation practices that affect the architecture of the root, such as trimming or pruning, might have an effect on the spatial synthesis and accumulation of bioactive compounds. Methods such as MALDI-MSI have visualized these spatial patterns in roots, showing how continuous cropping and management practices of the root system can drastically alter metabolic profiles and their distribution within the root system (Sun et al., 2021).

5.3 Crop rotation, intercropping, and relay cropping patterns

Continuous monoculture of *S. miltiorrhiza* results in the yield and secondary metabolite content declining due to soil fatigue and changes in microbial communities (Sun et al., 2021). Intercropping, especially with sesame, can

substantially increase the content of key metabolites, including tanshinone IIA, tanshinone I, and cryptotanshinone, while also improving root biomass and increasing microbial diversity. Intercropping with maize or soybean results in little benefit or is even deleterious (Zhang et al., 2024). These findings stress the importance of proper crop selection in rotation and intercropping systems for maintaining soil health toward enhancing metabolite accumulation.

5.4 Integrated optimization of cultivation patterns and agronomic management

These integrated methods synergistically improve not only the yield but also the quality by optimum planting density, appropriate pruning, and beneficial intercropping. For instance, application of arbuscular mycorrhizae along with proper cultivation pattern shows increased root biomass and secondary metabolite production (Wu et al., 2021). Crop rotation and intercropping to manage inter-root secretions and microbial communities overcome obstacles in continuous cropping for sustainability in production (Zhang et al., 2024).

6 Growth Regulators and Inducers in *Salvia miltiorrhiza*

6.1 Induction of secondary metabolites by plant hormones (ABA, GA, JA, SA, etc.)

Jasmonic acid and its derivative methyl jasmonate are the most potent elicitor for tanshinone and phenolic acid biosynthesis through transcriptional regulation of the biosynthetic genes by interaction with JAZ repressors and bHLH/ERF TFs (Lv et al., 2024). Gibberellin signals via induction of tanshinone accumulation mediated through GRAS TF, while abscisic acid and salicylic acid generally modulate the pathways of phenolic acid under stress conditions (Li et al., 2024).

6.2 Effects of ethylene and ROS signaling on metabolite synthesis

Ethylene and ROS signaling are closely related to stress responses and secondary metabolism. Overexpression of some stress-responsive transcription factors, such as AtMYB2, reduces ROS accumulation by enhancing antioxidant enzyme activity and thus increases the tanshinone and phenolic acid content under salt stress (Zuo et al., 2025). These pathways often interplay with hormone signaling in order to fine-tune metabolite production.

6.3 Abiotic and biotic stress inducers

Abiotic stresses, including drought, salinity, and UV irradiation, upregulate genes responsible for secondary metabolite biosynthesis mainly through hormone-dependent pathways, such as ABA and JA (Zhang et al., 2024). Biotic elicitors, like endophytic fungi and silver ions (Ag^{+}), are also able to induce tanshinone and phenolic acid biosynthesis through the activation of key biosynthetic genes and transcription factors involved (Cheng et al., 2023; Zuo et al., 2025).

6.4 Synergistic effects of hormones and environmental factors

Hormonal crosstalk and environmental signals act synergistically. For instance, MeJA and salt stress in concert regulate the SmJAZs-SmbHLH37/SmERF73-SmSAP4 module to balance biosynthesis of metabolites and tolerance to stresses (Lv et al., 2024). Such integration would ensure optimal secondary metabolite production and resilience of plants.

7 Multi-Omics Insights into Secondary Metabolite Regulation in *Salvia miltiorrhiza*

7.1 Transcriptomics revealing expression patterns of biosynthetic genes

Transcriptomic analyses have identified thousands of DEGs associated with the biosynthesis of key secondary metabolites, such as tanshinones, phenolic acids, and flavonoids. For example, transcriptome profiling under drought and nutrient stress has disclosed the upregulation of genes in the phenylpropanoid and terpenoid pathways and their controlling transcription factors, including MYB, WRKY, and bHLH (Yu et al., 2025). Dynamic regulatory hubs, such as the SmWRKY48-SmTCP4-SmWRKY28 module, orchestrating responses to metabolic pathway perturbations, were further unraveled by time-series transcriptomics (Jiang et al., 2024; Liu et al., 2025) (Figure 2).

