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Feature Review Open Access

Effects of Different Cultivation Substrates on the Growth and Quality Formation of *Dendrobium officinale*

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Abstract *Dendrobium officinale* Kimura et Migo is an important medicinal and edible traditional Chinese medicinal resource. During artificial cultivation, substrate conditions directly affect plant growth, bioactive compound accumulation, and medicinal quality formation. This review systematically summarizes the types, characteristics, and application effects of different cultivation substrates, including sphagnum moss, bark, coconut coir, peanut shells, rice husks, perlite, ceramsite, and composite substrates. It focuses on their effects on seedling survival, plant vigor, root development, biomass accumulation, and dry matter distribution in *D. officinale*, and further discusses the regulatory effects of substrates on the formation of quality-related constituents, such as polysaccharides, dendrobine, flavonoids, and phenolic compounds. Studies have shown that suitable cultivation substrates can promote root growth and nutrient uptake by improving rhizosphere moisture, aeration, nutrient supply, and microbial environment, thereby increasing plant biomass and the accumulation of medicinally active compounds. Composite substrates have great application potential in high-quality and efficient cultivation of *D. officinale* because they integrate water retention, aeration, physical support, and nutrient buffering functions. However, current research still faces problems such as inconsistent substrate evaluation standards, insufficient elucidation of quality formation mechanisms, and weak integration between substrate formulations and industrial applications. Future studies should strengthen the development of environmentally friendly composite substrates, further investigate substrate-microbe-quality formation mechanisms, and integrate smart agricultural technologies to establish standardized, large-scale, and sustainable cultivation systems for *D. officinale*.

Keywords *Dendrobium officinale*; Cultivation substrate; Growth and development; Quality formation; Bioactive compounds; Composite substrate

1 Introduction

Dendrobium officinale Kimura et Migo is a perennial epiphytic herb of the genus *Dendrobium* in the family Orchidaceae. It is also a valuable traditional Chinese medicinal plant and a medicinal-edible resource in China. Its stems have been officially recorded in the *Chinese Pharmacopoeia* and can be developed and utilized as both Chinese medicinal materials and functional food resources. Traditional medicine holds that *D. officinale* has the effects of nourishing Yin, clearing heat, benefiting the stomach, promoting fluid production, and strengthening the viscera. Modern studies have further shown that it is rich in various bioactive components, including polysaccharides, alkaloids, flavonoids, bibenzyls, phenanthrenes, and phenolic compounds, and exhibits multiple biological functions such as antioxidant, anti-inflammatory, immunomodulatory, gastrointestinal-protective, hypoglycemic, antitumor, cardiovascular-protective, and neuroprotective effects (Xu et al., 2022; Wang et al., 2025). In recent years, with the rapid development of the health industry, traditional Chinese medicine industry, and functional food market, the demand for *D. officinale* has continued to increase. It has gradually transformed from a rare wild resource into a large-scale artificially cultivated crop and has become an important medicinal plant industry with high economic value (Hou et al., 2025).

However, due to long-term overharvesting, habitat destruction, and slow natural regeneration, wild resources have declined significantly, and artificial cultivation, facility cultivation, and wild-simulated cultivation have gradually become the main sources of raw materials for *D. officinale* production (Chen et al., 2021; Liu et al., 2025). Alongside rapid industrial development, differences in cultivation regions, cultivation modes, harvest years, and processing methods have resulted in obvious variations in product quality. Therefore, how to coordinate yield improvement with quality optimization under artificial cultivation conditions has become an important issue in both industrial development and scientific research on *D. officinale* (Yuan et al., 2020; Zhang et al., 2023).

D. officinale is a typical epiphytic plant. Under natural conditions, it often grows attached to tree trunks, rock crevices, and other special habitats, and its roots have high requirements for the aeration, water retention, drainage, nutrient retention, and microecological environment of the growth medium. Therefore, in artificial cultivation systems, cultivation substrates are not only physical supports for plant attachment and growth, but also important factors regulating rhizosphere moisture, air, nutrients, and microbial environments. The commonly used substrates for *D. officinale* cultivation include pine bark, fern roots, sphagnum moss, biochar, mushroom residues, vermiculite, perlite, coconut coir, peanut shells, and composite substrates. These materials can, to some extent, simulate natural epiphytic habitats and provide roots with aeration, drainage, moisture retention, and nutrient-buffering conditions (He et al., 2022). Because different substrates vary significantly in pore structure, water-holding capacity, pH, nutrient content, and microbial composition, they exert important effects on root development, plant height, stem diameter, biomass accumulation, photosynthesis, stress resistance, and other growth indicators of *D. officinale* (Zhang et al., 2024). Previous studies have shown that pine bark-based substrates can improve the survival rate, plant height, stem girth, and dry weight of *D. officinale*, and show good production potential in some cultivation environments. Mixed substrates composed of pine bark and fern fiber can also support high acclimatization survival rates of tissue-cultured plantlets and favorable ex vitro growth performance (Luan et al., 2021; Wang et al., 2025). Meanwhile, substrates interact with ecological factors such as temperature, humidity, light, and nutrient status, thereby influencing the accumulation of polysaccharides, alkaloids, flavonoids, and other secondary metabolites, and ultimately determining the medicinal quality and commercial value of *D. officinale* (Yuan et al., 2020).

This review examines the effects of different cultivation substrates on the growth and quality formation of *D. officinale*. In recent years, related research has gradually expanded from simple comparisons of cultivation effects among different substrates to multiple aspects, including substrate physicochemical properties, rhizosphere microbial communities, ecological factor interactions, and quality formation mechanisms. Existing studies have shown that substrate selection and cultivation mode jointly affect the growth performance, survival rate, stress resistance, and bioactive compound accumulation of *D. officinale*. However, current research still has certain limitations. Many studies focus on single substrate formulations, specific regions, or individual indicators such as polysaccharide content, lacking systematic integration of multi-component quality evaluation involving polysaccharides, alkaloids, flavonoids, and phenolic compounds. In addition, the relationships among substrate characteristics, ecological factors, metabolite profiles, and molecular regulatory mechanisms have not yet been fully clarified, and substrate evaluation standards and industrial application specifications still require further improvement. Based on a review of relevant domestic and international studies, this paper systematically summarizes the types and characteristics of commonly used cultivation substrates for *D. officinale*, focuses on analyzing the effects of different substrates and related cultivation modes on plant growth and development, bioactive compound accumulation, and quality formation, and further discusses the possible mechanisms by which substrates regulate growth and quality, current research problems, and future development directions. This review aims to provide theoretical references and practical guidance for the scientific selection of cultivation substrates, optimization of artificial cultivation systems, and standardized, high-quality, and sustainable development of the *D. officinale* industry.

2 Types of Common Cultivation Substrates for *Dendrobium officinale*

2.1 Natural organic substrates such as sphagnum moss and bark

Natural organic substrates are widely used in the artificial cultivation of *Dendrobium officinale*. They are mainly derived from plant residues or natural organic materials and generally have good water retention, aeration, and root-attachment capacity, allowing them to partly simulate the natural epiphytic habitat of *D. officinale*. Among them, sphagnum moss is commonly used during tissue-cultured plantlet transplantation, seedling hardening, and greenhouse nursery stages because of its loose texture, strong water absorption capacity, favorable pore structure, and suitable pH. Studies have shown that, during the hardening stage of *D. officinale*, pure sphagnum moss promotes faster root emergence, enhances tillering, produces thicker leaves and stems, and increases plant biomass compared with bark alone, while maintaining a similar root-shoot ratio, indicating its clear role in promoting early adaptation and recovery growth of seedlings. In addition, compared with bark-based substrates, sphagnum moss substrates can also increase chlorophyll, carotenoid, and polysaccharide contents, suggesting that they not only favor vegetative growth but may also promote the accumulation of medicinal components.

Bark-based substrates mainly include pine bark, fir bark, and related materials, and are commonly used in seedbed cultivation, pot cultivation, and wild-simulated cultivation of *D. officinale*. Pine bark has high porosity and strong drainage capacity, providing a favorable aerated environment for the aerial roots of *D. officinale* and reducing the risk of root decay caused by prolonged high humidity. Meanwhile, during slow decomposition, pine bark can release certain organic nutrients and support sustained plant growth. Previous studies have shown that pine bark is widely used as an important component of seedbeds and mixed substrates for *D. officinale*. Under field-like cultivation conditions, it can support high survival rates, rapid growth, and high stem yield. During tissue-cultured plantlet acclimatization, the combined use of pine bark and fern fiber can achieve a 100% survival rate and favorable greenhouse growth performance in *D. officinale* (Luan et al., 2021).

From the perspective of quality formation, bark-based substrates may also affect the accumulation of secondary metabolites in *D. officinale*. Zuo et al. (2020) conducted metabolomic analysis of *D. officinale* stems cultivated in pine bark, coconut coir, and a 1:1 mixture of the two substrates, and found that pine bark alone was more conducive to the accumulation of flavonoids, with "flavonoid biosynthesis" identified as the main regulated pathway. This indicates that natural organic substrates not only affect root attachment and plant growth, but may also participate in quality formation by altering the rhizosphere environment and metabolic status. However, natural organic substrates still have certain limitations. For example, sphagnum moss largely depends on natural harvesting, and long-term use may face pressures related to resource conservation and rising costs. Bark-based substrates also have limited nutrient content, a long decomposition cycle, and considerable batch-to-batch variation. Therefore, improving the utilization efficiency of natural organic substrates and developing alternative, sustainable composite materials have become important directions in substrate research for *D. officinale*.

2.2 Agricultural waste-based substrates such as coconut coir, peanut shells, and rice husks

With the development of agricultural waste recycling and green cultivation concepts, agricultural by-products such as coconut coir, peanut shells, rice husks, mushroom residues, corncobs, and wood chips have gradually been applied in the cultivation of *D. officinale* and other *Dendrobium* species. These substrates are widely available and relatively low in cost. They can reduce environmental pressure caused by agricultural waste accumulation while lowering cultivation costs, and therefore have good ecological value and industrial application potential. Coconut coir and coconut husk are common organic substrates in *Dendrobium* orchid cultivation. Owing to their strong water-holding capacity, high porosity, and suitable aeration, they can support favorable survival and growth performance (Nuammee et al., 2024; Tt et al., 2024; Olasehinde, 2025).

In *D. officinale* cultivation, coconut coir can be used alone or mixed with materials such as pine bark. Zuo et al. (2020) found that, compared with pure pine bark, coconut coir alone or a 1:1 mixture of coconut coir and pine bark altered the stem metabolite profile of *D. officinale* but did not change the types of metabolites, indicating that it mainly affected metabolite contents rather than composition. In ornamental *Dendrobium* cultivars, pure coconut husk substrates can increase plant height, shoot number, inflorescence length, and floret number, and their overall performance is superior to that of most mixed substrates. This further demonstrates the importance of an appropriate water-air balance for the growth of *Dendrobium* plants (Tt et al., 2024). Therefore, coconut coir substrates have good substitution potential in green cultivation systems for *D. officinale*.

Peanut shells, rice husks, and other agricultural residues also have the advantages of light weight, good aeration, and structural improvement. After crushing, fermentation, composting, or disinfection, these materials can be used alone as cultivation substrates or combined with bark, sphagnum moss, perlite, and other materials. Previous studies have used spent mushroom residues, Chinese herbal residues, chestnut shells, peanut shells, mulberry branches, corncobs, wood chips, and soil or clay amendments to construct granular substrates for *D. officinale*. The results showed that such composite substrates significantly improved disease resistance and root health, increased the survival rate to more than 98%, and enhanced plant height, stem diameter, polysaccharide content, and yield. Rice husks and related materials are also considered effective structural improvement and moisture-regulating components in substrates for *Dendrobium* and other soilless crops (Figure 1) (Rahman et al., 2021; Hou et al., 2025). However, the application performance of agricultural waste-based substrates is greatly affected by raw material source, processing method, fermentation degree, and salt content. Insufficiently treated materials may carry risks such as pathogen residues, unbalanced nutrient release, or phytotoxicity. Therefore, in production practice, raw material pretreatment, fermentation and composting, sterilization, and scientific formulation should be strengthened to improve substrate stability and safety.

Figure 1 The growth of Dendrobium Shavin White orchid seedling in different substrate (Adopted from Rahman et al., 2021)
Image caption: A-T1; Rice husk+Chitosan, B-T3; Oil palm EFB+Chitosan, C-T4; Rice husk+Peat moss+Chitosan, D-T5; Rice husk+Peat moss+Oil palm EFB+Chitosan. Bar=1cm (Adopted from Rahman et al., 2021)

2.3 Perlite, ceramsite, and composite cultivation substrates

Inorganic substrates have attracted attention in facility cultivation and composite substrate construction for *D. officinale* because of their good physical stability, low bulk density, high porosity, and long service life. Perlite is a porous inert material produced by high-temperature expansion. It is lightweight and has strong drainage and good aeration, which can improve substrate structure and reduce the risk of compaction caused by long-term cultivation. Ceramsite, brick and tile fragments, charcoal, expanded minerals, and related materials are also commonly used as structural components to enhance mechanical support and root-zone aeration. Studies have shown that perlite and similar inert mineral materials are common inorganic components in soilless cultivation and orchid substrates, and their low bulk density, high porosity, and strong drainage capacity help improve the root environment (Nuammee et al., 2024; Carrasco et al., 2025).

Because a single inorganic substrate has weak nutrient-retention capacity and cannot fully meet the long-term growth and quality formation requirements of *D. officinale*, composite cultivation substrates are more commonly used in production practice. Composite substrates usually combine natural organic substrates, agricultural waste-based substrates, and inorganic substrates in specific proportions to balance water retention, aeration, structural stability, and nutrient supply. For example, pine bark combined with coconut coir, ceramsite, or perlite can simultaneously meet the needs of root aeration and moisture retention. Composite formulations containing bark, brick fragments, sphagnum moss, wood chips, and maize straw, after disinfection and fermentation, can stabilize substrate structure and reduce pathogen risk. During orchid acclimatization, mixed substrates containing brick fragments and charcoal together with water-retentive components such as sphagnum moss or fern fiber can improve root aeration and mechanical support, achieving survival rates of approximately 97~100% and supporting long-term growth (Nuammee et al., 2024).

The advantage of composite substrates lies in their capacity for targeted design according to different growth stages, cultivation modes, and regional environments of *D. officinale*. Compared with single substrates, composite substrates can not only improve seedling survival and plant growth rate, but may also promote bioactive compound accumulation and commercial quality by improving rhizosphere moisture, oxygen, nutrients, and microbial conditions. Studies on *Dendrobium* production have shown that potting media composed of coconut-derived organic materials mixed with brick fragments, charcoal, and tile fragments can achieve better vegetative growth and flowering traits than coconut coir alone. This indicates that composite substrates have important application value by integrating organic nutrient supply with inorganic structural stability (Ashokkumar et al., 2023; Tt et al., 2024). In the future, under the concepts of resource recycling, precision cultivation, and quality-oriented production, the development of functional, standardized, and sustainable composite substrates will become an important pathway for promoting the high-quality development of the *D. officinale* industry.

3 Effects of Different Cultivation Substrates on the Growth of *Dendrobium officinale*

3.1 Effects on seedling survival rate and plant vigor

Seedling survival rate is an important indicator for evaluating the cultivation effect of *Dendrobium officinale* and a direct basis for assessing substrate suitability. As *D. officinale* is an epiphytic plant, its seedling roots are relatively fragile and sensitive to changes in moisture, aeration, and environmental stability. Therefore, the water retention, aeration, structural stability, and disease-suppressive capacity of the substrate directly affect post-transplant survival. Existing studies have shown that sphagnum moss, pine bark, and their composite substrates can form a relatively stable moisture and air environment around the roots, reduce transplanting stress, and improve seedling survival. During the hardening stage, sphagnum moss can promote rapid root initiation, enhance tillering, and increase leaf thickness, stem diameter, plant height, leaf width, root length, root number, and biomass compared with bark treatment, making it more suitable for acclimatization and early transplantation of tissue-cultured plantlets.

Different substrates not only affect seedling survival rate but also significantly influence plant vigor. Suitable substrates can improve the rhizosphere environment and enhance water and nutrient use efficiency, thereby promoting plant height growth, stem thickening, and leaf development. Studies have shown that a granular substrate mainly composed of spent mushroom residues, Chinese herbal residues, and agricultural by-products such as chestnut shells, peanut shells, mulberry branches, corncobs, and wood chips can increase the transplant survival rate of *D. officinale* to more than 98%. After 1.5 years of cultivation, the average plant height reached approximately 78 cm and the stem diameter reached 7.5~8.2 mm, indicating good adaptability and growth vigor under field conditions. A cement-tile bed cultivation system using pine bark as the main substrate can also ensure a transplant survival rate of more than 98%, promote plant growth compared with traditional cultivation methods, advance flowering and stem formation, and increase yield per unit area. In addition, a 50:50 mixture of pine bark and fern fiber achieved a 100% survival rate 12 months after ex vitro transplantation and showed good performance in plant height, root number, fresh weight, and dry weight, suggesting that a rational combination of water retention and aeration is conducive to sustained seedling growth (Luan et al., 2021).

The substrate requirements of *D. officinale* vary among different growth stages. The seedling stage relies more heavily on strong moisture retention and environmental stability, whereas during the rapid growth stage, the requirements for substrate aeration, drainage, and nutrient supply gradually increase. Wood-based substrate combinations such as bark-sawdust mixtures can also support high survival rates and favorable growth. Among them, an alder bark:fine sawdust ratio of 5:1 showed good performance in plant height, stem diameter, root number, and leaf number, and was considered a suitable cultivation substrate. Therefore, rationally selecting or adjusting substrate types according to different growth stages of *D. officinale* is an important measure for improving seedling survival, enhancing plant vigor, and achieving stable production.

3.2 Effects on root development and nutrient uptake

Roots are important organs for water and mineral nutrient uptake in *D. officinale*, and their developmental status directly determines the subsequent growth potential of the plant. Cultivation substrates influence root morphogenesis and physiological activity by regulating rhizosphere moisture, oxygen, and nutrient supply. Substrate porosity, water-holding capacity, drainage, and nutrient status are key factors determining root development in *D. officinale*. Well-aerated substrates are conducive to root apical meristem activity and new root formation, whereas prolonged waterlogging or poor aeration can easily cause root hypoxia, inhibit root growth, and even induce root rot. During the hardening stage, sphagnum moss significantly increases root length, root number per cluster, and root biomass, indicating that a moist, fine-textured, and well-aerated medium facilitates rapid root proliferation and functional root formation in seedlings.

Bark-based substrates and composite substrates supplemented with structural materials such as fern fiber, perlite, and ceramsite are beneficial for increasing root length, root number, and root activity. A pine bark-based mixed substrate combined with fern fiber promoted rooting under greenhouse conditions over 12 months, enabling plants to develop more roots, longer roots, and higher fresh weight than other tested substrates (Luan et al., 2021). Some nutrient solutions and granular substrate formulations also aim to rapidly promote root emergence from stems and improve transplant survival. Reported results indicate that the cultivation period for complete plant formation can be shortened to approximately 25 days, with a high field survival rate, suggesting that nutrient-rich, well-buffered, and structurally suitable substrates can significantly promote root initiation and growth. For *D. officinale*, which has well-developed aerial roots, maintaining an appropriate air-water ratio is essential for healthy root development.

Substrates also serve as reservoirs and exchange interfaces for mineral nutrients and carbon sources. Widely targeted metabolomic studies have shown that pine bark, coconut coir, and their mixed substrates differ significantly in physicochemical properties, including water-holding capacity and nitrogen, phosphorus, and potassium contents, leading to marked changes in the stem metabolite profiles of *D. officinale*. This suggests that nutrient acquisition and metabolic status differ under different substrate conditions (Zuo et al., 2020). Ecophysiological studies have also found that total nitrogen, total phosphorus, pH, and available phosphorus in the soil are closely related to polysaccharide, total alkaloid, and flavonoid contents, and these parameters are all influenced by substrate selection in artificial cultivation systems (Yuan et al., 2020). In addition, mycorrhizal associations formed within or on the surface of substrates can enhance nutrient uptake. The growth-promoting fungus MF23 can increase root dry weight, root length, and seedling height in *D. officinale*, and upregulate genes related to nitrate, ammonium, amino acid, and peptide transporters, thereby promoting nitrogen uptake and assimilation (Figure 2) (Shan et al., 2021). Other mycorrhizal fungi can also enhance carbon acquisition from substrates, improve photosynthetic efficiency, and increase seedling biomass and polysaccharide content.

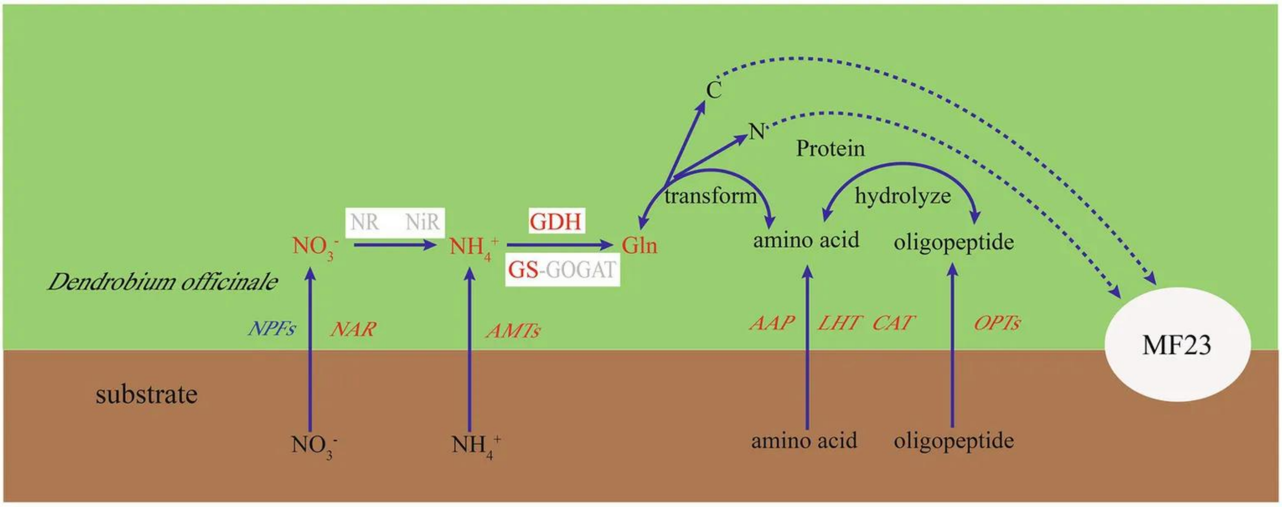

Figure 2 Putative nitrogen uptake and metabolism in the *D. officinale*-MF23 symbiosis (Adopted from Shan et al., 2021)
Image caption: Black font represents the background subjects; red, blue, and gray font represent up-, down-, and undifferentiated-regulated genes or metabolites, respectively. White boxes represent enzymes (Adopted from Shan et al., 2021)

3.3 Effects on biomass accumulation and dry matter distribution

Biomass accumulation is the result of the combined effects of photosynthesis, nutrient uptake, and material metabolism, and it is also an important indicator for evaluating substrate performance. Suitable substrates can provide stable moisture, oxygen, and nutrient conditions for *D. officinale*, promote the formation and transport of photosynthetic products, and thereby increase plant fresh weight and dry weight. Studies have shown that granular substrates rich in organic residues can produce an average yield of approximately 580 kg/mu in *D. officinale*, with a polysaccharide content of 42.5%, indicating that optimized substrates with high nutrient density are conducive to the synchronized accumulation of stem biomass and medicinal components. Pine bark seedbed cultivation can increase growth rate, advance flowering and stem formation by 1~3 years, and produce more than 250 kg/mu, suggesting that coarse, durable bark substrates can sustain high aboveground biomass accumulation over multiple years when combined with appropriate fertilization and management.

Different cultivation substrates also affect the distribution of dry matter among roots, stems, and leaves. The main medicinal part of *D. officinale* is the fleshy stem; therefore, the extent of dry matter accumulation in the stem is closely related to medicinal material yield and quality. Under suitable substrate conditions, plants can maintain high photosynthetic efficiency and nutrient transport capacity, allowing more assimilates to be transported to and stored in the stems, thereby promoting stem thickening and improving medicinal yield. Container cultivation studies have shown that turf-bark substrates can significantly increase the fresh weight and dry matter content of tissue-cultured plantlets, while sphagnum moss substrates not only promote growth but also increase polysaccharide content. This suggests that different substrates may guide biomass allocation toward structural growth or toward storage and medicinal component accumulation, respectively.