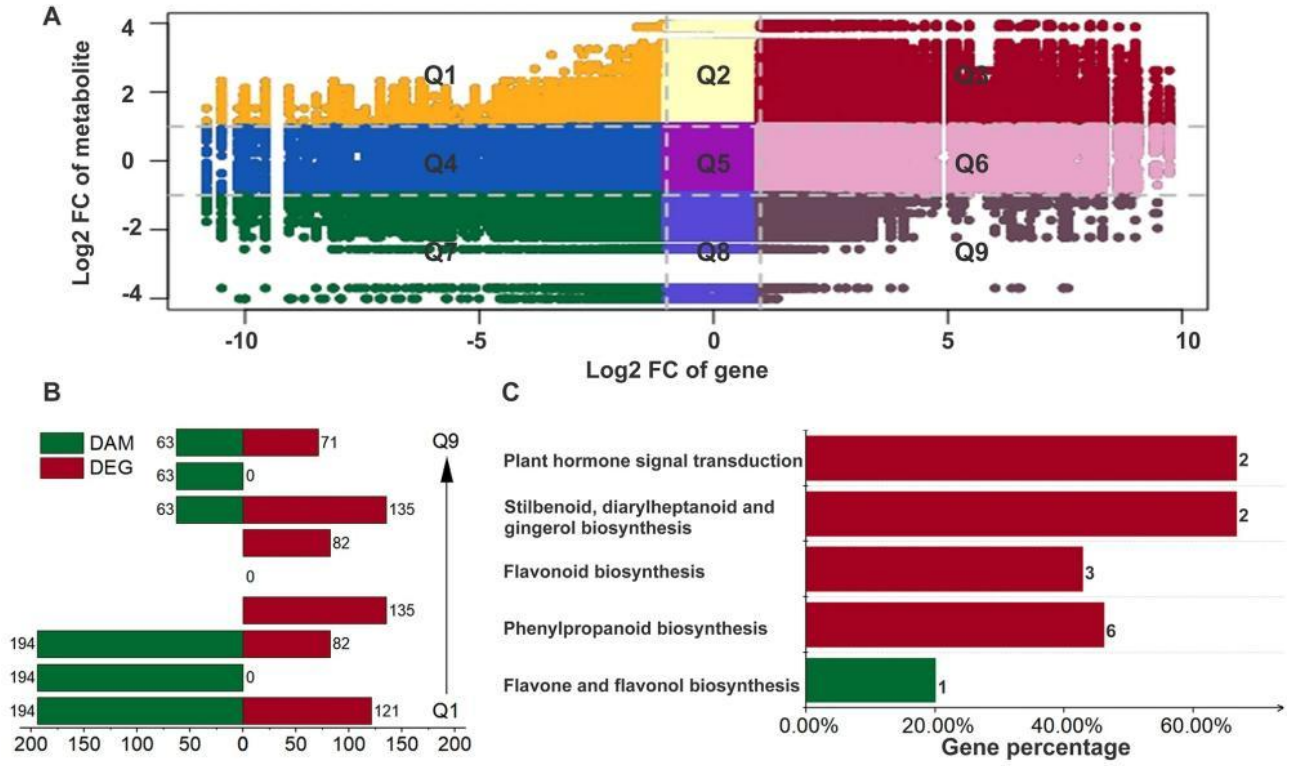


Figure 2 Integrated analysis of DAMs and DEGs in *S. miltiorrhiza*. (A) The nine-quadrant map of metabolites and genes. Each point represents a pair of correlated metabolites and genes with $|r| \geq 0.85$ and p value ≤ 0.05. The X-axis represents the log2 (fold change) of the gene, and the Y-axis represents the log2 (fold change) of the metabolite. (B) Number of DAMs and DEGs in each quadrant. Each row represents a quadrant, corresponding to Q1 to Q9 in (A) from bottom to top. Green represents DAMs and red represents DEGs. (C) The KEGG analysis of metabolites. Red represents metabolites in quadrant 3. Green represents metabolites in quadrant 7. The X-axis represents the proportion of metabolites in Q3 or Q7 to the total metabolites identified on the pathways (Adopted from Jiang et al., 2024)