In addition, biomass accumulation is closely related to the formation of bioactive components. Sufficient dry matter accumulation not only provides a material basis for plant growth, but also supplies carbon sources and energy for the synthesis of polysaccharides, alkaloids, and other secondary metabolites. Mycorrhizal cultivation studies have shown that MF23 inoculation significantly increases root and stem dry weight, root length, and seedling height compared with axenic culture, and its promoting effect becomes stronger over time (Shan et al., 2021). Compared with non-mycorrhizal controls, ex vitro seedlings associated with mycorrhizal fungi have greater increases in fresh and dry weight, taller plants, thicker stems, and more new roots and tillers, indicating that mycorrhizal symbiosis can coordinately increase total biomass and promote biomass allocation to the stems, which are harvested as medicinal materials. From a broader ecological perspective, stem, leaf, and total biomass of *D. officinale* vary significantly among different provenances and environmental conditions, indicating that substrate-related environmental factors and genetic conditions jointly drive patterns of dry matter distribution. Therefore, from the dual goals of yield and quality improvement, selecting suitable substrates and combining them with beneficial microbial regulation is an important approach for promoting biomass accumulation and optimizing dry matter distribution in *D. officinale*.

4 Effects of Different Cultivation Substrates on Quality Formation in *Dendrobium officinale*

4.1 Effects on polysaccharide accumulation

Polysaccharides are among the most important bioactive constituents of *Dendrobium officinale* and serve as a core indicator for evaluating its medicinal quality. In addition to possessing immunomodulatory, antioxidant, and metabolic regulatory activities, polysaccharides directly influence the medicinal value and market competitiveness of *D. officinale*. Previous studies have demonstrated that polysaccharide content is highly responsive to growth conditions. Cultivation mode, root-zone physicochemical environment, nutrient availability, and water status can all affect polysaccharide accumulation, and these factors are largely regulated by cultivation substrates (Yuan et al., 2020). Comparative studies conducted across different production regions and cultivation systems have shown that variations in light intensity, temperature, water availability, and nutrient conditions can lead to substantial differences in polysaccharide content, indicating that polysaccharide biosynthesis exhibits considerable environmental plasticity (He et al., 2022).

Substrates with favorable water-holding capacity, aeration, and nutrient-buffering ability are generally more conducive to polysaccharide formation and accumulation. Pine bark, sphagnum moss, and their composite substrates provide a relatively stable rhizosphere environment, promoting photosynthate production, carbon accumulation, and carbohydrate metabolism, thereby enhancing polysaccharide content. Reviews have emphasized that appropriate artificial substrates and cultivation systems are among the most important agronomic strategies for increasing polysaccharide yield in modern *D. officinale* production systems (Chen et al., 2021). At present, epiphytic cultivation and wild-simulated cultivation have become major production approaches. These systems typically employ bark- or tree-based substrates and aim to produce green, organic medicinal materials with high polysaccharide content. Comparisons among cultivation sites and production techniques indicate that plants grown under more favorable microclimatic conditions and substrate-nutrient environments are more likely to meet or exceed the polysaccharide standards specified in the Chinese Pharmacopoeia, whereas lower compliance rates are often observed in environmentally less suitable regions (He et al., 2022).

It should be noted that polysaccharide accumulation does not necessarily increase in parallel with plant growth. Instead, it is jointly influenced by genotype, cultivation age, cultivation mode, and substrate conditions. Multi-year metabolomic analyses have shown that carbohydrates and glycosides are the predominant metabolites in *D. officinale*, and the third cultivation year may represent the optimal harvest period based on carbohydrate accumulation patterns. In standardized cultivation systems, tetraploid breeding materials have exhibited nearly double the stem polysaccharide content of diploid plants, indicating that polysaccharide accumulation depends not only on substrate optimization but also on genetic improvement and harvest timing management (Pham et al., 2019). Therefore, cultivation practices should balance yield and quality by optimizing substrate structure, nutrient supply, and harvest age to achieve the coordinated enhancement of both polysaccharide content and biomass production.

4.2 Effects on dendrobine, flavonoids, and other bioactive constituents

In addition to polysaccharides, dendrobine, flavonoids, phenolic compounds, bibenzyls, and phenolic glycosides are important functional constituents of *D. officinale*. Dendrobine and related alkaloids possess potential anti-inflammatory, neuroprotective, and immunomodulatory activities, whereas flavonoids and phenolic compounds are closely associated with antioxidant activity, free-radical scavenging, and stress defense. The accumulation of these bioactive compounds is regulated not only by genetic background but also by cultivation environment and substrate conditions. By altering rhizosphere moisture, oxygen availability, nutrient supply, and the microecological environment, different substrates influence the allocation of resources between primary and secondary metabolism, thereby regulating the biosynthesis and accumulation of dendrobine, flavonoids, and related compounds.

Widely targeted metabolomic analyses comparing *D. officinale* stems cultivated in pine bark, coconut coir, and a 1:1 mixture of the two substrates revealed that although the overall metabolite categories remained similar among treatments, significant differences occurred in metabolite abundance. Among the 529 detected metabolites, flavonoids exhibited the most pronounced variation, with most flavonoid compounds preferentially accumulating in plants grown on pure pine bark. KEGG enrichment analysis further demonstrated that flavonoid biosynthesis was the only pathway significantly affected by substrate-induced metabolic changes, indicating a direct relationship between substrate selection and flavonoid metabolic regulation (Figure 3) (Zuo et al., 2020). These findings suggest that bark-based substrates not only facilitate root attachment and vegetative growth but may also promote the accumulation of specific bioactive compounds through alterations in metabolic pathway activity.

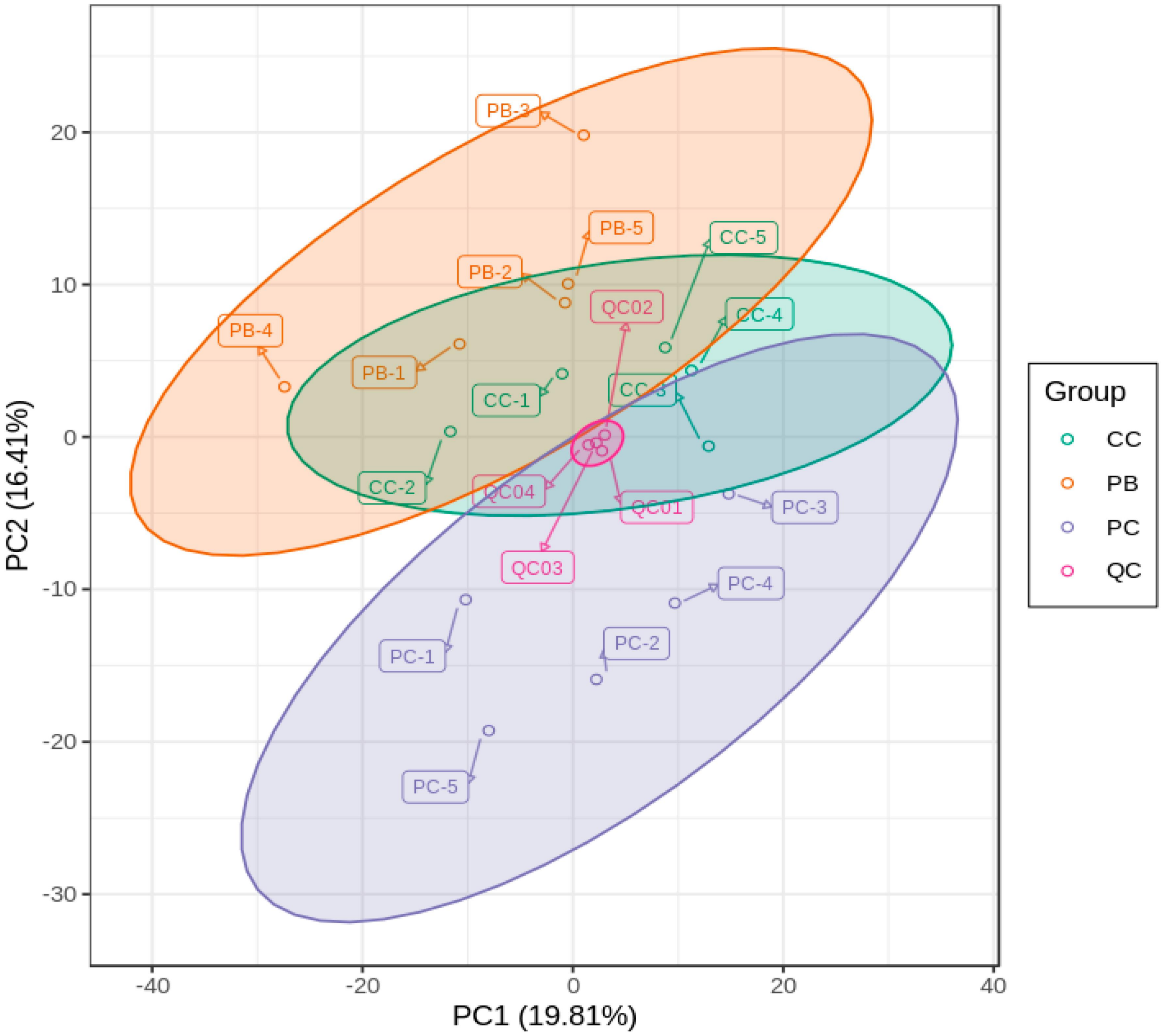

Figure 3 Score plot of principal component analysis (PCA) for *D. officinale* samples (Adopted from Zuo et al., 2020)
Image caption: Planted in pine bark (PB), coconut coir (CC), pine bark: coconut coir 1:1 mix (PC), and quality control (QC) samples; PC1 represents the first principal component and PC2 represents the second principal component (Adopted from Zuo et al., 2020)

In addition to substrate comparison studies, investigations involving different production regions and cultivation systems have also demonstrated that low-molecular-weight bioactive compounds are highly sensitive to environmental conditions. Metabolomic analyses of wild-simulated cultivation systems and materials from different geographical origins have identified numerous differentially accumulated metabolites, with significant enrichment of flavonoid and flavonol biosynthesis pathways and substantial variation in flavonoid content among habitats (Lan et al., 2022; Luo et al., 2023). Integrated proteomic-metabolomic studies have further shown that phenylpropanoid and flavonoid biosynthesis pathways are key targets affected by environmental variation. Critical enzymes such as phenylalanine ammonia-lyase and chalcone synthase exhibit differential regulation among production regions. Significant regional differences have also been reported for dendrobine and related alkaloids, suggesting that cultivation conditions, including substrate properties and soil nutrient status, can influence alkaloid accumulation (Guan et al., 2025). Therefore, selecting substrates with appropriate physical structure, nutrient characteristics, and moderate ecological stimulation effects may facilitate the accumulation of flavonoids, alkaloids, and other bioactive compounds, thereby enhancing the medicinal quality of *D. officinale*.

4.3 Effects on comprehensive evaluation of medicinal and commercial quality

Quality evaluation of *D. officinale* encompasses not only chemical indicators such as polysaccharides, alkaloids, and flavonoids, but also antioxidant capacity, morphological traits, stem quality, tissue texture, and commercial grading characteristics. High-quality *D. officinale* typically exhibits thick stems, uniform internodes, bright coloration, well-developed tissues, and elevated levels of bioactive constituents. Consequently, the dual effects of cultivation substrates on plant morphology and active constituent accumulation ultimately determine both medicinal and commercial quality. Previous studies have indicated that the medicinal quality of *D. officinale* is determined by a comprehensive profile of polysaccharides and various low-molecular-weight compounds, and is closely associated with functional activities such as antioxidant capacity (Chen et al., 2021; Xu et al., 2022; Wang et al., 2025; Yang et al., 2026).

In medicinal quality assessment, reliance solely on polysaccharide content has certain limitations. Comparative studies involving materials from different regions and cultivation environments have demonstrated that high polysaccharide levels do not necessarily coincide with elevated concentrations of flavonoids, phenolic glycosides, or other low-molecular-weight compounds. In some cases, regions producing materials with high polysaccharide content have exhibited relatively low levels of certain small-molecule constituents (He et al., 2022). Metabolomic and bioactivity studies have shown that flavonoids and phenolic acids are major contributors to the antioxidant capacity of *D. officinale*, and strong correlations have been observed between specific flavonoid glycosides and antioxidant indicators (Luo et al., 2023). Therefore, substrates or cultivation environments that promote flavonoid accumulation, such as pine bark-based systems, may enhance certain biological functions even when polysaccharide content remains relatively unchanged (Zuo et al., 2020; Lan et al., 2022).

From the perspectives of commercial quality and industrial application, substrate selection also influences stem thickness, fresh weight, uniformity, and processing suitability, thereby affecting commercial grading and market acceptance. Numerous studies have suggested that quality evaluation systems for *D. officinale* should incorporate representative low-molecular-weight biomarkers and biological activity indicators in addition to polysaccharides, because cultivation conditions—including substrate characteristics—can alter the balance among different classes of compounds, and such changes may not be directly reflected in appearance or yield (Chen et al., 2021; He et al., 2022). Regional comparisons under artificial shading cultivation have shown that *D. officinale* produced in southern cultivation regions generally contains higher levels of polysaccharides, flavonoids, and total polyphenols than material produced in newly established northern production areas, indicating that differences in regional environments and rhizosphere conditions may influence overall nutritional and medicinal value even under similar cultivation techniques. Therefore, future quality-oriented cultivation strategies should incorporate rational substrate selection and establish comprehensive evaluation systems that simultaneously consider polysaccharides, dendrobine, flavonoids, phenolic compounds, morphological traits, and commercial grade, thereby meeting the requirements of pharmacopoeial standards, functional food development, and market quality expectations.

5 Mechanisms by Which Cultivation Substrates Influence Growth and Quality of *Dendrobium officinale*

5.1 Regulatory effects of substrate physicochemical properties on the rhizosphere environment

The physicochemical properties of cultivation substrates are fundamental factors influencing the growth and quality formation of *Dendrobium officinale*. These properties mainly include porosity, bulk density, water-holding capacity, aeration, pH, cation exchange capacity, and nutrient contents such as nitrogen, phosphorus, and potassium. As a typical epiphytic plant, *D. officinale* possesses roots that are highly sensitive to oxygen availability and fluctuations in water status. Therefore, substrates with good aeration and appropriate water retention can maintain normal root respiration, nutrient uptake, and metabolic activities, thereby creating a stable rhizosphere environment for plant growth. In contrast, substrates with poor aeration, excessive bulk density, or prolonged waterlogging may lead to root-zone hypoxia, suppress root activity, and even induce root rot, ultimately impairing plant growth and quality formation.

Significant differences exist among substrates in terms of water retention, drainage capacity, and nutrient availability, and these variations further influence metabolic processes within the plant. Zuo et al. (2020) conducted a widely targeted metabolomic analysis of *D. officinale* stems cultivated in pine bark, coconut coir, and a 1:1 mixture of the two substrates. Their results showed substantial differences among substrates in water-holding capacity and nutrient contents, particularly nitrogen, phosphorus, and potassium, which were closely associated with distinct metabolite profiles in the plants. Although the overall categories of metabolites were similar among substrate treatments, considerable differences were observed in metabolite abundance. Multivariate analyses, including principal component analysis (PCA) and orthogonal partial least squares-discriminant analysis (OPLS-DA), clearly distinguished samples derived from different substrates, indicating that substrate physicochemical properties exert strong regulatory effects on plant metabolism (Zuo et al., 2020). Furthermore, studies comparing greenhouse cultivation, simulated-natural cultivation, and wild growth conditions demonstrated that soil pH, total nitrogen, total phosphorus, and available phosphorus are important environmental factors affecting polysaccharide, total alkaloid, and flavonoid contents in *D. officinale*, further highlighting the close relationship between root-zone chemical environments and medicinal quality (Yuan et al., 2020).

The hydraulic characteristics of substrates also influence root-zone water-oxygen distribution and plant performance. Studies on coconut coir-and perlite-based soilless media have shown substantial differences in water retention curves, saturated hydraulic conductivity, pore-size distribution, and bulk density among substrates. These characteristics collectively determine the distribution of water and air within the confined root zone. Substrates possessing high total porosity, appropriate levels of plant-available water, and adequate aeration space generally create a low-stress rhizosphere environment that supports healthy growth in container cultivation systems (Gohardoust et al., 2020). Research on other horticultural crops has similarly demonstrated that combining organic materials such as coconut coir with inorganic components such as perlite and tuff can optimize water retention and aeration, thereby improving nutrient-use efficiency, plant growth, and yield (Tang et al., 2024). Therefore, for *D. officinale*, substrates capable of maintaining a balance among water retention, drainage, aeration, and nutrient buffering are more conducive to sustaining stable root-zone water-oxygen dynamics and nutrient supply, thereby promoting both growth and quality formation.

5.2 Effects of substrate microorganisms on nutrient uptake and metabolic activities

In addition to physicochemical properties, microbial communities within cultivation substrates are important factors affecting the growth and quality formation of *D. officinale*. Cultivation substrates serve not only as physical supports for root attachment and growth but also as habitats for diverse microorganisms, including bacteria, fungi, and actinomycetes. These microorganisms participate in organic matter decomposition, nutrient cycling, rhizosphere metabolism, and plant stress regulation, thereby exerting substantial effects on root development, nutrient acquisition, and metabolic activities. In orchids such as *D. officinale*, rhizosphere and endophytic microorganisms not only enhance the uptake of water and mineral nutrients but may also contribute to the biosynthesis of quality-related metabolites, including polysaccharides, alkaloids, and flavonoids.

Studies of the *D. officinale* microbiome have provided important evidence for understanding substrate-microbe-plant interactions. Wang et al. (2022) conducted metagenomic analyses of *D. officinale* growing in nutrient-poor Danxia habitats and identified highly diverse microbial communities in both rhizosphere and endophytic compartments. These communities included plant growth-promoting rhizobacteria such as *Massilia*, *Pseudomonas*, *Bradyrhizobium*, *Paenibacillus*, and *Streptomyces*, as well as beneficial fungi including *Tulasnella* and *Serendipita*. Functional annotation revealed significant enrichment of pathways related to carbohydrate, amino acid, and energy metabolism, indicating that these microorganisms facilitate nutrient mobilization and transformation, thereby supporting plant survival and growth under low-fertility conditions (Wang et al., 2022). A review of rhizosphere microbiomes in *Dendrobium* species further suggested that plant growth-promoting bacteria and fungi can enhance nitrogen and phosphorus uptake, produce phytohormones such as indole-3-acetic acid and gibberellins, and suppress pathogens, collectively improving plant growth, stress tolerance, and quality (Sarsaiya et al., 2025).

Different cultivation systems and root-zone conditions may also alter microbial community composition and their influence on metabolite production. Studies on *Dendrobium denneanum* cultivated under tree-mounted, rock-mounted, and pot cultivation systems showed that soil properties, particularly total phosphorus and pH, simultaneously affected root microbial communities and metabolite profiles. Correlation analyses revealed associations between specific microorganisms, including *Occallatibacter* and *Clonostachys*, and the pharmacologically active compound gigantol, suggesting that root-associated microorganisms participate in regulating secondary metabolite biosynthesis (Chen et al., 2023). Broader rhizosphere microbiome studies have likewise demonstrated that the rhizosphere represents a hotspot for nutrient cycling and root nutrition, with enrichment of genes involved in organic compound transformation, nitrogen fixation, and denitrification relative to bulk soil (Ling et al., 2022). In crops such as maize and pea, arbuscular mycorrhizal fungi and rhizobia have been shown to enhance phosphorus and nitrogen uptake, reshape rhizosphere bacterial communities, and improve yield and nutrient-use efficiency (Lu et al., 2023; Calderon and Dangi, 2024). Collectively, these findings suggest that substrate-associated microbiomes may be regarded as extensions of root function in *D. officinale*, influencing growth and medicinal quality through enhanced nutrient acquisition, improved stress resistance, and regulation of metabolic pathways.

5.3 Relationship between substrate-induced stress and secondary metabolite accumulation

The formation of plant secondary metabolites is regulated not only by genetic factors but also by environmental conditions. Bioactive constituents of *D. officinale*, including polysaccharides, dendrobine, flavonoids, and phenolic compounds, are closely associated with plant responses to environmental stimuli. By altering water availability, aeration, salinity, nutrient balance, and rhizosphere microecological conditions, different cultivation substrates may impose varying degrees of physiological stress on plants, thereby influencing defense responses and the activation of secondary metabolic pathways. Moderate substrate-induced stress may stimulate defense mechanisms, redirecting carbon, nitrogen, and energy resources toward the biosynthesis of flavonoids, alkaloids, and other protective metabolites. However, excessive stress can inhibit photosynthesis and biomass accumulation, resulting in reduced growth and quality.

Previous studies investigating salt, temperature, and osmotic stresses have provided valuable insights into the relationship between environmental stimuli and the accumulation of quality-related metabolites in *D. officinale*. Under treatment with 250 mmol/L NaCl, significant transcriptomic and metabolomic reprogramming occurred in leaves, including marked changes in phenylalanine metabolism, flavonoid biosynthesis, and α-linolenic acid metabolism. Genes involved in jasmonic acid biosynthesis were upregulated, accompanied by increased levels of flavonoids, carbohydrates, and alkaloids. These findings suggest that jasmonic acid may act as a signaling molecule promoting flavonoid biosynthesis, enabling plants to adapt to salt stress through enhanced secondary metabolite production. Similarly, diurnal temperature fluctuation treatments increased polysaccharide and total flavonoid contents in protocorm-like bodies and induced numerous differentially expressed genes enriched in secondary metabolite and flavonoid biosynthetic pathways. Stress-related genes, including heat shock proteins (HSPs) and heat shock transcription factors (HSFs), were strongly induced, indicating a close relationship between mild temperature stress and the accumulation of quality-related metabolites (Chen et al., 2024).

Root-zone water status and osmotic conditions, which are strongly influenced by substrate characteristics, also play important roles in regulating secondary metabolism. In vitro studies have shown that osmotic stress simulated by PEG-6000 disrupts water metabolism and antioxidant systems in *D. officinale* seedlings, increases cell membrane permeability, and induces physiological disorders such as hyperhydricity, indicating that unfavorable osmotic conditions can damage tissues and alter metabolic processes (Gao et al., 2020). Reviews of dynamic changes in functional constituents of *D. officinale* have further emphasized that environmental factors such as light, temperature, and water availability significantly affect the biosynthesis and accumulation of polysaccharides, alkaloids, flavonoids, and phenolic compounds, with characteristic accumulation peaks occurring at specific developmental stages (Wang et al., 2025). Moreover, metabolomic comparisons among plants cultivated on different substrates revealed that although the overall metabolite profile remains relatively stable, flavonoids are highly sensitive to substrate conditions and preferentially accumulate under pine bark cultivation, where flavonoid biosynthesis was identified as the only significantly enriched KEGG pathway (Zuo et al., 2020). Collectively, these findings indicate that substrate-induced stresses-including salinity, temperature fluctuations, water imbalance, and nutrient stress-can function as regulatory signals that activate hormonal and stress-response networks, thereby enhancing or redirecting secondary metabolite biosynthesis and ultimately altering the medicinal quality of *D. officinale*.

6 Current Challenges in Research

6.1 Lack of unified standards for substrate evaluation

In recent years, the expansion of large-scale cultivation of *Dendrobium officinale* has led to a substantial increase in studies investigating different cultivation substrates. However, a unified framework for evaluating substrate performance has yet to be established. Considerable variation exists among studies in terms of evaluation criteria, experimental duration, and management practices, making direct comparisons difficult. Some studies primarily focus on growth-related parameters, such as plant height, stem diameter, root development, and biomass accumulation, whereas others emphasize the contents of bioactive compounds, including polysaccharides, alkaloids, and flavonoids. Consequently, a comprehensive evaluation system that simultaneously incorporates physicochemical properties, plant growth performance, quality attributes, economic costs, and ecological benefits has not yet been developed. Research on substrates for orchids and other epiphytic plants has also indicated that growers often formulate substrate mixtures empirically to balance aeration, water retention, pH, and cost. Since no single material can adequately satisfy all these requirements, substantial variation exists in substrate formulations and evaluation methods.

From a broader perspective, the lack of standardized evaluation criteria has become a major obstacle to the application and dissemination of research findings in soilless cultivation systems. Plant performance in soilless horticulture is often assessed under different experimental designs, management regimes, and evaluation parameters, ranging from visual quality ratings to biomass, yield, and product quality. Such inconsistencies make it difficult to compare results across studies and hinder the development of widely applicable cultivation recommendations (Barrett et al., 2016). Moreover, substrate properties are strongly influenced by raw material sources, processing methods, and composting conditions. This is particularly evident for peat substitutes and organic substrates, whose nutrient contents, biological activities, and physicochemical stability may vary considerably, further complicating the establishment of universal fertilization and management protocols (Atzori et al., 2021; Cacini et al., 2021).

Another limitation in current substrate evaluation research for *D. officinale* is the emphasis on short-term performance while neglecting long-term stability. Some substrates exhibit promising growth-promoting effects during short-term trials; however, their pore structure, water-holding capacity, salinity levels, and nutrient-release patterns may change over extended cultivation periods, thereby influencing subsequent plant growth and quality formation. In addition, climatic conditions, cultivation systems, and irrigation and fertilization practices differ among regions, meaning that the same substrate may perform differently under various production environments. Therefore, future research should establish unified physical, chemical, and biological evaluation standards while providing detailed descriptions of irrigation, fertilization, and pest management conditions. Such efforts would facilitate the interpretation of substrate performance under commercial production conditions and provide comparable and reliable scientific evidence for substrate selection and practical application in *D. officinale* cultivation (Barrett et al., 2016).

6.2 Insufficient understanding of quality formation mechanisms

Current studies on the effects of cultivation substrates on the quality of *D. officinale* primarily focus on changes in the contents of bioactive compounds such as polysaccharides, dendrobine, and flavonoids, whereas the underlying regulatory mechanisms remain insufficiently understood. Existing research generally suggests that substrates promote the accumulation of bioactive constituents by improving the rhizosphere environment, regulating water and nutrient availability, and influencing rhizosphere microbial communities. However, systematic evidence is still lacking regarding how substrate-derived signals affect metabolic pathways, enzyme activities, and gene expression associated with quality formation. With advances in molecular biology and omics technologies, the quality formation of *D. officinale* has increasingly been recognized as the result of interactions among genetic background, environmental signals, and metabolic regulation. Nevertheless, the specific roles and regulatory pathways of substrate-related factors remain poorly characterized.

Significant progress has been made in elucidating the molecular mechanisms underlying key quality traits in *D. officinale*. For example, integrated metabolomic and transcriptomic analyses demonstrated that high light intensity induces the expression of *DoHY5*, which subsequently activates genes involved in flavonoid and polysaccharide biosynthesis, resulting in increased accumulation of anthocyanins and mannose-rich polysaccharides. Other studies have clarified the regulatory role of the MYB-bHLH transcriptional complex in anthocyanin biosynthesis and identified candidate genes associated with the organ-specific accumulation of polysaccharides, alkaloids, and flavonoids (Wang et al., 2021; Zhao et al., 2025). Comparative omics analyses between *D. officinale* and *Dendrobium nobile* further revealed that differences in polysaccharide and alkaloid accumulation are closely associated with differential expression of glycosidase-related genes and terpene biosynthesis pathways (Zhang et al., 2024).

Despite these advances, most studies have focused on genetic and signaling regulation under controlled in vitro conditions, light treatments, or elicitor-induced responses, while substrate-driven rhizosphere factors have rarely been integrated into the analysis. Research on soilless cultivation has shown that substrate type, nutrient dynamics, and rhizosphere microbial communities can substantially alter root-zone environments; however, knowledge regarding microbial community structure, functional stability, and their regulatory effects on plant metabolism within organic substrates remains limited (Tuxun et al., 2025). In *D. officinale*, systematic links among substrate physicochemical properties, root-microbe interactions, carbon-nitrogen metabolic balance, and the activation of specific biosynthetic genes or transcription factors have not yet been established. Therefore, future studies should integrate transcriptomic, metabolomic, proteomic, and microbiome analyses to elucidate how different substrates regulate the biosynthesis of polysaccharides, dendrobine, flavonoids, and other bioactive constituents, thereby providing a theoretical basis for the precise improvement of medicinal quality.

6.3 Insufficient integration of substrate formulations with industrial applications

Although numerous novel and composite substrate formulations have been developed in recent years, many remain at the experimental stage and have not been widely adopted in commercial production. On one hand, some substrate formulations are overly complex, relying on unstable raw material sources, high-cost components, or labor-intensive processing methods, making large-scale implementation difficult. On the other hand, many studies emphasize short-term biological effects while giving insufficient consideration to economic costs, resource-use efficiency, operational convenience, supply-chain stability, and compatibility with certification standards. As a result, a gap remains between research outcomes and industrial demands.

Experiences from soilless cultivation and protected agriculture indicate that substrates intended for commercial application must be compatible with mechanized production systems, integrated fertigation technologies, pest management programs, and standardized production workflows. However, many experimental studies do not adequately simulate such practical conditions and often fail to provide management details necessary for large-scale implementation (Barrett et al., 2016). Research has shown that conventional substrates such as rockwool remain widely used in certain crops largely because of their high uniformity and compatibility with fertigation systems. In contrast, more sustainable materials, including coconut coir, biochar, compost, and wood fiber, although demonstrating promising agronomic performance in experimental trials, still face challenges related to supply stability, salinity control, substrate standardization, and compatibility with automated production systems (Atzori et al., 2021; Fussy and Papenbrock, 2022).

For medicinal orchids such as *D. officinale*, the insufficient integration of substrate formulations with industrial production is also reflected in the limited translation of research findings into quality standards. Current commercial production still relies primarily on traditional substrates such as sphagnum moss and bark. Although some composite substrates have shown superior effects on growth promotion and quality improvement, standardized formulations, technical production specifications, and long-term validation remain lacking. Agricultural and agro-industrial residues, including coconut fiber, carbonized rice husks, coffee husks, and sugarcane bagasse, offer ecological and economic advantages as orchid cultivation substrates. However, their application is constrained by issues such as pathogen contamination risks, fluctuations in salinity, nutrient immobilization, difficulties in controlling root-zone biological activity, and unstable supply chains (Atzori et al., 2021; Cacini et al., 2021). Therefore, future research should place greater emphasis on aligning substrate development with industrial requirements. While maintaining favorable growth performance and quality enhancement, efforts should focus on establishing standardized substrate production processes, quality control systems, and application protocols. Such measures will facilitate the transformation of research achievements into scalable, certifiable production systems that comply with pharmaceutical and functional food standards, thereby supporting the sustainable development of the *D. officinale* industry.

7 Future Perspectives and Development Trends

7.1 Development of green and environmentally friendly composite cultivation substrates

With the increasing emphasis on ecological agriculture, green production, and resource recycling, the development of resource-efficient and environmentally friendly composite cultivation substrates has become an important direction for the *Dendrobium officinale* industry. Future substrate design should focus not only on growth-promoting effects but also on sustainability, cost-effectiveness, raw material availability, and ecological safety. Research on soilless cultivation media indicates that the global trend is shifting from traditional materials such as peat and rockwool toward renewable resources and agricultural waste utilization, following the principles of “reduce-reuse-recycle” while maintaining suitable physical, chemical, and biological properties for root growth (Barrett et al., 2016). For *D. officinale*, although traditional substrates such as sphagnum moss exhibit excellent moisture retention and root-promoting properties, concerns regarding resource availability, environmental conservation, and long-term costs have increased. Therefore, developing alternative composite substrates based on coconut coir, rice husks, peanut shells, wood fibers, green compost, and biochar is of considerable practical significance (Gruda, 2019; Atzori et al., 2021).

Future research on composite substrates should place greater emphasis on functional optimization and resource integration. Different substrate materials possess distinct advantages in water retention, aeration, nutrient-holding capacity, structural stability, and microecological regulation. Through scientific formulation, complementary properties can be combined to improve overall substrate performance. For example, combining bark-based materials with coconut coir, perlite, expanded clay, or biochar can simultaneously satisfy the requirements for root aeration, drainage, moisture retention, and nutrient buffering, thereby creating a more suitable environment for the epiphytic root system of *D. officinale*. Studies on soilless cultivation have demonstrated that materials such as biochar, coconut coir, wood fibers, and organic residues can provide appropriate porosity, aeration space, and water-holding capacity after proper blending and stabilization. However, waste-derived materials may still exhibit variability in raw material quality, excessive salinity, phytotoxic compounds, and changes in substrate properties during cultivation. Therefore, standardized production, testing, and characterization procedures are required (Barrett et al., 2016; Gruda, 2019; Atzori et al., 2021).

In addition, the development of novel functional substrates is expected to become a major research focus in *D. officinale* cultivation. Recent advances in soilless cultivation systems provide valuable insights for substrate optimization. For instance, hydrochar derived from spent grains and combined with vermiculite and perlite can retain nutrients, reduce nitrogen and phosphorus losses, and provide low bulk density and high porosity, thereby improving crop growth (Miao et al., 2024). Bio-based hydrogel substrates composed of pectin and chitosan networks have been shown to promote seed germination, root vigor, yield, and polysaccharide accumulation in medicinal dandelion while enabling controlled nutrient release (Guo et al., 2026). Chitin and chitosan, owing to their high water-holding capacity, nutrient-binding ability, antimicrobial activity, and potential to stimulate plant hormones and beneficial microorganisms, have been recognized as promising substrate materials for future vertical farming systems (Jia et al., 2024). Applying these concepts to *D. officinale* cultivation suggests that future efforts should focus on developing peat-free, waste-based, biopolymer-enhanced, and microbe-carrier composite substrates. Such substrates could evolve from simple growth media into integrated platforms capable of water and nutrient buffering, rhizosphere regulation, and quality enhancement.

7.2 Strengthening research on substrate-microbe-quality interactions

In recent years, studies on rhizosphere ecology and plant microbiomes have emerged as important research areas in medicinal plant quality formation. For *D. officinale*, cultivation substrates not only determine the root growth environment but also influence the structure and function of rhizosphere and endophytic microbial communities, thereby regulating nutrient uptake, stress tolerance, metabolic activities, and the accumulation of bioactive compounds. Previous studies have shown that plant-associated microbial communities can promote plant growth, enhance stress resistance, and regulate the biosynthesis of secondary metabolites that determine medicinal quality (Lv et al., 2024). Reviews focusing on medicinal plants further indicate that rhizosphere and endophytic microorganisms can improve nutrient acquisition, restore degraded soils, induce systemic resistance, and directly stimulate the biosynthesis of alkaloids, phenolics, and other specialized metabolites, thereby enhancing medicinal quality and reducing contaminant accumulation (Kumari et al., 2023).

Future studies should pay particular attention to the roles of beneficial microorganisms, including mycorrhizal fungi, plant growth-promoting bacteria, and endophytic fungi, in the growth and quality formation of *D. officinale*. In *D. officinale* and related *Dendrobium* species, diverse endophytic fungi such as *Trichoderma*, *Epulorhiza*, and *Phomopsis*-related taxa have been associated with yield improvement, resource utilization, and plant protection, indicating their potential as microbial fertilizers and quality-enhancing agents. At the same time, plant secondary metabolites and microbiomes exhibit bidirectional interactions. On one hand, plant exudates and secondary metabolites shape rhizosphere microbial communities; on the other hand, microorganisms can reshape plant metabolomes through hormonal regulation, nutrient provision, induction of stress responses, and direct activation of defense pathways (Pang et al., 2021; Laffon et al., 2024; Lv et al., 2024). Therefore, merely comparing the effects of different substrates on growth and quality is no longer sufficient. Future studies should integrate substrate types, microbial communities, and metabolite profiles into a unified analytical framework.

With the rapid development of high-throughput sequencing, metagenomics, metabolomics, and transcriptomics, multi-omics approaches are expected to become essential tools for elucidating the mechanisms underlying quality formation in *D. officinale*. Controlled substrate-microbe interaction experiments could be employed to identify key microorganisms and optimal substrate conditions that synergistically enhance the accumulation of polysaccharides, dendrobine, flavonoids, and phenolic compounds. Furthermore, synthetic microbial consortia or endophyte-based inoculants may be developed to improve the production of specialized metabolites (Cheng et al., 2019; Laffon et al., 2024; Liu et al., 2025). On this basis, quality-oriented “substrate-microbe integrated products,” such as biofortified composite substrates, mycorrhiza-assisted seedling substrates, and functional microbial slow-release carriers, could provide innovative technological solutions for high-quality *D. officinale* cultivation.

7.3 Establishing high-efficiency cultivation systems for large-scale production

The *D. officinale* industry is gradually transitioning from wild harvesting and small-scale cultivation toward facility-based, large-scale, standardized, and modern production systems. Advances in propagation technologies, substrate improvement, and integrated cultivation practices have enabled the industry to shift from dependence on wild resources to large-scale protected cultivation and environmentally friendly production systems (Liu et al., 2025). Nevertheless, cultivated products still face challenges related to inconsistent quality and efficacy, lack of unified standards, and the need to balance high productivity with resource conservation and environmental sustainability (Cheng et al., 2019). Therefore, the development of high-efficiency cultivation systems suitable for large-scale production should be based on standardized substrate formulations integrated with irrigation and fertilization management, environmental control, pest and disease management, and standardized harvesting and processing protocols.

Future efforts should focus on systematically evaluating the performance of different substrates and identifying standardized formulations suitable for diverse ecological regions, cultivation facilities, and production systems. Simultaneously, substrate production standards, quality inspection protocols, and application guidelines should be established to improve product consistency, reproducibility, and industrial compatibility. Green composite substrates should also be integrated with microbiome-informed management strategies, enabling the transition from empirical substrate selection to precision substrate design. For large-scale commercial production, substrates must not only satisfy the physiological requirements of *D. officinale* roots and support quality formation but also be compatible with mechanized filling systems, automated irrigation, integrated fertigation, disease monitoring, and product traceability systems, thereby enhancing production efficiency and quality stability.

With the advancement of smart agriculture technologies, *D. officinale* cultivation is expected to move toward increasingly digitalized and precision-based management. Studies have shown that PLC-SCADA-based greenhouse systems can accurately monitor and control temperature, moisture, humidity, and light intensity, achieving prediction errors below 2.5% and providing reliable decision support for precision cultivation management. Edge-computing and digital-twin platforms developed for *D. officinale* production can further improve environmental control accuracy, increase yield by more than 20%, and reduce energy consumption by over 40%, thereby providing scalable frameworks for intelligent cultivation systems (Li et al., 2025). In addition, big-data approaches can be applied to identify and manage experimental outliers in digital cultivation datasets, improving the reliability of growth, yield, and quality modeling as well as decision-making processes. In the future, integrating standardized composite substrates, microbiome-based management strategies, intelligent greenhouses, Internet of Things (IoT) monitoring technologies, and digital-twin models is expected to facilitate the establishment of a modern *D. officinale* production system characterized by high yield, superior quality, low production costs, traceability, and long-term sustainability.

8 Conclusions

Existing studies consistently indicate that, under artificial cultivation conditions, cultivation substrates are fundamental factors determining the growth performance and morphogenesis of *Dendrobium officinale*. Differences in substrate physicochemical properties, such as porosity, water-holding capacity, aeration, bulk density, pH, and cation exchange capacity, directly affect the root-zone microenvironment, thereby regulating seedling survival, root architecture, and aboveground biomass accumulation. Natural organic materials, such as sphagnum moss and bark, as well as properly treated agricultural wastes, such as coconut coir, rice husks, and peanut shells, generally provide favorable support and buffering effects. In contrast, unsuitable substrates characterized by excessive compaction, poor drainage, or nutrient imbalance may cause root rot, nutrient deficiency, or growth stagnation. Empirical comparisons further show that mixed substrates with complementary properties often perform better than single materials, indicating that rational substrate design and precise management are essential for achieving stable, high-yield, and high-quality production of *D. officinale*.

In addition to affecting growth, cultivation substrates also significantly influence the accumulation of key bioactive constituents and the overall medicinal quality of *D. officinale*. Variations in substrate nutrient supply, organic matter composition, and associated microbial communities can regulate primary metabolism and redirect carbon and nitrogen fluxes toward secondary metabolite biosynthesis, thereby altering the contents of polysaccharides, flavonoids, alkaloids, and other functional components. Studies have shown that substrates with moderate nutrient levels, good aeration, and may promote the accumulation of certain bioactive constituents and improve pharmacologically relevant indicators, whereas overly fertile or unsuitable substrates may lead to excessive vegetative growth, which is unfavorable for the accumulation of effective constituents. Moreover, substrate-induced changes in stem morphology, tissue density, appearance, and storage properties can also affect commercial grade and market acceptance. Therefore, the scientific selection and formulation of cultivation substrates that coordinate robust growth with enhanced bioactive compound accumulation represent an important approach for improving both the medicinal and economic value of artificially cultivated *D. officinale*.

Looking ahead, systematic optimization of composite substrates and in-depth clarification of the mechanisms by which substrates regulate growth and quality formation will become important directions in *D. officinale* research. At the applied level, multiple organic materials, agricultural by-products, and inorganic materials should be integrated to develop green, environmentally friendly, cost-controllable, and easily standardized substrate systems suitable for different cultivation modes and regional conditions, supported by unified evaluation criteria and long-term production validation. At the theoretical level, greater attention should be paid to the interactions among substrate physicochemical properties, rhizosphere microbial communities, plant nutrient uptake, signal transduction, and secondary metabolism. Systematic studies should be conducted using omics technologies, metabolite profiling, and microecological analysis. By combining substrate optimization with mechanistic elucidation and integrating these advances into facility cultivation, precision management, and breeding of substrate-adapted varieties, efficient and sustainable production models can be established to further support the high-quality development of the *D. officinale* industry.

Conflict of Interest Disclosure

The author affirms 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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Meta Analysis Open Access

Analysis of the Integrated Development Pathways between Medicinal and Edible Utilization of *Polygonatum* and Understory Cultivation Industry

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Abstract *Polygonatum* spp. are important medicinal-and-edible plant resource in China, with abundant nutritional components and considerable potential for functional development. With the increasing demand for health-oriented products and the transformation of the traditional Chinese medicine industry, the utilization pattern of *Polygonatum* resources is shifting from conventional medicinal material production toward medicinal-food product development and ecological cultivation. However, the sustainable development of the *Polygonatum* industry is restricted by several challenges, including the decline of wild resources, weak germplasm foundations, incomplete cultivation technology systems, and insufficient integration across the industrial chain. This study explores the integrated development of medicinal-and-edible utilization and understory cultivation of *Polygonatum*, analyzing its major nutritional components and bioactive compounds, the current status of medicinal-food product development, and the limitations affecting industrial development. Considering the biological characteristics of *Polygonatum*, including its perennial growth habit, shade tolerance, and adaptation to forest ecosystems, this study further discusses understory cultivation models and the effects of ecological factors on yield formation and quality improvement. Based on these analyses, strategies are proposed to enhance resource utilization and industrial value through the selection and genetic improvement of high-quality germplasm, establishment of green standardized cultivation systems, advancement of processing technologies, construction of an integrated industrial chain of "understory cultivation-product processing-brand marketing", and integration with forest wellness tourism and ecological industries. In the future, the *Polygonatum* industry should develop toward high-value product innovation, ecological industrial system construction, and digital precision management to promote resource conservation, industrial upgrading, and sustainable utilization.
Keywords *Polygonatum*; Medicinal and edible utilization; Understory cultivation; Industrial integration; Resource utilization

1 Introduction

Polygonatum is an important medicinal-and-edible plant genus with long-standing ethnomedicinal use and growing industrial value. Across Eurasian medical traditions, *Polygonatum* species have been used for more than 2 000 years as tonic herbs for fatigue reduction, metabolic disorders, age-related conditions, and digestive or respiratory complaints, while several species are also consumed as vegetables, teas, functional foods, and famine-relief starch resources (Shu et al., 2026). This dual-use value is rooted in a rich chemical basis: *Polygonatum* contains polysaccharides, steroidal and triterpenoid saponins, flavonoids, lectins, alkaloids, and related metabolites, and current reviews link these components to immunomodulatory, hypoglycemic, hypolipidemic, antioxidant, anti-inflammatory, anti-fatigue, neuroprotective, and anti-osteoporotic activities (Liu et al., 2024). Several reviews therefore identify *Polygonatum* as a promising raw material for pharmaceuticals, functional foods, cosmetics, and preventive health products, with relatively low toxicity after appropriate processing and strong market utilization potential (Yang et al., 2025). At the same time, recent scholarship emphasizes that research attention is shifting from traditional medicinal use alone toward integrated development in the food sector and broader bio-based industries, indicating a clear industrialization trend for *Polygonatum* resources (Li et al., 2023).

Against this background, the industrial development of *Polygonatum* has accelerated, but it also faces a resource and supply constraint that makes cultivation-based expansion necessary. Multiple studies note that rising utilization and market demand have made continued reliance on wild resources unsustainable, while overharvesting has already caused serious depletion of some medicinal *Polygonatum* resources and exposed problems of germplasm degradation and unstable quality (Liao et al., 2023; Cheng et al., 2026). Artificial cultivation is therefore regarded as a feasible response to resource scarcity, and *Polygonatum* has increasingly been positioned as an understory economic crop or forest-based specialty industry with both ecological and economic relevance in southern China and other forest regions (Wang et al., 2023). Understory cultivation is attractive because it uses forest land, light, and heat resources efficiently and can contribute to forest resource protection, biodiversity maintenance, and sustainable forestry development. For example, intercropping *Polygonatum* cyrtonema in moso bamboo forests improved soil quality relative to monoculture bamboo, and an appropriate bamboo density increased tuber yield, suggesting that agroforestry systems can simultaneously support ecological restoration and product output (Xu et al., 2023). Likewise, under-forest wild-imitating planting methods for *P. kingianum* have been reported to reduce cultivated land use, lower pesticide and fertilizer residues, improve product quality, increase forest-land returns, and remain suitable for larger-scale corporate operation.

However, the transition from traditional use to large-scale industrial development requires more than simple expansion of planting area. Historically, *Polygonatum* utilization has centered on rhizomes as medicinal materials such as Huangjing and Yuzhu, derived mainly from *P. sibiricum, P. kingianum, P. cyrtonema,* and *P. odoratum*, while local food use has included direct consumption of rhizomes and, in some cases, longstanding intake of specific taxa by local communities (Cheng et al., 2026). Yet recent work shows that the edible value of *Polygonatum* is broader than traditional rhizome use alone: tender shoots of P. odoratum contain essential nutrients, amino acids, minerals, and bioactive compounds, and appropriate agronomic management can improve the quality of both edible aerial parts and underground medicinal parts (Zheng et al., 2025). Even so, several obstacles still constrain scale-up, including germplasm confusion, indiscriminate seedling introduction across regions, lack of elite varieties, immature technical systems, weak service and regulatory capacity, poor market alignment, and high trial-and-error costs in understory production (Liao et al., 2023; Guo et al., 2026). Biological and ecological matching also matters: *Polygonatum* species differ significantly in yield and medicinal composition, *P. cyrtonema* can reach 7.5 t/ha in Zhejiang under suitable conditions, and provenance, altitude, temperature, moisture, and tree species all influence growth, metabolite accumulation, disease incidence, and economic returns (Wang et al., 2023). Some germplasm, such as *P. kingianum* var. *grandifolium*, may also offer industrial advantages through shorter seedling periods, higher biomass, repeated sprouting, and adaptability to both forest canopy and open-field conditions.

This study explores the integrated development pathways linking the medicinal utilization, edible application, and understory cultivation of *Polygonatum*, considering these three aspects as an interconnected industrial system. From the perspectives of resource foundation, traditional utilization patterns, production organization, and ecological-industrial coupling, this study systematically analyzes the key components and optimization strategies for the development of the *Polygonatum* industry. In response to current research gaps, including insufficient systematic comparisons among different species and medicinal-food utilization pathways, incomplete understory cultivation technologies and standard systems, weak coordination between production and market demand, and limited research on the development of medicinal-and-edible plants within large-scale forest management systems, this study aims to establish an analytical framework for the efficient utilization of *Polygonatum* resources and coordinated industrial development.

The findings provide important references for the breeding of elite *Polygonatum* varieties, quality evaluation, and sustainable resource utilization. Previous studies have shown that *Polygonatum* quality formation is strongly influenced by provenance, and that growth traits are associated with the accumulation of medicinal components. Ecological cultivation, agroforestry system design, and rhizosphere microbiome regulation may further improve the quality of *Polygonatum* resources. Therefore, clarifying the integration pathways between medicinal-and-edible development and understory cultivation of *Polygonatum* will not only contribute to wild resource conservation and the stable supply of high-quality raw materials but also promote coordinated development of the traditional Chinese medicine industry, functional food industry, and understory economy within a sustainable forestry framework.

2 Foundations and Current Status of Medicinal and Edible Development of *Polygonatum*

2.1 Nutritional components and bioactive compounds of *Polygonatum*

Polygonatum has a strong medicinal-and-edible material basis because its rhizomes and some aerial parts contain both nutritional substances and multiple classes of bioactive compounds. Reviews across the genus identify polysaccharides, saponins, flavonoids, alkaloids, lectins, and phenylpropanoids as major constituents, and recent summaries report that as many as 501 compounds have been identified in *Polygonatum* species (Liu et al., 2024). Among these, polysaccharides are most consistently described as the primary functional components and one of the key active ingredients supporting both nutritional and health value (Hu et al., 2023; Yang et al., 2025). *Polygonatum* is also increasingly recognized by nutrition researchers because it performs well as a nutrient source, and *P. sibiricum* and *P. odoratum* have been included in China's Medicinal Food Directory due to their high safety profile (Gong et al., 2023). In *P. cyrtonema*, rhizomes have historically served as a famine food because of high carbohydrate content comparable to staple crops, showing that *Polygonatum*'s value is not limited to pharmacological activity alone (Cheng et al., 2026).