7.2 Proteomics and metabolomics uncovering regulatory networks

These mapped the accumulation of certain metabolites, such as anthocyanins, flavonoids, and tanshinones, to the expression of their corresponding biosynthetic enzymes and regulatory proteins through integrative proteomic and metabolomic studies. Such analyses have identified key enzymes and transcription factors whose abundance correlates with metabolite levels, and further revealed environmental and genetic factors driving ecotype-specific metabolite accumulation (Jiang et al., 2020; Yu et al., 2025). Proteomic data integrated with transcriptomics underlined the role of WRKY transcription factors, such as SmWRKY61, in promoting tanshinone content.

7.3 Signal transduction and metabolic pathway integration

Multi-omics approaches unraveled the way in which hormone signaling, for example, ABA, JA, and auxin, is integrated with secondary metabolism. Examples include that transcriptome and metabolome analyses under stress conditions reveal a tight link between hormone signal transduction pathways and the activation of biosynthetic genes of secondary metabolites, where transcription factors act as central nodes that interlink these pathways (Jiang et al., 2024; Liu et al., 2025). This thus enables plants to coordinate their growth, defense, and metabolite production according to environmental cues.

7.4 Application of molecular markers and gene regulation in agronomic optimization

Multi-omics have identified the key regulatory genes and molecular markers, thus providing targets for molecular breeding and optimization of agronomic practices. For instance, genes such as *SmWRKY40* and *SmWRKY61*, among others, together with ABC transporters, are implicated in enhanced metabolite accumulation and improved stress tolerance, hence strategies toward improvement of cultivars and precision agriculture (Yu et al., 2025). These support the development of high-yield and high-quality varieties of *S. miltiorrhiza*.

8 Concluding Remarks

Agronomic practices such as light management, irrigation, nutrient supplementation, planting density, pruning, and hormone application have consistently demonstrated influence on accumulation of the key secondary metabolites in *Salvia miltiorrhiza*. Both tanshinones and salvianolic acids respond dynamically to environmental and cultivation factors, and their optimal combination results in enhanced biosynthesis, hence a higher metabolite content. Integration of physiological, biochemical, and molecular observation disclosed that specific agronomic measures could effectively regulate the biosynthetic pathways.

The control of secondary metabolite accumulation is highly complex due to interactions among multiple environmental and genetic factors. Multifactorial studies integrated with transcriptomic, proteomic, metabolomic, and epigenomic analyses enable holistic investigations into the underlying biosynthetic mechanisms. Such an integrative approach becomes of utmost importance in deciphering the signaling networks, transcriptional regulators, and metabolic fluxes that underlie metabolite production.

Notwithstanding these advances, several lacunas still exist. The exact mechanisms by which individual agronomic parameters affect secondary metabolite biosynthesis are not yet well defined. Long-term effects, as well as interactions among multiple variables of cultivation and their impact on different development stages, are incompletely investigated. Finally, considerable challenges still lie in the translation of such laboratory-based studies into large-scale field cultivation under variable environmental conditions.

Based on multi-omics and integrative studies, a comprehensive understanding of agronomic regulation presents a basis for standardized cultivation strategies with the purpose of attaining maximum yield and quality of bioactive compounds in *S. miltiorrhiza*. These insights are crucial to sustainable production with consistent therapeutic quality and the expansion of industrial applications of Danshen in medicine, functional foods, and nutraceuticals.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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