Current evidence links these compounds to broad bioactivities, especially immunomodulatory, antioxidant, anti-inflammatory, anti-fatigue, hypoglycemic, hypolipidemic, neuroprotective, and anti-osteoporotic effects (Zhao et al., 2018; Gong et al., 2023). Mechanistic reviews focused on diabetes further indicate that *Polygonatum* polysaccharides, flavonoids, and saponins act through pathways such as improving insulin resistance, promoting insulin secretion, regulating intestinal microecology, inhibiting advanced glycation end-product accumulation, suppressing carbohydrate digestion and absorption, and modulating gluconeogenesis. Species-level studies add that *Polygonatum* extracts show strong antioxidant activity linked to flavonoids and polyphenols, while saponins appear especially important in regulating intestinal flora and lipoprotein metabolism, and polysaccharides contribute substantially to anti-inflammatory effects through cytokine regulation (Liu et al., 2024). Beyond rhizomes, tender shoots of *P. odoratum* are rich in essential nutrients, complete amino acids, mineral elements, and bioactive components, indicating that the edible resource base of *Polygonatum* can be expanded from underground organs to aerial tissues (Zheng et al., 2025).

2.2 Current status of medicinal and edible product development of *Polygonatum*

The current medicinal-and-edible product development of *Polygonatum* is characterized by a transition from traditional herbal use toward functional food and diversified industrial utilization. Across the literature, *Polygonatum* species are described as long-used tonic herbs and dual-use plants whose rhizomes are consumed as medicines, vegetables, teas, foods, and functional foods, with more than 2 000 years of application history in some species such as *P. odoratum* (Bi et al., 2023). Recent reviews emphasize that the genus has already entered the pharmaceutical, functional food, and cosmetic industries, and that research attention is shifting from medicinal application alone to integrated food-sector development (Li et al., 2024). This trend is supported by the low toxicity reported after proper processing and by the broad expectation that *Polygonatum* can serve as a raw material for health-oriented products (Shu et al., 2026).

At the product level, current development remains centered on rhizome-based medicinal materials and processed foods, but the resource spectrum is widening. Huangjing and Yuzhu are the canonical medicinal products derived from official *Polygonatum* sources, while *P. kingianum* var. *grandifolium* has long been consumed locally as food and is already circulated in the market as Polygonati Rhizoma (Cheng et al., 2026). Reviews on food applications argue that *Polygonatum* should be developed both as an ingredient and as a whole food, and polysaccharide-focused studies specifically highlight opportunities in functional foods, eco-friendly carriers, and other bio-based materials (Hu et al., 2023). Agronomic studies further show that product development can connect directly with cultivation innovation: *P. cyrtonema* can achieve yields of 7.5 t/ha under suitable conditions in Zhejiang, and P. odoratum tender shoots harvested at S2-S3 have edible value while S3-stage management can also improve subterranean yield and quality (Liao et al., 2023; Zheng et al., 2025). Understory and agroforestry systems also expand the industrial pathway by improving soil quality, supporting tuber yield, and increasing forest-land output benefits, making them compatible with large-scale medicinal-and-edible product supply (Xu et al., 2023).

2.3 Major constraints in the development of the *Polygonatum* medicinal and edible industry

The major constraints in the development of the *Polygonatum* medicinal-and-edible industry begin with resource pressure and biological inconsistency. Rising utilization and market demand have made dependence on wild resources increasingly unsustainable, and wild resource depletion has already become a stated challenge for sustainable utilization. At the same time, substantial variation exists among species, provenances, and growing environments in yield and medicinal composition, including significant differences in polysaccharides, saponins, flavonoids, and total phenolics (Liao et al., 2023; Cheng et al., 2026). This heterogeneity creates practical problems for standardization and breeding, especially because current cultivation still suffers from germplasm confusion, lack of elite varieties, indiscriminate cross-regional introduction of seedlings, and insufficient utilization of authentic medicinal sources. Research reviews also note that comparative understanding of the chemical differences among key medicinal species remains incomplete, which weakens standardization of medicinal-food uses across *Polygonatum* resources (Zhao et al., 2018; Yang et al., 2025).

A second set of constraints lies in the industrialization system itself, especially in understory cultivation and downstream market conversion. Field investigations across several provinces show that understory medicinal herb cultivation still faces an underdeveloped service system, insufficient regulatory capacity, low market alignment, immature technical systems, and weak research support. Specific production bottlenecks include high input with low output, mismatch between forest canopy density and plant light requirements, and unclear policy boundaries between ecological protection and commercial utilization, all of which raise trial-and-error costs in technology adoption (Guo et al., 2026). Although studies show that interplanting mode, tree species choice, and microbial regulation can improve soil quality, metabolite profiles, and medicinal value, these findings also imply that successful development depends on precise ecological matching rather than simple area expansion (Xu et al., 2023; Wang et al., 2023). More broadly, current reviews agree that food-sector applications remain underdeveloped relative to medicinal research, underlying mechanisms are still insufficiently clarified, and stronger technical standards, quality certification, and market-oriented product systems are still needed for large-scale, high-quality development (Li et al., 2024; Shu et al., 2026).

3 Understory Cultivation Models and Ecological Adaptability of *Polygonatum*

3.1 Biological characteristics of *Polygonatum* and its suitability for understory cultivation

Polygonatum is biologically well suited to understory cultivation because several species are perennial, rhizomatous herbs that naturally occur in shaded forest habitats and function as characteristic understory plants. *P. cyrtonema* is explicitly described as thriving in shaded understory habitats at 500~2 100 m and has been identified as a key understory economic crop in southern China (Figure 1) (Cheng et al., 2026). More broadly, understory cultivation systems are designed around the symbiosis between forest stands and medicinal plants and make use of forest land, light, and heat resources, which fits *Polygonatum*'s ecological niche.

Species-level evidence also supports strong adaptability within the genus. *P. kingianum* var. *grandifolium* can grow normally both under forest canopy and in the open field, while showing rapid emergence, repeated sprouting, evergreen adult plants, and rhizome biomass more than one time higher than that of *P. cyrtonema*, indicating unusual plasticity and production potential for forest-based cultivation. Transplantation experiments likewise found that this taxon was more adaptive than *P. kingianum* or *P. sibiricum* because it achieved the highest rhizome fresh weight and polysaccharide content, linking ecological adaptability directly to both yield and quality. Common-garden work further shows that *Polygonatum* species differ significantly in yield, stem and leaf traits, and rhizome saponin and polysaccharide contents, so understory suitability is real but species and provenance selection remains essential (Liao et al., 2023; Cheng et al., 2026).

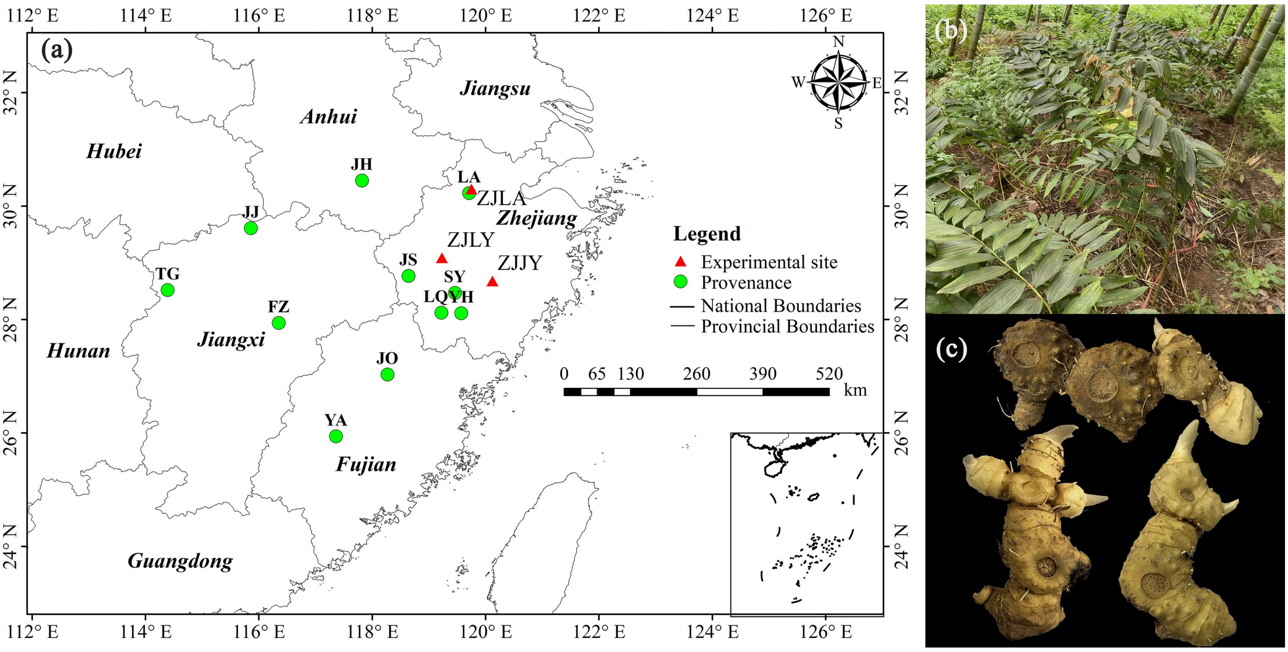

Figure 1 Distribution map of provenance collection sites and experimental sites for *P. cyrtonema* (Adopted from Cheng et al., 2026)
Image caption: (a) collection sites and experimental sites; (b) *P. cyrtonema* in Jinyun sites; (c) Rhizomes (Adopted from Cheng et al., 2026)

3.2 Effects of understory environmental factors on yield and quality formation of *Polygonatum*

Light is the most direct understory factor shaping *Polygonatum* growth. Shading experiments on *P. cyrtonema* show that shaded conditions increased chlorophyll a and b, net photosynthetic rate, stomatal conductance, transpiration, PSII efficiency, and total biomass, while reducing oxidative stress indicators, indicating that moderate shade improves physiological performance rather than suppressing it. The same study concluded that shading benefits rhizome yield and quality formation, with 65% light transmittance identified as especially suitable (Liang et al., 2019). Agroforestry evidence is consistent with this pattern: intercropping alters photosynthetic radiation and microclimate in ways that matter particularly for shade-tolerant *P. cyrtonema*, but excessive shading can cause lodging and inhibit growth, so canopy regulation is more important than maximizing shade (Xu et al., 2023).

Soil, altitude, moisture, pH, and rhizosphere biology jointly shape quality formation. Provenance trials found that saponin content increased with altitude and temperature, while flavonoid accumulation was promoted under drier conditions, showing that different active compounds respond to different environmental drivers (Cheng et al., 2026). Soil studies on *P. cyrtonema* showed that polysaccharides were associated with nutrient-rich soils and specific endophytic bacteria, whereas flavonoids were associated with relatively nutrient-poor soils, and Jingning material had the highest polysaccharide and saponin contents under higher AN, AP, and AK conditions (Zhang et al., 2024). Genotype-by-site adaptation studies further found that rhizome fresh weight and polysaccharide content peaked at soil pH 7.48~7.95 and declined with acidification, while beneficial rhizosphere microorganisms were associated with high-yield, high-quality materials and pathogenic taxa with poor performance. More generally, canopy plants can ameliorate solar radiation and heat stress while increasing understory soil moisture and carbon and nitrogen levels, which helps explain why forest microhabitats can favor shade-adapted medicinal plants when the tree layer is ecologically compatible (Abd-ElGawad et al., 2020; Shi et al., 2025).

3.3 Cultivation models and technical characteristics of understory *Polygonatum* production

Current understory *Polygonatum* production mainly follows intercropping, orchard underplanting, bamboo agroforestry, and under-forest wild-imitating planting models. In moso bamboo forests, intercropping significantly increased soil quality relative to bamboo monoculture, and the M1 density of 1 750 culms/ha produced the best combination of improved soil fertility and higher *Polygonatum* tuber yield (Xu et al., 2023). Stand density was the main factor controlling tuber yield in that system, exceeding the direct effects of altitude, SOC, and nitrate nitrogen, which means understory production technology must prioritize structural canopy management (Xu et al., 2023). In *Camellia oleifera* forests, intercropping with *P. cyrtonema* increased soil bacterial diversity, improved soil fertility, and enhanced tree-crop productivity, suggesting that *Polygonatum* can serve not only as an understory crop but also as a functional component of broader agroforestry systems (Kong et al., 2025).

Technical evidence also shows that understory models differ by tree species and by management intensity. For *P. sibiricum*, plants grown under oak trees showed better growth, less disease, and higher yield than those under citrus, Platycladus, pine, peach, or osmanthus, likely because deciduous stands formed thicker humus layers and better preserved soil moisture. Microbiome-metabolome work further found that understory interplanting increased rhizosphere bacterial and endosphere fungal diversity relative to field cultivation, and that metabolite changes were driven more strongly by rhizosphere than endosphere microorganisms (Wang et al., 2023). For *P. kingianum*, under-forest wild-imitating planting includes seedling selection, sand-bed pregermination, soil preparation, furrowing, transplanting, fertilization, disease control, and weeding, and it has been reported to shorten growth time, reduce pesticide and fertilizer residues, improve quality, and support both smallholder and corporatized production. In addition, crop regulation techniques such as topping in *P. odoratum* at the S3 stage while retaining 8~11 leaves can improve both edible shoot harvest and subterranean yield and quality, showing that understory production technology should integrate medicinal and edible targets rather than treat them separately (Zheng et al., 2025).

4 Integrated Development Pathways between Medicinal and Edible Utilization and Understory Cultivation of *Polygonatum*

4.1 Establishment of high-quality germplasm resources and standardized understory production systems

The first pathway is to build high-quality germplasm resources as the biological foundation of large-scale understory production. Provenance and common-garden studies show that *Polygonatum* differs significantly among species, provenances, and sites in yield, stem and leaf traits, and medicinal components, with substantial repeatability and clear selective-breeding potential. In *P. cyrtonema*, Songyang and Yunhe provenances achieved the highest comprehensive scores and are recommended as elite breeding materials, while long-term commercial validation is still needed because economic harvest usually occurs after 2~3 years rather than in a single screening season (Cheng et al., 2026). Species selection also matters at the cultivation stage: *P. cyrtonema* can reach 7.5 t/ha in Zhejiang, and stem diameter can be used as a practical harvest indicator in variety screening (Liao et al., 2023).

The second task is to convert germplasm advantages into a standardized understory production system. Current cultivation is constrained by germplasm confusion, lack of elite varieties, indiscriminate cross-regional seedling introduction, and weak use of authentic medicinal sources, all of which impede standardized industrial development (Liao et al., 2023). Molecular identification tools can directly address this bottleneck: an MNP-based fingerprinting system for *P. cyrtonema* distinguished all tested accessions with 99.90% accuracy and was proposed for cultivar authentication, seedling purity testing, germplasm conservation, and new-variety protection (Tang et al., 2026). At the production end, recent policy analysis recommends a variety-suitability framework based on canopy density classification, ecological cultivation protocols, and independent standards for understory medicinal herbs, which fits *Polygonatum*'s natural occurrence in shaded understory habitats and its role as a key forest economic crop (Guo et al., 2026).

4.2 Improvement of processing technologies and diversified product development of *Polygonatum*

The second pathway is to improve processing technologies so that raw *Polygonatum* resources translate into stable medicinal and edible value. Across the genus, polysaccharides are repeatedly identified as key active components, and reviews now cover extraction, purification, structural characterization, and structure-activity relationships as the basis for applications in foods, pharmaceuticals, cosmetics, and biomaterials (Gong et al., 2023; Shu et al., 2026). Processing is not a neutral step: different methods, including nine steaming and nine drying, wine processing, and honey processing, alter polysaccharide structure and biological activity, so product development should be based on targeted process optimization rather than generic primary processing (Zhao et al., 2026). Rapid quality evaluation technologies can support this transition, as near-infrared spectroscopy combined with chemometrics has already been reported for fast quantitation of polysaccharides and saponins in *P. cyrtonema* (Liao et al., 2023).

Processing upgrades should feed directly into diversified product development rather than remain limited to crude medicinal slices. *Polygonatum* is already recognized as a medicinal-and-food homologous resource with low toxicity after proper processing and broad application prospects in functional foods, pharmaceuticals, cosmetics, and preventive health products (Zhao et al., 2018; Hu et al., 2023). Current reviews emphasize that food-sector applications remain underdeveloped relative to medicinal research, even though P. odoratum has long been used as vegetables, foods, functional foods, and tea, and P. sibiricum and *P. odoratum* are already included in China's Medicinal Food Directory because of their safety profiles (Bi et al., 2023). A practical development route is therefore to expand from traditional rhizome products toward ingredient-based functional foods, whole-food products, eco-friendly carriers, and other bio-based materials built around polysaccharides and other active constituents (Yang et al., 2025).

4.3 Construction of an industrial chain model integrating "understory cultivation-product processing-brand marketing"

The third pathway is to construct an integrated industrial chain linking understory cultivation, processing, and brand marketing. Medicinal plant commercialization tends to fail when production, demand, and downstream quality requirements are disconnected, and value-chain research shows that successful commercialization requires understanding both demand systems and production systems rather than treating cultivation alone as the core problem (Palash et al., 2021). For *Polygonatum*, this means aligning planting mode, varietal selection, processing standards, and product positioning with market demand, a need echoed by recent understory-cultivation policy analysis that calls for stronger market alignment, quality certification, and regulatory frameworks that enable premium pricing (Guo et al., 2026). Certification, traceability, and safety are especially important because they shape buyer decisions and determine whether producers can enter higher-value markets.

An effective chain model also requires organization beyond the farm gate. Integrated value-chain approaches can shorten supply chains, strengthen backward and forward linkages, improve farmer bargaining power, and support certification adoption and premium realization, while intersectoral partnerships can improve the position of small-scale producer organizations (Volenzo and Odiyo, 2020). Evidence from medicinal-plant business studies likewise shows that lack of modern production and business techniques, weak finance, inadequate training and extension, and unstable price and demand constrain the full marketing system, whereas suitable planning across production, processing, and marketing can improve long-run performance (Palash et al., 2021). For *Polygonatum*, brand marketing should therefore be built on origin authenticity, standardized quality, safety certification, and the combined identity of "medicinal, edible, ecological, and wellness-oriented" products rather than on raw-material sales alone (Cheng et al., 2026; Tang et al., 2026).

4.4 Integration of ecological conservation with emerging industries such as forest wellness tourism

The fourth pathway is to integrate ecological conservation with forest wellness tourism and related emerging industries. Understory medicinal-plant cultivation already plays a positive role in the protection and sustainable use of forest resources, biodiversity, and the ecological environment, which makes *Polygonatum* suitable for development models that combine production with ecological services (Cheng et al., 2026). At the same time, wild-resource exploitation without effective domestication and governance can intensify ecological degradation, so conservation-oriented cultivation and value-chain design are necessary preconditions for expansion (Volenzo and Odiyo, 2020). This supports a shift from extractive utilization toward forest-based composite industries that include standardized cultivation, conservation education, and ecological branding.

Forest wellness research suggests that forests support psychological, physiological, and social wellbeing, but effective initiatives require integrated management across forestry, health, planning, and community sectors rather than forest management alone (Doimo et al., 2020). Applied tourism studies further emphasize protecting diverse tourism resources, improving infrastructure, building eco-friendly facilities and educational trails, and using adaptive, cross-sector governance with community participation, sustainability certification, and environmental education. These studies provide a transferable reference for *Polygonatum*-producing areas, this supports an integrated model in which understory cultivation landscapes, medicinal-food culture, wellness experiences, and conservation education are jointly developed to create employment, diversify rural income, and keep ecological protection as the limiting condition of industrial growth (Wang et al., 2024).

5 Key Issues and Optimization Strategies for the Integrated Development of the *Polygonatum* Industry

5.1 Strengthening germplasm conservation and genetic improvement research

The first key issue is that *Polygonatum* industrial expansion is constrained by wild resource depletion, germplasm degradation, and persistent confusion among closely related species and cultivars (He et al., 2025; Cheng et al., 2026). Morphological identification alone is often unreliable because *Polygonatum* shows strong phenotypic variation, interspecific similarity, hybridization, seasonal dormancy, and environmentally plastic rhizome traits, which can lead to uneven quality and even medication-safety risks (Figure 2) (Huang et al., 2026). Research across SCoT, ISSR, SSR, transcriptome-derived SSR, IRAP, and molecular fingerprinting systems consistently shows high genetic diversity in *Polygonatum germplasm* and supports molecular identification as a practical basis for conservation, classification, and breeding (Jiao et al., 2018). Core-collection construction is especially important because it preserves maximum allelic diversity with lower redundancy and management cost; in one recent study, a C78 core set retained 84.59% of alleles and was proposed to streamline ex situ conservation and germplasm regeneration (Zhu et al., 2025).

The main optimization strategy is to combine in situ conservation, ex situ core collections, and marker-assisted breeding into one germplasm innovation system. Multi-site provenance trials show highly significant genotype, site, and genotype-by-environment effects for growth and medicinal traits, with strong repeatability and clear selective-breeding potential (Cheng et al., 2026). Songyang and Yunhe provenances performed best in *P. cyrtonema* and are already recommended as elite breeding materials, while common-garden experiments indicate that *P. cyrtonema* is particularly suitable for introduction and cultivation in Zhejiang-like environments (Liao et al., 2023). Marker systems now go beyond diversity description: transcriptome-derived SSRs include markers associated with polysaccharide biosynthesis, and MNP or IRAP fingerprints can support cultivar authentication, seedling purity testing, germplasm protection, and intellectual-property management (He et al., 2025; Huang et al., 2026; Tang et al., 2026). A practical path is therefore to establish a national germplasm bank, define conservation priorities for geographically distinct groups, integrate molecular IDs with medicinal-component traits, and use diverse parental materials for crossbreeding high-yield, high-quality, and understory-adapted varieties (Zhu et al., 2025).

5.2 Improving green cultivation technologies and quality evaluation systems

The second key issue is that *Polygonatum* cultivation still lacks a sufficiently mature green production technology system and stable quality-evaluation framework. Species and provenance differ markedly in yield, polysaccharide and saponin contents, and agronomic traits, and these differences are further shaped by the climatic conditions of origin and cultivation environment (Liao et al., 2023). Understory production adds another layer of complexity because yield responds strongly to stand density and soil conditions; in bamboo-*Polygonatum* agroforestry, tuber yield increased as culm density decreased, with the M1 mode at 1750 culms/ha producing the best soil fertility and yield outcome (Xu et al., 2023). Cultivated *P. cyrtonema* also appears to offer quality advantages over wild material for industrial use, including higher average saponin content, stronger in vitro antioxidant activity, and more stable polysaccharide levels, although wild material can contain more alkaloids, amino acids, and coumarins (Peng et al., 2025). These findings support a shift from experience-based planting toward ecology-based, region-specific green cultivation protocols (Cheng et al., 2026).

Figure 2 Morphological images of four *Polygonatum germplasm* resources (Group II) (Adopted from Huang et al., 2026)
Image caption: (A) Fruit of *P. kingianum*; (B) Red flower of *P. kingianum*; (C) Yellow-green flower of P. kingianum; (D) rhizome of *P. kingianum*; (E) rhizome of *P. sibiricum*; (F) Flower of *P. sibiricum* (H58); (G) Flower of *P. sibiricum* (H14); (H) Fruit of *P. sibiricum;* (I) Immature fruit of *P. cirrhifolium*; (J) Mature fruit of *P. cirrhifolium*; (K) Flower of *P. cirrhifolium*; (L) rhizome of *P. zanlanscianense*; (M) Leaf and mature fruit of *P. zanlanscianense* (Adopted from Huang et al., 2026)

The corresponding optimization strategy is to standardize the full chain from nursery to harvest, while building rapid, multi-index quality evaluation. Existing standardized planting patents already cover seed reservation, breeding, seedbed management, greenhouse construction, seedling-stage management, and dormancy management, and show that standardized cultivation can simultaneously secure quantity and quality. Broader medicinal-plant standardization experience further shows the need to define provenance conditions, seed and root standards, seedling techniques, pest control, harvest processing, pesticide and heavy-metal residue limits, active-ingredient thresholds, and storage and transport rules. On the quality side, near-infrared spectroscopy combined with chemometrics enables rapid assessment of polysaccharides and saponins and can support raw-material selection and grading more efficiently than conventional assays (Liao et al., 2023). At the same time, optimized extraction and analytical methods remain necessary for key actives: ultrasonic-assisted extraction and HPLC quantification have already been optimized for steroidal saponins in P. kingianum, providing a practical reference for processing-linked quality control across production areas (He et al., 2022).

5.3 Enhancing industrial chain coordination and market competitiveness

The third key issue is that *Polygonatum* still faces weak industrial-chain coordination and insufficient market competitiveness, a pattern that matches the broader medicinal-plant sector. Medicinal-plant value chains are often long, weakly integrated, and poorly coordinated across producers, collectors, processors, and traders, with little vertical integration and limited horizontal collaboration (Chandra and Kumar, 2021). Comparable value-chain studies identify recurrent bottlenecks at farm, trader, and consumer stages, including low prices, weak demand, poor post-harvest technology, limited finance, inadequate training, and weak communication among chain actors (Palash et al., 2021; Geyo, 2024). Market studies also show that MAP sectors increasingly compete against lower-cost imports and need more innovation, actor agreements, and digital upgrading to remain competitive (Spina et al., 2023; Lestari et al., 2026).

The main optimization strategy is to build an integrated *Polygonatum* chain around producer organization, processing, branding, certification, and market networks. Cross-sector MAP research identifies market development, certification and labelling, and transformation and processing as core strategic priorities, while experts consistently rank new product design, producer-consumer networks, geographic branding, and proper raw-material storage and processing as high-value actions. Certification schemes that document origin, product quality, organic or forest-management compliance, and sustainable harvesting are particularly important because consumers weigh geographical origin, tradition, and the people behind the product in purchase decisions (Taghouti et al., 2022). Participation in broader value chains can improve product quality, market access, and innovation, but it requires technological upgrading, stronger partnerships, managerial training, and institutional support (Palash et al., 2021; Lestari et al., 2026). For *Polygonatum*, this implies a coordinated model led by enterprises, cooperatives, and producing areas that links understory cultivation bases with standardized processing, differentiated medicinal-food products, traceable regional brands, digital marketing, and farmer-oriented benefit-sharing mechanisms.

6 Development Trends and Prospects

6.1 Transition from resource utilization to high-value product development

The future direction of *Polygonatum* development is a clear shift from primary resource utilization toward high-value product development based on bioactive compounds, processing science, and diversified end uses. Current reviews consistently identify *Polygonatum* as a medicinal-and-edible genus with substantial market utilization value, especially because its polysaccharides are major active components with antioxidant, immunoregulatory, anti-inflammatory, anti-osteoporotic, and antidiabetic functions (Yang et al., 2025; Zhao et al., 2026). Research attention has already moved beyond traditional crude use toward extraction, structural characterization, and food-oriented application of functional ingredients, with specific emphasis on functional foods, pharmaceuticals, cosmetics, and bio-based materials (Li et al., 2023). This trend is especially strong for *Polygonatum* polysaccharides, which have entered the food system as beverages, health foods, additives, and packaging-related materials, indicating that *Polygonatum* is moving from raw medicinal material supply toward ingredient innovation and deep processing.

The main prospect is not only more products, but better differentiated products through processing control, species selection, and quality-oriented functional design. Processing methods such as nine steaming and nine drying, wine processing, and honey processing alter polysaccharide structure and bioactivity, so future competitiveness will depend on targeted process optimization rather than simple primary processing (Zhao et al., 2026). Product upgrading can also come from fermentation and flavor engineering: in *P. cyrtonema* beverage development, Lactiplantibacillus plantarum fermentation increased free amino acids, polyphenols, and flavonoids, improved antioxidant and digestive enzyme inhibitory activity, and reduced the herbal odor while increasing fruity and woody notes (Xie et al., 2026). At the same time, chemometric polysaccharide fingerprinting can distinguish major medicinal species and link structural differences to antioxidant activity, supporting species-specific raw material grading and higher-value functional food development (Liu et al., 2025). Overall, *Polygonatum* appears poised to move from selling rhizomes as generic raw materials toward a portfolio of precision-processed medicinal, food, nutraceutical, and biomaterial products (Hu et al., 2023; Yang et al., 2025).

6.2 Transition from single cultivation to an ecological industrial system

A second major trend is the transition from single-crop planting toward an ecological industrial system built around understory cultivation, agroforestry, and multi-functional forest use. Understory medicinal plant cultivation is increasingly valued because it makes efficient use of land, light, and heat resources, while also contributing to forest-resource protection, biodiversity maintenance, and sustainable forestry development. Agroforestry more broadly is recognized as a resource-complementary land-use system that improves soil functions, microclimate, biodiversity, and resilience compared with monocropping, which makes it a strong structural fit for *Polygonatum* and other shade-tolerant medicinal plants (Fahad et al., 2022). Evidence from compound forest-medicinal plant systems further shows that introducing medicinal plants in the understory can improve soil nutrient status, enrich rhizosphere microbial communities, and enhance soil carbon-source utilization, indicating that future *Polygonatum* development can create ecological as well as economic returns (Yu et al., 2023).

The likely next stage is therefore a forest-based composite industry, not a planting industry alone. Studies on medicinal plant agroforestry report higher species richness, better soil health, and increased farmer income, while also reducing pressure on wild medicinal plant populations, which aligns directly with *Polygonatum*'s dual need for conservation and industrial supply (Kholiya et al., 2025). However, this transition requires coordination beyond cultivation because present understory systems still face weak service systems, low market alignment, high input-low output problems, and unclear boundaries between ecological protection and utilization (Guo et al., 2026). Long-term agroforestry research also emphasizes that future management must evaluate multifunctionality, temporal dynamics, and trade-offs among yield, soil fertility, ecological services, and socioeconomic outcomes rather than optimize one variable in isolation (Cardinael et al., 2020). For *Polygonatum*, the most promising prospect is an integrated system combining understory production, ecological restoration, forest economy, and rural livelihood diversification rather than simple expansion of planted area.

6.3 Transition from experience-based production to digital and precision management

A third trend is the transition from experience-based cultivation toward digital and precision management. Precision agriculture is increasingly defined as a data-driven management approach that uses sensors, IoT, remote sensing, AI, and machine learning to improve production efficiency while reducing input losses and environmental impact (Sishodia et al., 2020; Miller et al., 2025). These systems enable real-time monitoring of soil moisture, pH, plant stress, water status, pest occurrence, and environmental conditions, which supports targeted irrigation, fertilization, pest management, and yield forecasting (Fuentes-Peñailillo et al., 2024; Mansoor et al., 2025). Remote sensing and UAV platforms have become especially important because they provide high-resolution crop monitoring, disease and pest detection, irrigation management, and yield prediction, while cloud computing and machine learning expand the ability to process large image and sensor datasets.

For *Polygonatum* understory systems, this means future production can shift from generalized field experience to site-specific ecological regulation. Smart sensing and spectroscopic/remote-sensing technologies under stress, enabling earlier intervention and better management of plant health and yield formation (Mansoor et al., 2025). AI-integrated sensing, high-throughput phenotyping, and automated platforms can also lower labor intensity and improve the precision of harvest, sorting, weed detection, and growth regulation, although the evidence is still mostly from general agriculture rather than Polygonatum-specific systems. The main constraints are clear: high initial costs, technical skill requirements, data management complexity, interoperability problems, privacy concerns, and weak connectivity in remote areas all still limit adoption (Fuentes-Peñailillo et al., 2024; Miller et al., 2025). Even so, the direction is clear that future *Polygonatum* production will increasingly rely on sensor networks, remote monitoring, AI analytics, and user-friendly decision systems to support standardized, efficient, and sustainable understory cultivation (Sishodia et al., 2020).

7 Conclusion

The medicinal-and-edible development of *Polygonatum* has substantially enhanced the utilization value of its resources because the genus combines nutritional attributes with diverse pharmacological functions and therefore supports both traditional medicine and food-oriented applications. *Polygonatum rhizomes* are officially recognized medicinal materials derived mainly from *P. cyrtonema, P. sibiricum*, and *P. kingianum*, while their inclusion in medicine-food use reflects the practical convergence of health care and dietary consumption. Their value is rooted in abundant active and nutritional constituents, especially polysaccharides and saponins, which are widely treated as major quality markers and linked to hypoglycemic, immune-regulating, anti-aging, antioxidant, and other health-promoting activities. At the same time, *Polygonatum* has food-security and nutritional significance because it has been described as having potential to address chronic and hidden hunger, and *P. cyrtonema* rhizomes historically served as a famine food with carbohydrate content comparable to staple grains. This dual value supports a transition from simple raw-resource use toward higher-value development based on breeding, quality control, extraction, and differentiated medicinal-food products.

Understory cultivation promotes the green development of the *Polygonatum* industry because it aligns with the plant's natural ecological traits while reducing dependence on increasingly depleted wild resources. *Polygonatum* naturally thrives in shaded forest habitats, and studies identify it as a key understory economic crop with strong potential in forest-based cultivation systems. Evidence from bamboo-polygonatum agroforestry shows that intercropping can significantly improve soil quality compared with monoculture, and that a bamboo density of 1750 culms/ha produced the best combination of soil fertility improvement and tuber yield. These systems also help restore ecological and economic functions of forest land by improving productivity, diversifying output, and creating more sustainable use pathways for shaded land resources. Yet green development depends on standardization rather than simple expansion, because cultivation outcomes vary significantly across species, provenances, and environments, and current production still faces germplasm confusion, weak technical systems, and the need for standardized seedling, field, and dormancy management. The long-term significance of understory cultivation is therefore not only higher output, but the formation of an ecologically compatible production mode that links conservation, artificial domestication, and quality-oriented forest farming.

Industrial integration is the key pathway for the sustainable upgrading of the *Polygonatum* industry because isolated cultivation cannot by itself solve bottlenecks in value realization, market access, and competitiveness. Broader medicinal-plant value-chain research shows that supply chains are often long, weakly integrated, and dependent on poorly coordinated actors, with middlemen playing a large role and with limited communication, innovation, and market responsiveness. For *Polygonatum*, this means that sustainable upgrading requires coordinated development of germplasm conservation, standardized cultivation, processing technologies, quality evaluation, certification, and branded product systems rather than continued reliance on raw rhizome sales. Molecular identification tools, core germplasm construction, and rapid quality assessment methods already provide technical support for this transition by improving variety authentication, breeding efficiency, and raw-material grading. At the market end, future competitiveness depends on product innovation, certification and labeling, digital upgrading, actor agreements, and stronger partnerships that connect producers, processors, and downstream markets. Taken together, the sustainable upgrading of the *Polygonatum* industry depends on transforming a fragmented resource-based sector into an integrated system that combines understory cultivation, deep processing, value-chain coordination, and ecological economic development.

Conflict of Interest Disclosure

The author affirms 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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Research Insight Open Access

Construction of an Efficient Production and Quality Control Technology System for *Ganoderma lucidum* Spore Powder

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Abstract This article analyzes the construction of an efficient production and quality control technology system for *Ganoderma lucidum* spore powder, focusing on key technical aspects including elite strain selection, culture medium optimization, precise regulation of cultivation environments, establishment of high-yield spore production models, spore collection and processing technologies, and quality evaluation methods. The available evidence indicates that breeding high-spore-yield and contamination-resistant strains is an important foundation for improving production efficiency. Optimization of medium composition and environmental factors such as temperature, humidity, light, and aeration can promote spore formation and the accumulation of bioactive components. Sporoderm-breaking and sporoderm-removal technologies can improve the release efficiency of active compounds, but they should be developed with consideration of both bioactive preservation and processing safety. For quality control, a multi-indicator comprehensive evaluation system should be established by integrating appearance characteristics, physicochemical parameters, multi-component detection, authenticity identification, and safety assessment. Meanwhile, standardized production processes, digital environmental monitoring, and industrial chain extension will further promote the transformation of the *G. lucidum* spore powder industry from experience-based management toward precision and intelligent production. This study provides a theoretical basis and technical reference for high-quality production, quality control, and industrial upgrading of *G. lucidum* spore powder.

Keywords *Ganoderma lucidum* spore powder; strain breeding; cultivation regulation; quality evaluation; standardized production

1 Introduction

Ganoderma lucidum is a medicinal and edible fungus with a long history of use in Asia, and its modern industrial development has accelerated as its bioactive components and health-related applications have become better characterized. Recent reviews describe *G. lucidum* as an important source of polysaccharides, triterpenoids, sterols, lipids, proteins, and other secondary metabolites with immunomodulatory, antioxidant, anti-inflammatory, antitumor, antidiabetic, hepatoprotective, and antimicrobial potential (Swallah et al., 2023; Ahmad et al., 2024). Against this background, *G. lucidum* products have expanded from traditional decoctions to powders, capsules, nutraceuticals, functional foods, and pharmaceutical preparations, and the international development of *G. lucidum*-based products is continuing to grow (Yeung et al., 2022). Among these products, spore powder is widely recognized as a high-value form because it concentrates the reproductive essence of the fungus and has become extensively consumed as a functional food and dietary supplement, especially in China (Ren et al., 2025). Studies further note that *G. lucidum* spore powder contains abundant active constituents, and some reports indicate that the contents of major ingredients such as polysaccharides can exceed those of the fruiting body, while wall-broken or wall-removed spores improve the release and absorption of these compounds because the natural sporoderm is difficult to digest and degrades poorly (Shen et al., 2020; Tang et al., 2023). Consistent with this utilization value, recent chemical studies have identified 142 compounds in spore powder, including lipids, triterpenes, alkaloids, organic acids, sterols, and fatty acids, providing a material basis for its continued development in health foods, medicines, and related high-value products (Zhang et al., 2024).

However, the rapid expansion of the *G. lucidum* spore powder market has also exposed prominent constraints in production efficiency, raw material stability, and product consistency. Natural resource limitations, strict growth requirements, and difficulty maintaining stable yield and quality across cultivation batches still restrict large-scale development and utilization. At the cultivar level, current spore-oriented production remains overly dependent on a limited number of strains; in particular, “Longzhi No.1” has been widely used for spore production, yet its poor resistance to competing microorganisms has reduced its suitability for industrial cultivation, creating an urgent need for new varieties with both high spore yield and stronger resistance (Tang et al., 2023). Even after raw materials are obtained, quality variation remains substantial. Commercial and regional comparisons show marked differences in triterpenoid content, physicochemical properties, antioxidant activity, enzyme inhibition, and overall chemical composition among different sources, years, and producing areas, which directly affects the medicinal value, functional performance, and market credibility of downstream products (Yeung et al., 2022; Zhang et al., 2023; Li et al., 2026). These findings indicate that production of *G. lucidum* spore powder still lacks a sufficiently integrated technical system linking strain selection, cultivation management, harvest timing, wall-breaking or wall-removal processing, and quality evaluation.

In addition to inconsistency, authenticity and safety risks remain major obstacles to standardization. Adulteration is a documented problem in the market, with dyed starch being deliberately mixed into *G. lucidum* spore powder to reduce production costs, prompting the development of rapid near-infrared and chemometric methods for authenticity identification and adulteration quantification (Shi et al., 2022). Fraudulent labeling of geographic origin is also a concern because active ingredient levels and commercial value vary significantly by origin, while cultivation region, stage, substrate, and cultivar can all affect elemental, isotopic, and chemical profiles; isotope-based traceability models have therefore been proposed as quality control tools with high classification accuracy (Wadood et al., 2023; Zhang et al., 2023). Safety control must also address contaminants introduced during processing and commercialization. Excessive phthalate plasticizers have been found in *G. lucidum* spore oil, highlighting process-related quality risks, while population exposure assessments for potentially toxic elements and the need for microbial and heavy-metal limits are consistent with broader calls for stronger safety assurance across the industrial chain (Qi et al., 2025). At the same time, manufacturing technology itself influences efficacy: wall-removed spore powder contains higher polysaccharide and triterpenoid levels and shows stronger antitumor effects than wall-broken powder, while process optimization based on industrial data can raise critical quality-property performance for moisture, fineness, crude polysaccharides, and total triterpenes to acceptable process capability levels (Shi et al., 2021; Zhong et al., 2023).

This study explores the construction pathway of an efficient production and quality control technology system for *Ganoderma lucidum* spore powder. It systematically analyzes key technical aspects, including elite strain selection, efficient cultivation, standardized harvesting, optimized sporoderm-breaking or sporoderm-removal processing, authenticity identification, quality traceability, and multi-indicator comprehensive evaluation. Existing standard systems have provided a certain foundation for the standardized development of the *G. lucidum* spore powder industry. However, previous studies have shown that current standard limits alone cannot fully address challenges associated with germplasm variation, changes in cultivation environments, regional quality differences, product authenticity, and alterations in active-component release and safety during processing. Therefore, this study further integrates key technical processes involved in *G. lucidum* spore powder production to establish a comprehensive technology system covering strain breeding, cultivation regulation, harvesting and processing, and quality evaluation. The proposed system aims to improve spore powder yield and batch stability, ensure product authenticity and safety, strengthen the control of characteristic active components, and provide a theoretical basis and technical reference for promoting the transformation of the *G. lucidum* industry from traditional experience-based management toward standardized, precise, and data-driven production models.

2 Biological Basis of Spore Powder Production

2.1 Growth and development characteristics of *Ganoderma lucidum* and spore formation process

Ganoderma lucidum is a white-rot basidiomycete that naturally grows on wood or lignocellulosic substrates, and its life cycle proceeds from basidiospore germination to primary mycelium formation, substrate colonization, primordium differentiation, young fruiting body formation, maturation, and finally spore release (Ren et al., 2025). Basidiospores can germinate rapidly under suitable nutritional conditions; one cultivation study reported efficient germination in coconut water gelatin within 72 h, after which the sporoderm produced a single germ tube that elongated, septated, and branched into monokaryotic primary mycelia. During fruiting, visible morphogenesis follows a recognizable sequence including mycelial coat hardening, primordial initiation, antler-like development, basidiocarp maturation, and spore liberation, indicating that efficient spore production depends on precise coordination between vegetative growth and reproductive differentiation. Recent developmental transcriptome analyses further divide fruiting and sporulation into sequential stages from mycelium, primordium, and young fruiting body to mature and post-sporulation stages, with large transcriptomic shifts especially at the mycelium-to-primordium and young-to-mature fruiting transitions (Liu et al., 2022).

Spore formation itself occurs on the abaxial side of the pileus and is closely linked to structural differentiation of pores, tube tissues, basidia, and spore walls (Cai et al., 2021). Ultrastructural work showed that young tubes first appear as slight depressions in the tramal surface, accompanied by extensive hyphal death and disintegration, while surviving hyphae become coated with extracellular matrix; developing basidia then push through this matrix into the tube lumen, where basidiospores are formed. Nuclear migration into spores begins only after lipid droplets start to coalesce and the spore wall has begun to form, and the mature *G. lucidum* spore wall comprises an outer primary layer, inter-wall pillars, and an inner secondary wall, features that help explain the robust sporoderm of commercial spore powder materials. At the molecular level, sporulation is associated with differential expression of genes involved in meiosis, carbohydrate metabolism, and transcriptional regulation; meiosis-related genes such as *DMC1*, *MSH4*, *HOP1,* and *Mek1* are highly expressed during development, while genes for trehalose and malate synthesis are upregulated during spore morphogenesis, implying active energy provisioning and carbohydrate accumulation in mature spores (Liu et al., 2022).

2.2 Selection of elite strains and optimization of germplasm resources

Efficient production of *G. lucidum* spore powder begins with elite germplasm, because strain differences strongly affect growth rate, resistance, fruiting performance, and basidiospore yield. A major current limitation is that most cultivated varieties were bred for fruiting body production rather than spore powder, and "Longzhi No.1" has been one of the few varieties widely used for spores despite poor resistance to competing microorganisms, which has reduced its production suitability (Tang et al., 2023). Accordingly, recent breeding work has focused on selecting high-spore-yield, disease-resistant, and stable strains through mutation breeding, molecular identification, antagonism testing, and multi-site cultivation evaluation (Viceconte et al., 2021; Feng et al., 2024). This direction is consistent with broader industrial demand for fast-growing, high-yield strains capable of supporting the growing market for medicinal and nutraceutical *Ganoderma* products (Swallah et al., 2023).

Several studies now provide concrete breeding examples. UV mutagenesis of the high-spore-yield parent strain G0109 produced mutant UV119, which showed strong resistance to undesired microorganisms and increased fruiting body and basidiospore yields by 8.67% and 19.27% relative to the parent, with basidiospore yield 20.56% higher than "Longzhi No.1" (Tang et al., 2023). Another breeding study reported that strain XZ-2, obtained through tissue isolation and radiation treatment, delivered fruiting body yields 9.7%~30.1% higher and basidiospore yields 20.2%~45.7% higher than control strains across locations and years, while maintaining stable annual performance and elevated polysaccharide and triterpenoid levels. Atmospheric room-temperature plasma mutation combined with microbial microdroplet screening also yielded stable mutants YB05, YB09, and YB18 with faster growth, stronger antagonism, and higher biomass or triterpenoid production across five generations, showing that high-throughput breeding can accelerate germplasm improvement for industrial fermentation (Feng et al., 2024). Comparative local strain screening likewise identified G8 and Bendi as superior strains with faster mycelial growth, stronger spore-producing ability, higher biological efficiency, and better production characteristics, further indicating that regional germplasm evaluation remains an important complement to mutation breeding.

2.3 Optimization of culture medium and nutritional regulation technologies

After elite strains are obtained, efficient spore production depends on matching genotype with suitable carbon sources, nitrogen balance, substrate structure, pH, temperature, illumination, aeration, and spawn materials, because *Ganoderma* species have specific physiological requirements and growth performance varies sharply with medium composition and environmental control (Ahmad et al., 2024). Experimental optimization studies show that mycelial growth can be markedly improved under defined conditions. For example, one study found that coconut water gelatin at pH 6.0, under sealed and lighted conditions at 32 ℃, gave the most efficient mycelial growth, while corn grit was the most suitable grain spawn and a substrate of 70% rice straw and 30% sawdust produced the shortest fructification period of 17.33 days. These results support the view that low-cost agricultural residues can be effectively converted into production substrates, and that rational control of physical and nutritional parameters is a prerequisite for industrial cultivation (Akçay et al., 2025).

Nutritional regulation also affects not only biomass and fructification, but the accumulation of target active components relevant to spore powder quality. In submerged culture, sucrose favored mycelial growth, corn flour supplementation promoted biomass with an optimum around 7.0~7.5 g/L, and an optimized natural medium containing potato extract, sucrose, and corn flour achieved a mycelial yield of 7.51 g/L together with higher triterpenoid and intracellular polysaccharide contents than a nutrient-rich comparison medium (Zheng et al., 2026). Substrate composition likewise alters yield and chemical quality: coconut sawdust and other lignocellulosic substrates can improve biological efficiency, while supplements such as olive oil and copper enhance triterpenoid and phenolic contents (Zhu, 2024). Waste-based substrate screening further showed strong substrate dependence, with oak wood 91%+wheat bran 9% giving the highest mushroom yield at 46 g/kg, whereas corn husk gave the lowest, demonstrating that lignocellulosic composition and bran supplementation materially influence production performance (Akçay et al., 2025). At the level of developmental physiology, active component accumulation is stage-dependent: triterpenoids, steroids, and polyphenols peak in the budding stage, whereas polysaccharides, flavonoids, and purines are higher in the maturation stage of basidiospores, indicating that nutritional regulation and harvest timing should be coordinated to balance yield with the desired chemical profile (Gao et al., 2024). Together, these findings show that an efficient production system for *G. lucidum* spore powder must integrate superior strains, substrate engineering, and stage-specific nutritional regulation to achieve high yield, stable sporulation, and consistent quality (Ren et al., 2025).

3 Key Technologies for Ganoderma Spore Powder

3.1 Precise regulation technologies of cultivation environmental conditions

The efficient production of *G. lucidum* spore powder depends first on stage-specific control of the cultivation environment, because mycelial growth, primordium initiation, fruiting body development, and spore release do not share the same optimal requirements (Zhou, 2017). Studies of solid cultivation report that *G. lucidum* generally performs well at 18~25 ℃ and 85~90% humidity during growth, while fruiting body development is favored around 24~28 ℃ and high humidity, and temperatures below 20 ℃ can cause yellowing and growth arrest (Chanshorphea, 2019). Under subtropical bag cultivation, exposure of spawn bags to (30±1) ℃ and 90~95% RH supported primordium initiation and completion of the crop cycle, showing that local production systems can shift the operating window upward when substrates and strains are adapted to those conditions. Medium-level physiological studies likewise found strong environmental sensitivity: mycelial growth was most efficient on a pH 6.0 medium under sealed, lighted conditions at 32 ℃, and a separate comparative study identified 30 ℃ as the best temperature, pH 6 as optimal, and darkness or alternating light as more favorable than continuous light for vegetative growth (Al-Kaabi and Hussien, 2025).

Environmental regulation must therefore be precise rather than uniform, especially for light, air exchange, and contamination control. Controlled-room experiments showed that light quality materially changes morphology and composition: red light inhibited fruiting body differentiation, while green light increased fruiting body weight by 21.4%, raised pileus triterpenes by 28.1%, and enhanced multiple extracellular enzyme activities, indicating that optimized spectral management can improve both yield formation and metabolite accumulation (Liu et al., 2024). Air supply is also a critical control variable, because in static culture systems it significantly increased triterpenoid accumulation, supporting the broader principle that oxygen availability and ventilation influence secondary metabolism and probably later sporulation performance (Hu et al., 2018). At the production-house scale, sanitation management is equally important: repeated cultivation can favor antagonistic fungi such as *Trichoderma* and *Mucor*, whereas waterlogging-based sanitation sharply reduced their colonization, restored fruiting body development to about 90%, and enabled spore yields of about 5 kg per house where the untreated control failed (Tong et al., 2020). Taken together, efficient environmental regulation for spore production should integrate temperature-humidity coordination, pH adjustment, spectral light management, adequate aeration, and strict sanitary control to stabilize fruiting and maximize subsequent spore formation.

3.2 Optimization of high-yield spore production cultivation models

High-yield spore production also requires choosing cultivation models that shorten the cropping cycle, reduce contamination, and improve substrate conversion efficiency. Reviews and cultivation studies show that *G. lucidum* can be produced by bottle procedures, sawdust bags, short wood segments, tree stumps, wood logs, and liquid-state culture, but for fruiting bodies and spores the dominant industrial direction has shifted from natural logs toward sawdust-based bag or synthetic log systems (Jeewanthi et al., 2017; Zhou, 2017). Earlier wood-log cultivation required a long cropping cycle of roughly 6~24 months and generally lower yield, whereas lignocellulosic bag substrates permit more controlled and efficient biomass transformation (Thiribhuvanamala and Krishnamoorthy, 2021). Direct comparisons in Cambodia found higher contamination in log culture than bag culture for *G. lucidum*, and sawdust substrates gave higher yield and biological efficiency, supporting the superiority of bag cultivation where cleanliness and standardization are priorities (Chanshorphea, 2019). This shift is consistent with the broader ecological advantage of *G. lucidum* cultivation, namely the conversion of agricultural and forestry residues into medicinal biomass using relatively low-cost solid substrates (Thakur et al., 2024).

Within sawdust-based systems, substrate design and strain-model matching are decisive for high spore yield. Substrates of 70% rice straw and 30% sawdust shortened the fructification period to 17.33 days, coconut wood log sawdust with wheat bran produced 77.5 g per 175 g substrate and 44.3% bioefficiency, and indigenous Pakistani material performed best on sawdust+wheat straw, showing that optimized lignocellulosic combinations can substantially improve production efficiency (Thiribhuvanamala and Krishnamoorthy, 2021). Other local evaluations similarly found that rubber sawdust, mango sawdust, or their mixtures maintained relatively high yield and biological efficiency, while sawdust outperformed paddy straw, sugarcane bagasse, maize stalk, and coir pith for total yield in another recent comparison (Sethi and Chinara, 2025). Spawn medium optimization matters as well: corn grit produced rapid mycelial growth in one study, while barley grains were the most appropriate spawn medium in another, indicating that cultivation models should be regionally adapted rather than fixed to one recipe (Ghafoor et al., 2025). Finally, high-yield models depend on elite strains; the UV-mutant strain UV119 increased basidiospore yield by 19.27% over its parent and 20.56% over “Longzhi No.1,” while also improving resistance to microbial invasion, so the most effective cultivation model is an integrated system that combines superior germplasm, low-contamination bag culture, and substrate formulas tailored for rapid colonization and sustained sporulation (Figure 1) (Tang et al., 2023).

3.3 Optimization of spore powder collection and processing technologies

After sporulation, efficient production depends on standardized collection and processing technologies that preserve bioactive components while improving release from the hard sporoderm. *G. lucidum* spores are rich in polysaccharides and triterpenoids, but their wall is composed mainly of chitin, cellulose, and lignin, making the contents difficult to digest and absorb unless wall disruption is performed (Qi et al., 2024). Mechanical rolling, room-temperature milling, ultrafine grinding at low temperature, ball milling, and combined chemicophysical methods have all been proposed as effective sporoderm-breaking approaches (Wang et al., 2017). The common technical target is high wall-breaking efficiency with minimal damage to active ingredients; reported methods include low-temperature vibration pulverization under protective gas, which achieved a 98% breaking rate without additives or obvious deterioration, and broken-sporoderm machine or ball-mill processing, both of which exceeded 95% wall breaking. In addition, fermentation with *Lactobacillus plantarum* achieved a wall-breaking rate of 52.38% after 48 h, suggesting that biological pretreatment can complement physical disruption where mild processing is desired.

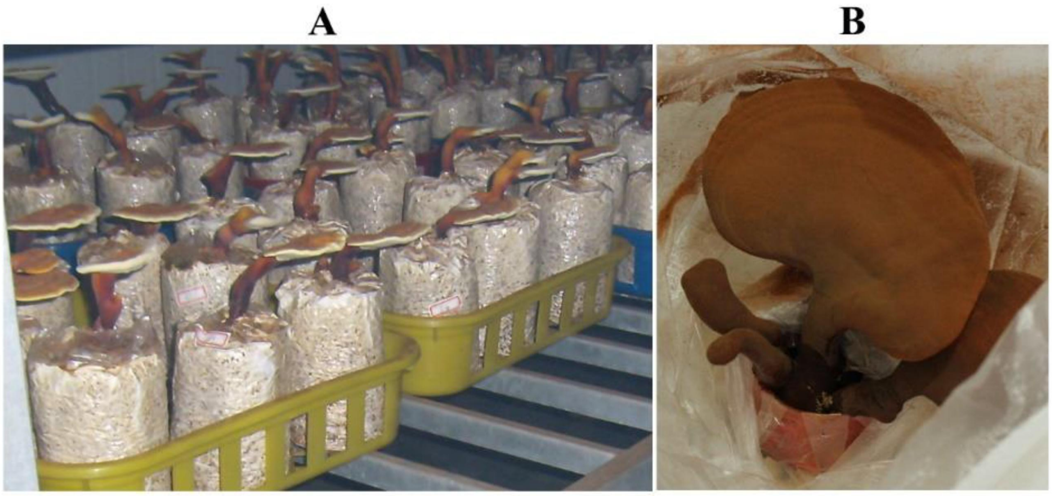

Figure 1 Fruiting of the 1st, 5th, 10th and 15th generations of the mutagenic strain UV119 (Adopted from Tang et al., 2023)
Image caption: (A): Fruiting situation of different generations of UV119; (B): collection of spores powder (Adopted from Tang et al., 2023)

Processing optimization should not be judged by wall-breaking rate alone, because different methods produce different nutrient release and bioactivity outcomes. In vitro digestion experiments showed that broken spores released substantially more polysaccharides and triterpenes than unbroken spores, and that bioaccessibility increased with specific surface area; after the intestinal phase, polysaccharide bioaccessibility rose from 29.52% in unbroken powder to 39.73~72.45% after room-temperature milling and 44.53~104.18% after low-temperature ultrafine grinding. Low-temperature ultrafine grinding also outperformed conventional milling in bioaccessibility despite a lower specific surface area, implying that structural preservation during processing can be as important as particle-size reduction (Qi et al., 2024). Studies comparing sporoderm-removal with ordinary sporoderm-broken powder found even larger differences: sporoderm-removal increased total polysaccharides by nearly 12-fold, yielded more abundant triterpenoids, and produced stronger antioxidant activity, while another study reported that broken spores extracted 3~4 times more bioactive compounds than non-broken spores. Therefore, spore powder collection and processing technologies should be built around clean collection, low-temperature drying, protective and efficient wall-breaking, and post-process quality evaluation based on release efficiency and active-component retention, so that the final product achieves both high yield and high functional quality.

4 Quality Control of Ganoderma Spore Powder

4.1 Evaluation of appearance quality and basic physicochemical indicators

The quality control of *Ganoderma lucidum* spore powder should begin with a combined evaluation of appearance, microscopic traits, and basic physicochemical indicators, because single-index assessment does not adequately capture source differences, processing status, or market adulteration. Early quality studies on wall-broken spore powder used character inspection, microscopy, physicochemical identification, and main-component assays together, and showed that these indices were stable and operable for preliminary quality valuation. Regional comparison further shows that spore powders differ measurably in color and physicochemical properties, confirming that appearance is not only a sensory trait but also a useful external reflection of internal quality variation (Li et al., 2026). Because quality is strongly affected by producing area, cultivation environment, and harvest conditions, the appearance evaluation system should record color uniformity, fineness, agglomeration, odor, and wall-breaking-related morphology together with origin and batch information (Ran et al., 2025).

Basic physicochemical testing should then focus on moisture, ash, and related compositional indicators that can reveal processing quality and raw-material purity. Moisture is especially suitable for rapid routine control, and near-infrared models have predicted moisture content in *G. lucidum* with good accuracy, supporting its use for fast non-destructive screening in production settings (Ni et al., 2023). Ash content also has discriminating value: one study found lower ash in Xiuyan samples than in first-grade Shandong spore powder, while third-grade Shandong samples had higher ash, indicating that mineral residue can reflect grade or impurity burden. Since pulverization changes sample homogeneity and may alter optical behavior, standardized sampling, particle-size control, and wall-breaking-rate evaluation are necessary to make physicochemical indicators comparable across lots (Ran et al., 2025). For rapid authenticity and sensory-style discrimination, emerging tools such as electronic nose, NIR, and hyperspectral imaging can complement conventional tests, especially for batch screening before confirmatory analysis (Figure 2) (Shi et al., 2022; Ran et al., 2025).

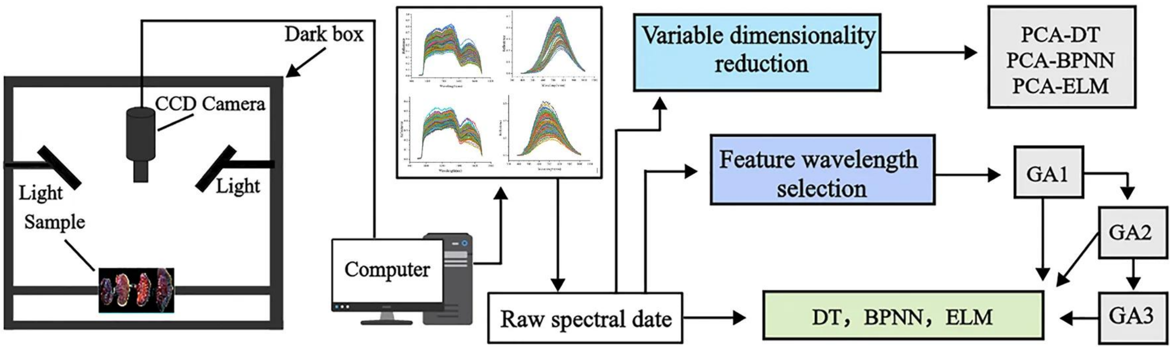

Figure 2 Schematic diagram of *Ganoderma lucidum* sample program analysis (Adopted from Ran et al., 2025)

4.2 Detection of active components and quality evaluation methods

Active-component control should center on polysaccharides, triterpenoids, sterols, lipids, proteins, and selected nucleoside-related markers, because these are the principal material basis of spore powder quality and function (Ran et al., 2025). Triterpenoids and polysaccharides are the most widely accepted core quality markers, and they are already used officially for *Ganoderma* quality assessment (Wu et al., 2017). Yet the evidence also shows marked quantitative variability across commercial products and regions: tested *Ganoderma* samples ranged from 0.22% to 3.31% polysaccharides and 0.21% to 10.56% total triterpenes, while LC-MS/MS-targeted triterpenes ranged from 0.01% to 0.98%, indicating that a single bulk index is not sufficient for refined quality grading (Liu et al., 2025). Regional spore-powder comparisons likewise found large differences in total sugars, polysaccharides, lipids, proteins, phenolics, total triterpenoids, ergosterol, and nucleosides, with substantial corresponding differences in antioxidant and enzyme-inhibitory activities (Li et al., 2026).

Accordingly, the quality evaluation method should combine targeted quantification with fingerprinting and authenticity tools. HPLC-DAD fingerprinting has been established for *Ganoderma* products using 13 candidate compounds, with 11 ganoderma acids identified as useful chemical markers and the method validated as accurate and feasible for quality control and identity determination (Yeung et al., 2022). For spores specifically, UPLC-Q-TOF-MS/MS identified nine confirmed triterpenoids and supported an HPLC method for simultaneous determination of five triterpenoids, with good linearity, acceptable recovery, and large habitat-related differences in content (Qiao et al., 2024). Polysaccharide evaluation can be strengthened by saccharide mapping and HPSEC-MALLS-RID, which showed potential for routine quality evaluation of polysaccharides in supplements (Wu et al., 2017). Molecular identification should also be included, because ITS2 barcoding precisely detected 16 adulterants among 84 commercial Ganoderma samples, and authenticity testing by NIR with chemometrics can rapidly identify dyed-starch adulteration and quantify its level with calibration and validation correlations above

0.99 (Shi et al., 2022). At the process-evaluation level, wall-breaking technology must be assessed not only by breaking rate but also by nutrient release, since broken powders showed much higher intestinal bioaccessibility of polysaccharides and triterpenes than unbroken powders, and sporoderm-removed powders contained higher active-constituent levels and stronger antitumor activity than ordinary wall-broken powders (Qi et al., 2024).

4.3 Safety evaluation and quality standard system construction

The safety evaluation system for *G. lucidum* spore powder should cover authenticity, contaminant limits, and toxicological evidence rather than relying only on active-component content. Market studies show that product consistency is often poor: in a U.S. survey, only 5 of 19 products (26.3%) matched their label ingredients, indicating that identity auditing and adulterant screening are essential parts of quality control (Wu et al., 2017). Heavy metals remain a concrete concern in commercial Lingzhi products, with about one-third of tested samples exceeding allowable limits for arsenic and more than half exceeding limits for cadmium, while organochlorine pesticides were less problematic in the tested subset. These findings support setting mandatory limits for Pb, As, Hg, Cd, pesticide residues, and microbial contamination, together with strengthened GAP and GMP management across cultivation, harvesting, and processing.

The quality standard system should therefore integrate pharmacopoeial indicators, local or industry standards, and safety validation by toxicology. Existing standards already provide a regulatory basis, including the industry standard GH/T 1133-2017 for wall-broken *Ganoderma* spores and local food safety standards in Guizhou and Zhejiang (Li et al., 2026). Toxicological evidence is reassuring but still needs product-specific confirmation: a 26-week repeated-dose study found no significant systemic toxicity for sporoderm-removed spores in rats and established a NOAEL of 4.0 g/kg, about 20 times the human equivalent dose (Xia et al., 2023). Broader mushroom-powder toxicology also found no acute toxicity, no subchronic oral toxicity up to 2 000 mg/kg bw/day, and no genotoxic potential in tested *G. lucidum* powder preparations (Chrysostomou et al., 2024). However, safety reviews still note that high doses of spore extract should be used cautiously because some evidence raised concern about increased CA72-4 despite no clear organ toxicity, so the final standard system should include routine toxicology review, batch traceability, and post-market monitoring in addition to compositional release tests (Thuy et al., 2023).

5 Standardization and Industrial Application of *Ganoderma lucidum* Spore Powder Production

5.1 Whole-process standardized production model of “strain-cultivation-collection-processing”

A whole-process standardized production model for *Ganoderma lucidum* spore powder should begin with elite strain selection and then connect strain, substrate, cultivation environment, collection, and processing into one closed technical chain. High-spore-yield strains are a core upstream variable, because most existing cultivars were originally bred for fruiting bodies rather than spores, while the mutant strain UV119 achieved 19.27% higher basidiospore yield than its parent and 20.56% higher yield than “Longzhi No.1,” with stronger resistance to undesired microorganisms (Tang et al., 2023). Standardization at the cultivation stage then requires procedural control of culture material preparation, sterilization, inoculation, mycelial growth, land or bag management, and fruiting management, because complete workflow designs for spore production patents already define sequential operations from strain selection through inoculation and field management to spore collection. These workflow designs also show that collection is not an isolated terminal step but part of the cultivation system itself, with sleeve barrels, filter-cloth wrapping, film laying, packaging, drying, sieving, and storage all treated as standardized downstream operations that influence purity, recovery, and marketable quality.

A mature whole-process model therefore needs to align production standards with regulatory standards so that each link has measurable control points. The Chinese Pharmacopoeia already specifies identification, content determination, and microbial limits for *Ganoderma* spore powder, with minimum limits of 0.90% polysaccharides and 0.50% triterpenes and sterols, while GB/T 29344-2023 provides technical specifications for harvesting and processing and NY/T standards provide methods for wall-breaking rate, ganoderic acid, and total triterpenoid determination. International standardization is also advancing, because ISO 21315:2018 established the first global standard for *G. lucidum* fruiting bodies and an ISO standard for spore powder is under development, providing a basis for harmonized testing, packaging, storage, and trade. At the enterprise level, whole-process standardization should further emphasize purity and contamination control, since wild-imitating collection systems have reported>99.9% purity, while dedicated collecting techniques reported high yield, lower cost, and heavy metals controlled within national standards.

5.2 Application of digital technologies in production management

The next step is to digitize production management so that environmental regulation, disease prevention, and process traceability shift from experience-based control to real-time data-driven control. Across mushroom production systems, IoT platforms have been used to monitor temperature, humidity, light intensity, and substrate moisture in real time through sensors connected to cloud-based mobile and web applications, with autonomous feedback control of the cultivation chamber (Irwanto et al., 2024). This is directly relevant to *G. lucidum* spore powder because mushroom growth is highly sensitive to environmental instability, and digital systems are designed precisely to stabilize those parameters that are otherwise difficult to maintain under traditional management (Irwanto et al., 2024). IoT architectures now also support remote visualization, automated actuation of humidifiers, heaters, lighting, and exhaust fans, and cloud dashboards for continuous decision-making, which reduces dependence on manual inspection and improves consistency between batches (Chong et al., 2023).

Evidence from broader mushroom systems suggests that these digital tools can deliver practical production gains, not only monitoring convenience. A low-cost centralized IoT ecosystem increased controlled-room yield by about 49% over ordinary cultivation while also integrating disease detection, agronomist advisory support, and e-commerce functions (Guragain et al., 2024). Another IoT cultivation study found about 28% higher production and better yield consistency than conventional methods, while TinyML-based monitoring enabled on-device processing of temperature, humidity, CO2, light, soil moisture, pH, and soil temperature with low latency and improved environmental stability (Rukhiran et al., 2023; Adebayo et al., 2025). For *G. lucidum* production specifically, digital management can be extended beyond greenhouse control to process simulation and bioprocess optimization, since industrial-scale modeling showed that reactor scale strongly changes cost, reducing modeled production cost from 6.82 USD/g at 2 m^3 to 0.8 USD/g at 20 m^3, and specialized bioreactor design improved fungal biomass and exopolysaccharide production under optimized pH, glucose, agitation, and aeration conditions (Araque et al., 2020; Supramani et al., 2023).

5.3 Industrial chain extension and product development directions

The industrial application of *G. lucidum* spore powder is moving beyond raw health supplements toward multi-level product development in foods, nutraceuticals, pharmaceuticals, and functional ingredients. Spore powder has already become a new resource for health products and pharmaceuticals, and the broader *G. lucidum* industry is expanding internationally as demand grows for dietary supplements, herbal products, and functional foods (Tang et al., 2023). This industrial extension is scientifically plausible because the spores contain genetic material and active components similar to the fruiting body, and wall-breaking and extraction technologies have substantially expanded their research and application value (Xu and Li, 2019; Chen et al., 2025). Product development should therefore target both direct-use spore powder and processed functional fractions, because bioactive triterpenoids from spore powder can be efficiently extracted by optimized dual-mode sonication and show antioxidant, antibacterial, and potential anticancer activity, while proteoglycans prepared from cracked or uncracked spore powder have shown antioxidant, hypoglycemic, antibacterial, and antitumor functions (Zhu et al., 2019).

Industrial-chain extension should also emphasize high-value by-product utilization and diversified consumer products. Spore powder after oil extraction still retains substantial bioactive substances and improved intestinal barrier dysfunction in mice by enriching beneficial microbiota and increasing tight-junction protein expression, indicating that oil-extracted residues are not waste but candidate secondary raw materials for gut-health products (Zhong et al., 2025). In the food sector, broken spore powder functioned as a feasible raw material for Chinese steamed bread, and 0.5%~1% addition gave the most suitable balance of quality and sensory performance, showing a concrete route for mainstream food incorporation (Chen et al., 2025). At the same time, related

Ganoderma powder processing technologies already demonstrate routes for fine powder manufacture, puffing, ultramicro-grinding, and digestibility improvement, which support development of standardized food-grade powders and compounded products. Overall, the industrial future of *G. lucidum* spore powder lies in linking standardized upstream production with digital management and downstream value-added product matrices, so that raw spores, extracted actives, oil-extracted residues, and food-formulation ingredients can all be incorporated into an integrated modern industrial chain (Araque et al., 2020).

6 Current Challenges and Future Development Directions

6.1 Further improvement of breeding technologies for high-yield and high-quality strains

A central challenge in *Ganoderma lucidum* spore powder production is that breeding for high spore yield, stable quality, and microbial resistance still lags behind breeding for fruiting bodies. Current industrial reliance on a very limited spore-oriented germplasm base remains a bottleneck, because "Longzhi No.1" has been widely used for spore production but shows weak resistance to competing microorganisms, and stable yield and batch quality remain difficult to control (Tang et al., 2023). Recent mutation breeding shows clear promise but also underscores that improvement is still incremental rather than complete: UV mutagenesis produced strain UV119 with 19.27% higher basidiospore yield than its parent and 20.56% higher yield than "Longzhi No.1," while atmospheric room-temperature plasma mutation identified strains with faster growth, 17.85~26.33% greater biomass, 15.72~32.10% higher triterpenoid production, and stability across five generations (Feng et al., 2024). Even outside established production regions, cultivation studies found large strain-to-strain differences in time to maturity and biological efficiency, but also very low overall productivity where substrates and cultivation conditions were poorly optimized, indicating that breeding gains cannot be separated from production context (Poyeri and Ohimain, 2024).

Future breeding should therefore move from empirical screening toward integrated molecular and physiological breeding systems. Synthetic biology reviews identify robust regulatory networks and low homologous recombination frequency as major obstacles to precise gene targeting in *G. lucidum*, but they also argue that modern molecular tools can accelerate pathway engineering and marker development (Azi et al., 2024). This direction is already supported by breeding studies showing that mono-mono crossing can create hybrids with both elevated polysaccharides and triterpenes, such as hybrid H-23 with 16.63 mg/g polysaccharides, 10.50 mg/g triterpenes, and satisfactory biological efficiency, and that genetic engineering combined with mating can raise individual ganoderic acids 1.75- to 2.69-fold in new dikaryons (Liu et al., 2017; Zhou et al., 2024). At the same time, future programs should widen the breeding target beyond nuclear genotype alone, because mitochondrial background affected basidiospore yield and polysaccharide and triterpenoid content, and local population studies found meaningful phenotypic diversity even where phylogenetic divergence was limited, supporting region-specific germplasm mining and multi-trait selection (Ye et al., 2022; Cortina-Escribano, 2024).

6.2 Enhancement of precision regulation levels in the production process

A second major challenge is that production control is still not precise enough across spawn preparation, environmental regulation, contamination management, and scale-up. Reviews consistently note that successful cultivation depends on meticulous substrate selection, efficient spawn production, and precise management of cultivation parameters, yet contamination remains a major barrier and genetic variability further complicates uniform production (Karunarathna et al., 2025). This is especially important for spore powder because strict growth requirements and unstable batch performance continue to restrict industrial development (Tang et al., 2023). Liquid spawn work shows that apparently minor upstream variables, including plate broth volume, mycelium picking position, and carbon-nitrogen concentration, significantly affect biomass and metabolic activity, while fermentor-prepared liquid spawn had better activity than smaller-scale preparations (Guo et al., 2023). Likewise, semi-industrial submerged culture studies found that controlled pH 5.5 markedly improved exopolysaccharide production, underscoring how strongly product output depends on tightly managed process variables.

The future direction is to build sensor-based, automated, and model-assisted production systems that reduce reliance on manual regulation. Automated environmental control studies for *G. lucidum* cultivation show that temperature, humidity, light, and CO_2 require continuous monitoring, that manual regulation is inconsistent and error-prone, and that sensor-triggered fogger or sprinkler systems can maintain humidity above 80% in mushroom houses. More broadly, bioprocess studies highlight the scale-up challenge of maintaining consistency, contamination control, and productivity when moving from laboratory to industrial systems, and call attention to cost and sustainability constraints that must be addressed simultaneously (Lim et al., 2024). Precision regulation should therefore evolve toward integrated digital management of environmental sensing, spawn quality, contamination risk, nutrient supply, and scale-up modeling, so that production can be optimized not only for yield but also for reproducibility, economic viability, and low-carbon operation (Karunarathna et al., 2025).

6.3 Improvement of quality evaluation and standardization systems

A third challenge is that the current quality evaluation framework for *G. lucidum* spore powder is still fragmented across identity, composition, and safety control. Although the Chinese Pharmacopoeia already specifies identification, content determination, and microbial requirements for spore powder, with minimum limits for polysaccharides and triterpenes/sterols, and although GB/T and NY/T standards cover harvesting, processing, wall-breaking rate, ganoderic acid, and total triterpenoid determination, these standards do not fully resolve the large commercial variability seen in real products. Commercial surveys found marked variation in polysaccharides and triterpenes across 84 batches of *Ganoderma* products, with total polysaccharides ranging from 0.22% to 3.31% and total triterpenes from 0.21% to 10.56%, while targeted LC-MS/MS showed triterpene contents of only 0.01% to 0.98% (Liu et al., 2025). Earlier spore-powder studies also found source-dependent differences in ash and triterpene content, and HPLC fingerprinting showed substantial year-to-year variability in Ganoderma chemical profiles (Yeung et al., 2022). These findings show that future quality control cannot rely on one or two bulk indicators alone.

Future standardization should therefore integrate molecular authentication, multi-component quantification, structural characterization, and international harmonization. ITS2 barcoding identified 16 adulterants among 84 commercial Ganoderma samples, while U.S. supplement testing found that only 26.3% of products matched their labels, showing that identity auditing needs to become routine rather than exceptional (Wu et al., 2017). More comprehensive quality systems are already emerging: HPLC-DAD fingerprinting supports simultaneous evaluation of multiple ganoderma acids, saccharide mapping and HPSEC-MALLS-RID provide improved polysaccharide assessment, and single-step extraction with fine structural evaluation can cut preparation time to one-sixth and save 50% of raw material while improving analytical efficiency (Yeung et al., 2022; Zheng et al., 2024). At the standard-system level, ISO 21315:2018 established the first international standard for *G. lucidum* fruiting bodies and an ISO standard for spore powder is under development, so the next step is to link domestic pharmacopoeial methods with internationally harmonized standards that cover authenticity, active components, wall-breaking efficiency, safety limits, packaging, storage, and traceability (Liu et al., 2025).

7 Conclusions

Efficient production technologies are the material foundation for improving the market competitiveness of *Ganoderma lucidum* spore powder, because the industry still faces strict growth requirements, unstable batch yield, and limited availability of high-spore-yield, contamination-resistant cultivars. Breeding progress shows that process competitiveness can be improved at the source: UV-mutant strain UV119 increased basidiospore yield by 19.27% over its parent and 20.56% over "Longzhi No.1," while also improving resistance to undesired microorganisms. At the cultivation stage, integrated workflows that link strain selection, substrate preparation, sterilization, inoculation, fruiting management, and dedicated powder collection can produce high-yield, high-purity spores, with one wild-simulating process reporting>99.9% purity and another collection technology reporting>32% higher selling income with heavy metals controlled within national standards. Process competitiveness also depends on rational medium design and cleaner collection schemes, including filter-cloth wrapping and substrate systems intended to reduce resource waste, pesticide residues, heavy metals, and low active-component accumulation. Taken together, the evidence indicates that elite strains+optimized cultivation+controlled collection and processing are the core technical basis for raising yield, lowering risk, and strengthening the industrial competitiveness of *G. lucidum* spore powder.

Quality control systems are the key guarantee for product value because *G. lucidum* spore powder shows large variability in composition, authenticity, and source-dependent quality, and these differences directly affect identity, efficacy, and safety evaluation. Existing regulatory frameworks already define important anchors, including Chinese Pharmacopoeia requirements for identification, microbial limits, and minimum contents of 0.90% polysaccharides and 0.50% triterpenes/sterols, as well as USP indicators for appearance, heavy metals, and active ingredients. However, single-index control is not sufficient: HPLC-DAD fingerprinting identified 11 ganoderma acids as useful chemical markers, multidimensional fingerprinting distinguished samples from different sources, and HPLC fingerprints combined with chemometrics successfully grouped *Ganoderma* by cultivated origin. Authenticity monitoring is equally essential, because commercial spore powder is often adulterated with dyed starch, NIR-chemometric models can quantify that adulteration with calibration and validation correlations>0.99, and combined HS-GC-IMS plus DNA mini-barcode approaches detected that some marketed products may contain non-*G. lucidum* species. Therefore, future quality control should integrate appearance and physicochemical indices, multi-component fingerprinting, authenticity testing, and contaminant limits into one coordinated value-guarantee system.

Standardization and digitalization are now the main drivers of industrial upgrading in *G. lucidum* spore powder production, because they convert dispersed empirical experience into traceable, controllable, and continuously optimized process systems. On the standardization side, China has already formed a relatively complete framework spanning the Pharmacopoeia, GB/T 29344-2023, food-safety standards, wall-breaking-rate testing, ganoderic-acid determination, and total triterpenoid determination, while ISO standardization for *Ganoderma* has also advanced internationally . On the digital side, industrial data-mining strategies for sporoderm-removal spore powder have already been used to identify process-parameter intervals that keep critical quality attributes such as moisture, fineness, crude polysaccharides, and total triterpenes at Ppk ≥1.33, showing that data-driven optimization has direct manufacturing value. More broadly, IoT, fuzzy logic, cloud dashboards, and TinyML systems in mushroom cultivation enable real-time sensing, autonomous control, remote visualization, disease support, and local low-latency decision-making, and related cultivation studies reported ~49% and ~28% yield gains under digital control as well as improved quality consistency and reduced labor dependence. Digital analytics are also extending into downstream process monitoring, as UV-Vis combined with CNN predicted nine ganoderic acids during extraction with $R^2 > 0.88$, indicating that digital tools can support not only cultivation management but also processing and release control.

Conflict of Interest Disclosure

The author affirms 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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Development of Local Characteristic Resources of *Tetrastigma hemsleyanum* and Optimization of Under-Forest Industry Development Pathways

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Abstract *Tetrastigma hemsleyanum* is an important characteristic medicinal plant resource in southern China, with traditional medicinal, edible, and modern functional product development value. With the continuous decline of wild resources and increasing market demand, artificial cultivation and ecological under-forest cultivation have gradually become important approaches for resource conservation and industrial development of *T. hemsleyanum*. Focusing on the development of local characteristic resources and the under-forest industry of *T. hemsleyanum*, this study systematically analyzes the distribution of germplasm resources, characteristics of local types, and differences in quality and ecological conditions among producing areas, and further elucidates the ecological basis of under-forest production in terms of light and temperature, moisture and soil conditions, and forest stand types. On this basis, under-forest wild-simulated cultivation and forest-medicinal plant integrated management models are compared, and the comprehensive utilization of tuberous roots, stems, leaves, and other resources, deep processing of characteristic products, and local brand development are further discussed. The results indicate that the current *T. hemsleyanum* industry still faces several major constraints, including insufficient conservation of wild and elite germplasm resources, limited supply of high-quality seedlings, low levels of standardization and large-scale under-forest cultivation, and insufficient product development, quality control, and industrial chain extension. Future development should strengthen local germplasm conservation and elite germplasm utilization, establish standardized under-forest cultivation technologies adapted to regional ecological conditions, promote whole-plant resource utilization, deep processing, quality traceability, and regional brand development, and ultimately establish an integrated industrial system linking “germplasm conservation-ecological cultivation-processing and value addition-brand development.” This study provides a reference for the sustainable utilization of *T. hemsleyanum* resources and the development of local characteristic under-forest industries.
Keywords *Tetrastigma hemsleyanum*; Local characteristic resources; Under-forest cultivation; Germplasm resources; Industrial development

1 Introduction

Tetrastigma hemsleyanum Diels et Gilg, commonly known as Sanyeqing, is a rare perennial vine and an important traditional Chinese medicinal plant widely distributed in subtropical regions of southern China, especially along the Yangtze River basin and in provinces such as Zhejiang, Fujian, and Guangxi. It has a long history of medicinal use, with records tracing back to ancient materia medica, where it was used for clearing heat, detoxification, promoting blood circulation, and treating high fever, pneumonia, hepatitis, snake bite, jaundice, and infantile febrile convulsions (Xia et al., 2023). Modern phytochemical and pharmacological studies further show that *T. hemsleyanum* contains abundant flavonoids, phenolic acids, polysaccharides, organic acids, terpenoids, steroids, and other constituents, with roughly 142~150 compounds reported to date (Hu et al., 2021).

These compounds support a broad spectrum of biological activities, including anti-tumor, anti-inflammatory, antioxidant, antipyretic, antiviral, immunomodulatory, hepatoprotective, analgesic, and antibacterial effects, which explains the strong and growing scientific and market interest in this species. Experimental studies have identified anti-cancer and anti-inflammatory effects in liver cancer cell models, inflammatory cell models, tumor-bearing mice, and ulcerative colitis models, while also linking activity to compounds such as chlorogenic acid, rutin, quercetin, kaempferol derivatives, alkaloids, and polysaccharides (Wang et al., 2018; Feng et al., 2024).

Polysaccharide fractions, in particular, have shown antitumor, anti-inflammatory, immune-regulatory, antioxidant, thermoregulatory, and metabolic-regulatory potential, with possible applications extending beyond medicine to food and cosmetic industries (Zhou et al., 2022).

Despite its high medicinal and economic value, the resource base of *T. hemsleyanum* faces significant pressure. Multiple reviews note that wild populations have been overexploited because of increasing demand, narrow habitat requirements, and the long-standing preference for wild medicinal materials, leaving this species on the verge of extinction in some areas and even placing it among preferentially protected crop germplasm resources in Zhejiang Province (Ji et al., 2021; Hu et al., 2021). More broadly, medicinal plant research in China shows that wild herbal resources are increasingly unable to meet market demand, making artificial cultivation the most feasible and inevitable route for conservation and stable supply (Rao et al., 2004). At the same time, the quality and clinical efficacy of Chinese medicinal materials depend directly on cultivation processes, and ecological planting, under-forest economy, intercropping, and industrialized production have become major research hotspots in recent years (Miao et al., 2024). For *T. hemsleyanum* specifically, current bottlenecks remain clear: its active material basis is not fully resolved, quality control standards are still imperfect, backward processing and storage problems persist, and physiological cultivation studies have focused mainly on light and fertilizer, leaving many production mechanisms insufficiently understood. These constraints limit industrial scaling, product standardization, premium branding, and the conversion of local germplasm advantages into a stable characteristic industry (Xia et al., 2023).

Against this background, developing local characteristic resources of *T. hemsleyanum* has clear practical significance at the ecological, economic, and regional development levels. Understory cultivation of medicinal plants makes fuller use of land, light, and heat resources, is based on forest-medicine symbiosis, and contributes to sustainable utilization of forest resources, plant diversity conservation, and ecological improvement (Li et al., 2025). Agroforestry more generally is well suited to shade-tolerant medicinal plants, offering a practical strategy for simultaneous cultivation and conservation while also creating remunerative alternative crops for smallholders (Rao et al., 2004). Chinese ecological agriculture research likewise argues that underwood planting and imitation-wild habitat cultivation are important pathways to achieve high-quality, efficient, and sustainable medicinal material production while increasing mountain-area incomes and reducing pressure on wild resources (Wang et al., 2020). Experimental evidence from forest-medicinal plant systems further suggests that understory planting can improve soil nutritional status, enrich rhizosphere microbial communities, and enhance soil carbon utilization, indicating that the forest-medicine compound model can generate both ecological and economic benefits (Yu et al., 2023). However, understory industries also face real constraints, including mismatches between canopy density and crop light demand, unstable input-output relationships, weak technical systems, insufficient regulation, and high trial-and-error costs, so optimization must be grounded in species traits, local forest conditions, and market demand (Wen et al., 2025).

This study will explore the development of local characteristic resources of *Tetrastigma hemsleyanum* and the optimization of its under-forest industrial development pathways by comprehensively analyzing its medicinal resource endowment, local ecological conditions, and current industrial development needs. Particular attention will be given to the intrinsic relationships among resource conservation, ecological cultivation, standardized production, and industrial utilization of *T. hemsleyanum* within the framework of the under-forest economy. On this basis, the study will systematically summarize the characteristics and development foundations of local germplasm resources, analyze the effects of different ecological conditions and under-forest production models on resource utilization and industrial development, identify the key constraints limiting the transformation of local resource advantages and the large-scale development of the under-forest industry, and propose corresponding optimization pathways in terms of elite germplasm utilization, selection of ecologically suitable forest sites, standardization of cultivation technologies, quality evaluation, deep processing of products, and brand development. By establishing a development framework of “resource conservation-ecological cultivation-processing and value addition-industrial integration,” this study aims to provide a reference for the conservation of elite *T. hemsleyanum* germplasm resources, rational utilization of forest-land resources, and ecological under-forest production. It also seeks to improve product quality consistency and market competitiveness, promote the transformation of local medicinal plant resource advantages into industrial advantages, and provide theoretical and practical support for the coordinated development of regional specialty agriculture, the under-forest economy, and the health industry.

2 Characteristics and Development Basis of Local *Tetrastigma hemsleyanum* Resources

2.1 Distribution of germplasm resources and characteristics of local types

Tetrastigma hemsleyanum is a perennial medicinal vine endemic to subtropical China and is distributed mainly in regions south of the Yangtze River, including Zhejiang, Fujian, Jiangxi, Hunan, Guangxi, Guizhou, Yunnan, Guangdong, Chongqing, and Taiwan, with Guangxi and Zhejiang recognized as areas with relatively abundant diversity (Chen et al., 2022; Han et al., 2026). Field and survey studies further show that this species typically occurs in valleys, shrubs, forests, gullies, slopes, moist grasslands, rock crevices, and valley streams, usually under scattered light and at elevations of about 300-1300 m, indicating a distinct dependence on shaded, humid, and relatively specific mountain habitats. In Guangxi, wild populations are concentrated mainly in the north and west, and the associated plant communities include tree, shrub, and herb layers with more than 50 accompanying species, which reflects the ecological complexity of the local germplasm habitat. Across its full range, the species spans broad longitudinal, latitudinal, and elevational gradients, which provides the environmental basis for the differentiation of local germplasm and adaptive types.

Local types of *T. hemsleyanum* show both shared species traits and geographically structured variation. Morphologically, the plant is a climbing liana with slender stems, trifoliate leaves, and spindle-, ovate-, or calabash-shaped tuberous roots, while root tubers from different regions generally retain similar external and microscopic diagnostic features, making simple morphology insufficient for origin discrimination (Dong et al., 2022). However, genetic studies consistently show clear differentiation among regional germplasms. ISSR analysis of 24 accessions detected definite genetic diversity and grouped samples into four clusters, with Zhejiang materials clustering independently and Guizhou germplasm forming a separate group. A larger ISSR-SRAP study of 27 accessions also found a clear clustering pattern corresponding to geographic distribution, higher similarity within populations than between populations, and higher similarity in cultivated than wild populations. Landscape genomics further resolved four major genetic groups corresponding broadly to Southwest, Central, South, and East China, confirming that local types are not only regional production concepts but genetically structured resource units shaped by long-term environmental differentiation.

2.2 Differences in resource quality and ecological conditions among different producing areas

The quality of *T. hemsleyanum* resources differs substantially among producing areas, and these differences are closely tied to both germplasm background and ecological conditions. Comparative genomic and pharmacognostic studies note that although root tubers from Zhejiang, Fujian, Jiangxi, Guangxi, and Sichuan are similar in external shape and microstructure, significant regional differences still exist in yield and medicinal quality, indicating that quality variation cannot be reliably judged by appearance alone. Evidence across several studies shows that samples from Zhejiang and Fujian had the highest total flavonoid contents and the strongest inhibitory activity against HepG2 cells, highlighting the importance of geographical origin in determining functional quality (Dong et al., 2022). Broader metabolomic work on 254 samples from eight areas identified 49 potential chemical markers and further linked origin to differences in metabolic profiles and antioxidant-related quality markers such as catechin and darendoside B (Chu et al., 2024). A multi-constituent comparison across southeastern and southwestern habitats likewise found significant differences in 60 bioactive compounds and concluded that southeastern samples were superior overall in quality evaluation (Chen et al., 2022).

Regional quality divergence is inseparable from ecological heterogeneity. *T. hemsleyanum* grows best under moist, shaded, acidic conditions, with suitable temperatures around 18~25 ℃, pH 5.0~7.0 soils, and mountain habitats that buffer excessive light and drought stress. Seasonal and climatic factors directly influence metabolite accumulation: under precipitation of 2.0~6.6 mm, temperature of 17.5~24.1 ℃, humidity of 67.3~80.2%, and sunshine duration of 3.4~5.8 h from April to May, total flavonoid content reached relatively high levels, and the flavonoid biosynthetic pathway showed clear environmental responsiveness (Shi et al., 2022). Genomic evidence indicates that climatic variation explains more genomic variation than geographical distance, with winter precipitation acting as the strongest predictor of contemporary genetic structure, which supports the view that producing-area differences reflect local climate adaptation rather than simple geographic separation. Even under cultivation, habitat conditions remain decisive: dryland systems can show 30~35% lower flavonoid concentrations than forest understory systems, while biochar-mediated improvement of soil enzymes and fungal communities can partly bridge this quality gap, demonstrating that local soil microecology is a major component of resource quality formation (Zhang et al., 2026).

2.3 Conservation of local characteristic resources and utilization of elite germplasm

The conservation of local characteristic *T. hemsleyanum* resources has become urgent because wild populations have been sharply reduced by overharvesting, slow natural growth, and strict habitat requirements. Reviews and field investigations note that the species usually needs 3~5 years to reach commercial medicinal standards, while excessive collection and ecological change have caused rapid contraction of wild distribution areas and serious depletion of natural reserves (Ji et al., 2021). In Guangxi, surveyed reserves were only about 24 441.20 kg, and the study explicitly recommended active protection measures to ensure sustainable utilization. Genetic evidence suggests that conservation should focus not only on preserving populations in situ, but also on promoting gene exchange among populations, because cultivated materials show higher within-group similarity and natural populations contain richer diversity needed for long-term utilization. Climate-change risk adds another layer of urgency, as landscape genomic modelling identified high genomic vulnerability in central-northern parts of the species range and supported proactive management for populations facing future genotype-environment mismatch.

The utilization of elite germplasm should therefore combine origin identification, resistant parent selection, ex situ preservation, and directed breeding. Molecular traceability tools based on chloroplast genomes, mutational hotspots, and trnL-trnN barcodes can distinguish major geographic groups and support the authentication of local characteristic materials, while isotope-element models with machine learning achieved 100% prediction accuracy for origin traceability in tested samples (Bai et al., 2025). For breeding, the Zhejiang ZJWZ strain showed the best overall stress resistance among five provincial strains and was identified as preferred parental material for resistance improvement. Ex situ conservation technologies are also increasingly feasible: slow-growth culture at 8 ℃ with 0.2 mg/L MH prolonged subculture to at least 10 months while maintaining genetic stability and stable flavonoid content, and callus studies indicate that subculture frequency should be controlled within four cycles for clonal fidelity or extended to 6-8 cycles when somatic variation is intentionally used for germplasm improvement. At the utilization end, differentiated use of roots, stems, and leaves and optimization of cultivation mode can raise the value of elite germplasm, since leaves contain significantly higher flavonoid and phenolic acid levels than roots and stems, and greenhouse plus stereoscopic planting improved both yield and quality, providing practical pathways for converting superior local resources into stable industrial advantages (Hu et al., 2023).

3 Ecological Basis for the Development of the Under-Forest *Tetrastigma hemsleyanum* Industry

3.1 Effects of under-forest light and temperature conditions on growth adaptability

Tetrastigma hemsleyanum is a shade-adapted species whose natural habitat is typically under forest cover, valley shade, rock crevices, moist grasslands, and mountain gullies, indicating that weak light and buffered thermal conditions are part of its basic ecological niche (Shi et al., 2022). Controlled shade experiments consistently show that excessive irradiance suppresses its photosynthetic performance and growth, while moderate canopy filtering improves leaf development and carbon assimilation. In one classic experiment, plants achieved the greatest leaf size and highest net photosynthetic rate under 67% shade, and light levels stronger than 50% shade depressed photosynthetic activity, whereas overly deep shade also reduced growth (Dai et al., 2009). A later gradient study reached a closely matching conclusion, finding that most photosynthetic indices peaked under 70% shading, with rapid-growth-stage values markedly higher than those in the slow-growth stage (Xu et al., 2018).

Physiologically, increasing shade raises chlorophyll a, chlorophyll b, and total chlorophyll content, while reducing the chlorophyll a/b ratio, which reflects adjustment to low-light capture under the canopy (Xu et al., 2018). Full sunlight and only light shading reduce electron transport and photochemical quenching while increasing non-photochemical quenching, showing that strong light imposes photoprotective stress rather than promoting efficient photosynthesis (Dai et al., 2009). Temperature interacts with shade rather than acting independently, because strong light, high temperature, and low humidity together reduce photosynthetic activity and slow growth, while seasonal evidence suggests a favorable temperature range around 17.5~24.1 ℃ for higher flavonoid accumulation and around 18 ℃ in natural habitats (Shi et al., 2022). More broadly, understorey ecology shows that shade modifies not only irradiance but also humidity, nocturnal temperature, and plant stress tolerance, so canopy conditions should be managed as a combined microclimatic system rather than as light reduction alone.

3.2 Effects of under-forest moisture and soil conditions on plant growth

Water availability and soil environment are major determinants of *T. hemsleyanum* growth because the species is best suited to moist hillsides or valleys and is recognized as drought-sensitive across its native range. Landscape-genomic analysis indicates that climatic variation explains more genomic variation than geographic distance, and precipitation-related variables are among the strongest predictors of population structure, which supports the ecological importance of moisture conditions for local adaptation. Seasonal metabolite studies further show that higher flavonoid levels occurred under moderate precipitation, 67.3~80.2% humidity, and 17.5~24.1 ℃ from April to May, while sterol accumulation was inhibited by excessively high humidity and temperature extremes. The same work found that phenolic accumulation was negatively correlated with precipitation and humidity but could be enhanced within controlled soil-moisture ranges, indicating that water supply must be sufficient but not excessive if both growth and quality are goals (Shi et al., 2022).

Soil effects extend beyond fertility to rhizosphere processes and microbial regulation of secondary metabolism. Wild Zhejiang material had higher total flavonoids and PAL activity than cultivated material, and its rhizosphere soil contained higher available phosphorus and potassium together with distinct microbial taxa and metabolic pathways linked to nitrogen, phosphorus, and phenylalanine metabolism. Stony soils supported larger tubers, greater bacterial diversity, and bacterial groups associated with phytohormone biosynthesis, photosynthesis, and stress resistance, showing that physical soil structure and microbiota jointly shape tuber development (Hong et al., 2021). Fertilization studies also show that biochar or pyrogenic organic matter improves plant height, fresh root weight, and total flavonoids by increasing soil pH, organic matter, available nutrients, and enzyme activities, and in bamboo-forest or forest-soil systems these effects appear partly mediated by reshaped fungal and bacterial communities (Zhang et al., 2020; Zhang et al., 2026).

3.3 Adaptability of *Tetrastigma hemsleyanum* to different forest stand types

Tetrastigma hemsleyanum shows real adaptability to multiple under-forest settings, but that adaptability is conditional on stand structure and microhabitat matching. Field surveys in Guangxi found it suitable in valleys, shrubs, and higher-altitude forests, where communities include tree, shrub, and herb layers with more than 50 accompanying species. The species occurs across warm-temperate evergreen forest regions spanning large climatic and elevational gradients, and populations from different regions show substantial morpho-agronomic, phytochemical, and genetic variation shaped by local climate adaptation. This means stand selection for industrial development should follow local provenance and ecological matching rather than assume uniform performance across forest types. Reviews of understorey medicinal-plant systems reach the same practical conclusion: under-forest cultivation can efficiently use land, light, and heat resources, but success depends on understanding the growth environment and forest-medicine symbiosis (Li et al., 2025).

Evidence from specific stand types suggests that some forest systems are especially promising. Under a Moso bamboo forest with about 80% canopy density, biochar-based organic fertilizer increased *T. hemsleyanum* biomass while improving soil pH, organic carbon, and microbial community structure, supporting bamboo-forest intercropping as a feasible under-forest pathway (Zhang et al., 2020). Simulated-wild cultivation under tree canopies in hilly mountain regions exposes plants to cooler, more heavily shaded, rain-fed conditions than greenhouse systems, and these environmental differences produce detectable physiological and isotopic distinctions between cultivation modes (Wang et al., 2026). At the same time, stand type involves tradeoffs: greenhouse plus stereoscopic planting improved both yield and quality relative to understory planting in one cultivation comparison, so under-forest systems are ecologically suitable but not automatically superior for all production targets (Hu et al., 2023). The under-forest industry basis of *T. hemsleyanum* lies in its moderate-shade preference, moisture dependence, and sensitivity to soil microecology, while the optimal stand should be chosen by balancing ecological suitability, target quality traits, and local management capacity.

4 Under-Forest Cultivation and Production Models of *Tetrastigma hemsleyanum*

4.1 Under-forest wild-simulated cultivation model

The under-forest wild-simulated cultivation model of *Tetrastigma hemsleyanum* is essentially an agroforestry production pathway that places the species under forest canopies or near-natural shaded habitats to reproduce the microenvironment of wild populations, especially moderated light, cooler temperature, higher humidity, and biologically active forest soils (Li et al., 2025). This model has become attractive because simulated-wild and wild-labeled *T. hemsleyanum* products command higher market prices than greenhouse-grown material, and existing evidence indicates that agroforestry-grown products are generally regarded as higher quality than conventionally cultivated counterparts (Wang et al., 2026). Its practical logic also matches the broader medicinal-plant literature, which shows that forest farming is a promising alternative to continued wild harvesting when natural populations are under pressure (Naud et al., 2010; Pang et al., 2024). For *T. hemsleyanum* specifically, the model is ecologically plausible because the species naturally grows under the shade of mountainous cliffs, requires 3-5 years to form tubers in natural environments, and is increasingly dependent on artificial cultivation because of overexploitation and harsh habitat constraints (Shi et al., 2022).

Current evidence supports the quality advantage of this model, but also shows that the advantage is not produced by shade alone. Forest understory cultivation of *T. hemsleyanum* typically produces flavonoid concentrations 30~35% higher than dryland greenhouse systems, and the likely reason is the combined effect of acidic forest soils, higher organic matter, and distinct microbial communities that conventional dryland soils do not provide (Zhang et al., 2026). Stable-isotope work also shows that simulated-wild and greenhouse products can be distinguished scientifically, with greenhouse tissues having more positive δ13C and δ15N values, which supports the idea that cultivation pathway leaves measurable ecological and metabolic signatures (Wang et al., 2026). At the same time, the wild-simulated model is not identical to undisturbed wild growth, because commercial systems often use in situ pots to avoid competition from dominant native species and to facilitate tuber harvest, so the model should be understood as a controlled approximation of wild habitat rather than a perfect replica. In production practice, its success therefore depends on matching the natural habitat as closely as possible while retaining operational control over planting density, harvest, and soil regulation (Wen et al., 2025; Zhang et al., 2025).

4.2 Forest-medicinal plant integrated management model

The forest-medicinal plant integrated management model goes beyond simple under-canopy planting and treats the forest and the medicinal crop as a coupled production system in which canopy structure, soil processes, microbial communities, and economic outputs are managed together (Yu et al., 2023). This model is widely recommended because understory medicinal-plant cultivation can make fuller use of land, light, and heat resources while promoting the protection and sustainable use of forest resources and biodiversity (Li et al., 2025). The agronomic premise is that stand structure and interspecific interactions are manageable variables rather than background conditions: tree species, stand density, canopy openness, crop position, and intercropping combinations all influence understory light, humidity, soil traits, and ultimately yield and active-compound formation (Zubay et al., 2021; Wen et al., 2025). In this sense, the model is especially relevant for *T.*

hemsleyanum, whose quality formation is sensitive to microecology, fungal composition, soil enzymes, and habitat-specific soil chemistry (Zhang et al., 2026).

Evidence from other medicinal-plant systems shows why this integrated approach matters. In a South China forest-medicine compound system, understory planting improved soil nutrient status, increased rhizosphere microbial communities, and enhanced microbial carbon-source utilization, indicating that compound management can generate both ecological and production benefits (Yu et al., 2023). Agroforestry trials in medicinal plants also show that management details shift outcomes: lower cocoa-tree density increased biomass and essential-oil yield for some species, whereas higher cocoa-tree density favored flavonoid accumulation in another species, showing that stand design must be linked to the target product trait rather than assumed uniform (Barazetti et al., 2022). Parallel understory studies found that inter-row positions can outperform under-canopy positions, with *Epimedium pubescens* yield increasing by 90~107% relative to under-canopy locations across three plantation types, and economic assessment identified a 75% shading treatment as optimal in one system (Zhang et al., 2025). For *T. hemsleyanum*, this implies that integrated management should include deliberate canopy regulation, stand selection, and soil amendment rather than simply planting beneath any available forest cover (Jaroszewicz et al., 2024).

4.3 Comprehensive comparison of different under-forest production models

Taken together, the main under-forest production options for *T. hemsleyanum* can be divided into a wild-simulated model, a more interventionist forest-medicinal integrated management model, and loosely managed or extensive under-canopy planting systems. Their strengths differ. Wild-simulated cultivation is closest to the species' native ecological niche and best aligned with market preferences for high-quality, near-natural products (Figure 1) (Shi et al., 2022; Wang et al., 2026). Integrated management is stronger for scaling, because it explicitly optimizes stand composition, light environment, fertilization, and forest-floor use efficiency (Barazetti et al., 2022). Extensive under-canopy planting has lower technical thresholds and can still be economically viable, but evidence from silvi-medicinal systems shows that open conditions often produce higher yields and returns than below-canopy conditions even when understory systems remain profitable, so low-input forest planting is not automatically the highest-performing option (Sanwal et al., 2016). Comparative work in other medicinal plants also shows that different planting environments can produce large differences in both quality and yield, and some forest types are clearly more suitable than others (Lan et al., 2023).

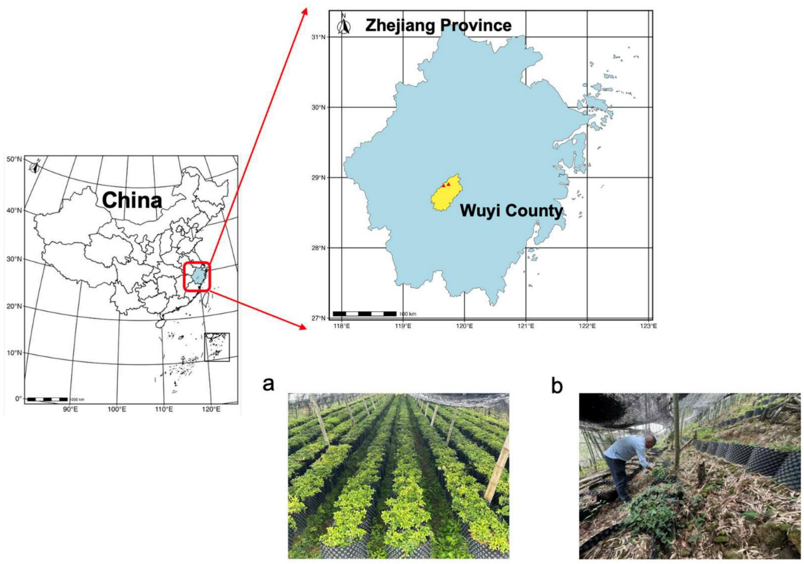

Figure 1 Location and set-up of the two cultivation sites for *Tetrastigma hemsleyanum* in Wuyi County, Zhejiang Province, East China (Adopted from Wang et al., 2026)

Image caption: (a) Greenhouse cultivation method; (b) simulated-wild cultivation method (Adopted from Wang et al., 2026)

The core tradeoff across models is between ecological authenticity, managerial controllability, and production stability. Under-forest systems can enhance active-compound accumulation, as seen in ginseng and *T. hemsleyanum*, but medicinal-plant studies repeatedly show that higher biomass and higher chemical quality do not always peak under the same conditions (Naud et al., 2010; Lan et al., 2023). The best model therefore depends on the development objective: if the goal is premium medicinal quality and ecological branding, wild-simulated cultivation under suitable forest stands is more advantageous; if the goal is standardized, scalable, and technically optimized supply, the forest-medicinal integrated management model is more appropriate (Duc et al., 2025; Le et al., 2026). For local industry development of *T. hemsleyanum*, the most practical pathway is likely a graded model in which core production areas adopt wild-simulated cultivation under high-quality forest habitats, while broader supply areas use integrated management with provenance-matched seedlings, canopy regulation, and soil-microecological improvement (Pang et al., 2024; Le et al., 2026; Zhang et al., 2026). In this sense, optimizing under-forest production models for *T. hemsleyanum* is not a choice of one fixed template, but a process of matching habitat quality, management intensity, and product positioning to local resource conditions.

5 Diversified Development and Utilization of Local Characteristic *Tetrastigma hemsleyanum* Resources

5.1 Comprehensive development of medicinal and aboveground resources

The diversified utilization of local *Tetrastigma hemsleyanum* should begin with a shift from root-centered use to whole-plant development, because current evidence shows that not only the tuberous roots but also the stems, leaves, whole grass, and aboveground fractions contain valuable bioactive constituents and practical medicinal functions (Li et al., 2023). Root tubers remain the traditional core medicinal part and are widely used in clinics and functional food products for fever, pneumonia, hepatitis, asthma, convulsions, and related inflammatory conditions (Sun et al., 2021; Shu et al., 2023). However, the aboveground parts already have recognized use value: leaves are consumed as functional tea or dietary supplements, and aerial portions have been developed as potential new traditional Chinese medicine preparations (Luo et al., 2022; Bai et al., 2022). This broader utilization route is especially important because the species grows slowly, usually requiring 3~5 years to meet medicinal standards, and overdependence on roots increases harvesting pressure on an already scarce resource (Figure 2) (Ji et al., 2021).

Figure 2 The aerial part (A), root tuber (B) and raw herb (C) of *T. hemsleyanum* (Adopted from Ji et al., 2021)

The evidence also shows that aboveground resources are not inferior by default and may be superior for some target products. Quantitative comparisons found that leaves contain significantly higher levels of flavonoids and phenolic acids than roots and stems, while metabolomic imaging detected higher abundance of most organic acids and flavonoids in leaves than in underground parts (Luo et al., 2022). Leaves also contain unique compounds, with 24 components detected only in leaves, compared with 3 unique to tuberous roots and 7 unique to fibrous roots, and both leaves and fibrous roots have been proposed as new medicinal parts for future development.

Functional evidence supports this direction: leaf phenolics were metabolized into bioavailable forms during digestion and fermentation, and leaf supplementation ameliorated DSS-induced colitis by improving tight-junction proteins, suppressing pro-inflammatory cytokines, activating Nrf2-related antioxidant defenses, and reshaping gut microbiota and short-chain fatty acids (Wu et al., 2021). Aboveground polysaccharides are also promising, since a novel pectic polysaccharide extracted from the aboveground part showed macrophage immune-enhancing activity and may contain a core active domain suitable for immune-regulatory product development (Tian et al., 2025).

5.2 Development of characteristic products and deep processing

The next step is to convert local raw materials into characteristic products through standardized extraction, processing, and value-added development. *T. hemsleyanum* already has both medicinal value and potential for food-related development, and its roots are widely used as functional tea, dietary supplements, and health-related food materials (Sun et al., 2021; Shu et al., 2023). Its chemical basis for product development is broad, with about 142~150 identified compounds, especially flavonoids and polysaccharides, and these components show antioxidant, anti-inflammatory, anti-tumor, immunoregulatory, antipyretic, and hepatoprotective activities (Hu et al., 2021; Ding et al., 2025). This supports development not only of traditional decoction pieces and health teas, but also of antioxidant extracts, immune-enhancing polysaccharide products, liver-protective preparations, and food, medicine, and cosmetic derivatives (Tian et al., 2025; Xu et al., 2026). At the same time, reviews note that backward processing methods, storage difficulties, and limited quality standards still constrain industrial upgrading, so deep processing must be coupled with stronger process control.

Several studies show that processing and extraction conditions materially change product quality, which makes post-harvest standardization central to deep processing. Extraction optimization increased the total yield of five key flavonoids to 788.12 mg/kg under optimized ethanol-ultrasound conditions, and the resulting extract showed strong DPPH scavenging activity (Shu et al., 2023). Extraction method matters more broadly: ethanol extracts showed better antioxidant and antiproliferative activity than water extracts, while bioactivity of water extracts declined as extraction temperature increased. Processing method also changes efficacy. Different drying methods caused large shifts in ten major constituents, especially rutin, proanthocyanidin B1, and catechin, and among three processed products, the freeze-dried extract preserved bioactive constituents best and showed the strongest hepatoprotective effect (Xu et al., 2026). For polysaccharide products, both extraction technology and structure-function analysis are advancing quickly: multiple extraction and purification methods have been developed, and a glucan isolated after optimized ultrasound-assisted extraction showed significant antipyretic activity through suppression of TNF-α, IL-1β, cAMP, and PGE2 (Ding et al., 2025). Biotechnological deep processing is another reserve pathway, because hairy roots can be induced at high efficiency and in some cases contain higher levels of several flavonoids and stronger antioxidant activity than 3-year true roots, suggesting a feasible alternative source of raw material for high-value extracts.

5.3 Local brand building and development of regional characteristic industries

Local brand building should rely on the joint logic of origin, quality, and regional identity. *T. hemsleyanum* is already embedded in Zhejiang’s regional medicinal identity: it is regarded as one of the new eight Genuine Medicinal Materials of Zhejiang and as the new “Zhebawei,” and it has been included in the medical insurance system of Zhejiang and other provinces (Bai et al., 2022). Product markets already distinguish by producing area, and root price varies with origin, which means local branding can build directly on demonstrated geographical quality differentiation (Chu et al., 2024). That differentiation is scientifically supportable: metabolomics across 254 samples from eight areas identified 49 potential chemical markers, including catechin and darendoside B as antioxidant-related quality markers, while origin studies across southern sites showed differences in quercetin and kaempferol and provided technical support for quality evaluation from different origins (Li et al., 2023). A strong local brand therefore needs provenance-linked quality standards, origin authentication, and differentiated product positioning rather than generic bulk sales.

Regional characteristic industry development also depends on organization and governance, not just on resource endowment. Research on medicinal-plant bioeconomies shows that geographical indication labeling can support value-added, but only when paired with cooperative organization, industrialization policy, phytopharmacovigilance capacity, and equitable collaboration with enterprises (Lindberg et al., 2023). For *T. hemsleyanum*, this implies a regional pathway that links under-forest cultivation bases, local processing enterprises, and county-level public brands around authenticated origin, standardized drying and extraction, and diversified products such as medicinal slices, health teas, antioxidant extracts, polysaccharide preparations, and functional-food derivatives (Sun et al., 2021; Guo et al., 2023; Chu et al., 2024). Because this species has high medicinal value but limited wild resources, local industry upgrading should emphasize resource-saving whole-plant use, high-value deep processing, and place-based brand premiums instead of simple expansion of raw root sales (Ji et al., 2021; Hu et al., 2021). In this way, diversified development of local characteristic *T. hemsleyanum* resources can support both conservation and the formation of a stable regional under-forest characteristic industry.

6 Major Problems in the Development of the Under-Forest *Tetrastigma hemsleyanum* Industry

6.1 Insufficient conservation of elite germplasm resources and limited supply of high-quality propagation materials

Wild resource depletion and incomplete elite germplasm conservation still restrict the long-term supply basis of the under-forest industry. Wild *T. hemsleyanum* resources are scarce because the species has strict habitat requirements and has been over-excavated for years (Hang et al., 2023). In Guangxi, field investigation found that wild reserves were only about 24 441.20 kg and that distribution areas were becoming increasingly limited under combined pressure from overcollection and ecological change. This pressure has already affected genetic diversity, with recent work noting that indiscriminate exploitation has severely reduced diversity and pushed the species toward potential extinction risk, while climate change and pollution further intensify survival pressure. Although the species has high medicinal value, its slow growth means it generally requires 3~5 years to reach medicinal standards, so losses of local germplasm cannot be quickly replaced through ordinary production cycles (Ji et al., 2021; Shi et al., 2022).

The second layer of this problem is that the supply of high-quality propagation materials remains limited, and breeding of elite, stress-resistant strains is still insufficiently developed. Seed yield is low, and conventional vegetative propagation by cuttings produces only limited numbers of plants, which directly constrains commercial expansion (Pang et al., 2024). Artificial cultivation has been established, but ensuring stable yield and quality still requires identification and expansion of resistant cultivated strains, while research on resilient-strain breeding remains limited. Recent stress-screening work identified the Zhejiang ZJWZ strain as promising parental material for resistance breeding, but this also shows that elite-strain selection is only beginning rather than already widely deployed. Tissue culture and conservation technologies provide solutions but have not yet fully translated into broad industrial supply: slow-growth storage can maintain genetically stable microplants for at least 10 months, and organogenesis protocols can achieve mass propagation with over 98% acclimatization survival, yet these are still technical pathways that need wider integration into breeding, nursery systems, and under-forest seedling supply chains (Pang et al., 2024).

6.2 Low levels of standardization and large-scale production in under-forest cultivation

The low level of standardization in under-forest cultivation weakens the reproducibility of both yield and quality.. Reviews note that current physiological research on *T. hemsleyanum* has focused mainly on light and fertilizer, while many other cultivation factors remain insufficiently studied. The species also faces a long cultivation cycle, low yield, and variable quality under artificial planting, and these are described as critical obstacles to industrial production (Hang et al., 2023). Current planting modes are described as chaotic and complicated, and comparative cultivation research was undertaken precisely because an optimal mode for jointly improving quality and yield had not been clearly established (Hu et al., 2023). This lack of standardization is especially problematic in under-forest systems, where habitat differences strongly affect quality formation: dryland cultivation can show 30~35% lower flavonoid concentrations than forest understory systems, and even corrective measures such as biochar have habitat-specific effects rather than universal ones (Zhang et al., 2026).

Large-scale production is further limited because suitable production parameters are not yet unified across provenance, habitat, and cultivation mode. Environmental studies show that metabolite accumulation changes markedly with temperature, humidity, precipitation, and season, indicating that large-scale cultivation cannot rely on a single fixed technical package across all producing areas (Shi et al., 2022). Under-forest planting under Moso bamboo can increase biomass when supported by biochar-based organic fertilizer, but this effect depends on changes in soil physicochemical properties and microbial communities, again showing that management standards must be ecologically specific. Even where more productive systems have been identified, they do not always align with the under-forest model: greenhouse cultivation combined with stereoscopic planting improved both yield and quality and outperformed understory planting in some comparisons, which suggests that under-forest cultivation still lacks a consistently validated standard model for industrial scaling (Hu et al., 2023). In practice, this means current under-forest development often remains fragmented, with uneven technical levels, weak nursery standardization, and limited capacity to build certified large-scale production bases despite policy interest in the under-forest economy (Zhang et al., 2020).

6.3 Insufficient product development, brand building, and industrial chain extension

Product development and deep processing still lag behind the resource base and pharmacological potential of *T. hemsleyanum*. Around 150 compounds have been isolated from the species, and the plant shows broad anti-inflammatory, anti-tumor, antioxidant, immunoregulatory, and related bioactivities, yet reviews explicitly argue that new clinical uses and more comprehensive utilization still need to be developed (Hu et al., 2021). The same reviews note backward processing methods, storage difficulties, and imperfect detection methods, all of which directly limit industrial upgrading (Ji et al., 2021). Mechanistic quality research also shows that the active material basis is still not fully clear and that the industry lacks a scientific, universal, and measurable quality-control system, making it difficult to support stable high-end products in market circulation (Xia et al., 2023). Although roots are already marketed as functional foods and their price varies by origin, this market differentiation is not yet equivalent to mature brand construction, because origin-linked metabolic profiles and bioactivity markers still need further clarification for credible product grading and certification (Chu et al., 2024).

Industrial chain extension is also insufficient because the species' aboveground resources, polysaccharides, and origin-authentication tools have not yet been fully converted into a coordinated local specialty industry. Leaves and fibrous roots contain many distinctive metabolites and have been proposed as potential new medicinal parts, but current commercialization remains far more root-centered than evidence would justify. Polysaccharides show broad potential in food, medicine, and cosmetics, and new aboveground pectic polysaccharides with immune-enhancing activity have already been characterized, but this remains an emerging development direction rather than a mature downstream sector (Tian et al., 2025). Brand building is further weakened by market-order problems: simulated-wild and greenhouse products differ measurably in isotopes, yet mislabeling of conventional products as higher-priced wild or simulated-wild material can occur for profit, showing that brand premiums are not secure without robust traceability systems (Wang et al., 2026). More broadly, even the genetic resource base is still incomplete, because the previous lack of mitochondrial-genome information was considered a limitation on breeding, conservation, and development, which underscores that industrial chain extension still depends on stronger upstream scientific infrastructure as well as downstream branding and processing (Han et al., 2026).

7 Optimization Pathways for Local Resource Development and Under-Forest Industrial Development of *Tetrastigma hemsleyanum*

7.1 Establishment of a system for local germplasm conservation and elite germplasm utilization

Establish an integrated system that combines in situ conservation, ex situ preservation, elite germplasm identification, and rapid propagation. *Tetrastigma hemsleyanum* remains under strong resource pressure because wild populations are scarce, growth is slow, and the species usually requires 3-5 years to reach commercial medicinal standards. This pressure is intensified by persistent market demand and overharvesting, and the species has already been listed among preferentially protected crop germplasm resources in Zhejiang Province (Hu et al., 2021). A local germplasm system should therefore begin with systematic surveys, provenance registration, and hierarchical conservation of wild and cultivated resources, especially materials from major producing regions and ecologically differentiated local populations (Bai et al., 2022). This is justified not only by conservation need, but also by utilization value, because the species contains abundant flavonoids, polysaccharides, and other metabolites with important medicinal and functional-food potential (Ji et al., 2021).

Elite germplasm utilization should then move from simple collection to targeted breeding and industrial seedling supply. Stress-screening evidence identified the Zhejiang ZJWZ strain as the strongest overall performer under cadmium, salt, and low-temperature stress, supporting its use as preferred parental material for resistance breeding. At the same time, large-scale production still suffers from low seed yield and limited cutting propagation, so micropropagation and organogenesis need to become routine components of germplasm utilization systems rather than isolated laboratory methods. Current regeneration protocols are already practical for this purpose, achieving a shoot proliferation coefficient of 6.73 within 30 days, 100% rooting of adventitious shoots, and over 98% survival after acclimatization (Pang et al., 2024). Beyond seedling multiplication, biotechnological approaches such as metabolic engineering and hairy-root systems should be incorporated into elite germplasm utilization strategy, because they can reduce dependence on wild materials and provide alternative routes for rapid production of target bioactive compounds.

7.2 Optimization of ecologically suitable and standardized under-forest cultivation technologies

Build ecologically matched and standardized under-forest cultivation technologies around the biological characteristics of the species. *T. hemsleyanum* naturally grows in shaded valley forests, cliffs, gullies, and moist mountain habitats, and both review and experimental evidence indicate that moderate shade is essential for stable growth and quality formation (Shi et al., 2022). The available physiological evidence shows that cultivation is most suitable under roughly 67% shade, while environmental studies further indicate that higher flavonoid accumulation occurs under moderate temperature, humidity, and seasonal moisture conditions rather than under uniformly intensified inputs. Standardization should therefore not mean uniform planting under any forest, but rather matching local provenance, canopy density, seasonal management, and site moisture to the ecological niche of the species. This is especially important because current studies still emphasize light and fertilizer more than broader under-forest ecological regulation, leaving many cultivation variables insufficiently standardized (Hu et al., 2021).

Standardization also needs to extend belowground, because quality formation depends strongly on soil properties, extracellular enzymes, and rhizosphere microbial communities. Biochar experiments show that dryland cultivation typically has 30~35% lower flavonoid concentrations than forest understory systems, but targeted amendment can partly bridge this gap by stimulating enzyme activity and restructuring fungal communities (Zhang et al., 2026). The same work indicates that medicinal quality depends more on functional bio-inorganic habitat regulation than on simple nutrient addition, which supports the use of rhizosphere engineering in non-native or degraded production sites. Controlled-environment studies suggest that UV treatments may provide a reference for quality-oriented stress regulation can markedly increase flavonoid accumulation and antioxidant-enzyme activity in leaves and roots (Bai et al., 2022). In practice, a standardized under-forest technical system should integrate provenance-matched seedlings, canopy-light regulation, moisture control, soil amendment, microbial optimization, and stress-quality monitoring to create production protocols that are both locally adaptable and reproducible across bases.

7.3 Promotion of deep processing, brand building, and integrated industrial development

Promote deep processing, whole-plant utilization, and regional brand construction so that local industries capture more value than raw-root sales alone. The development basis is already strong: around 142~150 compounds have been identified from *T. hemsleyanum*, especially flavonoids and polysaccharides, and these exhibit anti-inflammatory, antioxidant, antitumor, immunomodulatory, antipyretic, and hepatoprotective activities. Product development should therefore expand from tuber medicine into functional foods, antioxidant extracts, immune-enhancing polysaccharides, and aboveground-resource products (Hu et al., 2021; Ji et al., 2021). This broader route is supported by compositional studies showing that leaves contain significantly higher flavonoid and phenolic-acid levels than roots and stems, with 24 compounds detected only in leaves, while leaves and fibrous roots have been proposed as potential new medicinal parts (Luo et al., 2022). Functional studies strengthen that case: leaf phenolics and their metabolites ameliorated DSS-induced colitis through barrier protection, oxidative-stress reduction, and gut-microbiota regulation, while aboveground polysaccharides showed macrophage immune-enhancing activity (Wu et al., 2021; Tian et al., 2025).

Deep processing should be paired with quality-oriented process optimization and origin-based branding. Extraction studies show that process conditions strongly affect active-compound yield, with optimized ethanol-ultrasound extraction producing a total yield of 788.12 mg/kg for five major flavonoids and strong DPPH scavenging activity (Shu et al., 2023). Processing method also affects efficacy: freeze-dried products preserved bioactive constituents better and showed the strongest hepatoprotective effect among three processed forms (Xu et al., 2026). Polysaccharide deep processing is also advancing, as optimized ultrasonic extraction has yielded structurally defined glucans with significant antipyretic activity, providing a clearer route from local resource to high-value product (Ding et al., 2025). Finally, regional branding should rely on scientifically verified origin-quality relationships, because root price already varies by origin and metabolomic studies across eight producing areas identified 49 potential chemical markers, including catechin and darendoside B as antioxidant-related quality markers (Chu et al., 2024). Building local public brands around authenticated provenance, standardized processing, and diversified products would align well with the species' established identity as Zhejiang's “New Zhebawei” and help convert local characteristic resources into an integrated under-forest specialty industry (Bai et al., 2022).

8 Conclusions and Perspectives

Tetrastigma hemsleyanum possesses traditional medicinal, edible, and modern pharmacological value, making it a local characteristic medicinal plant resource with considerable industrial potential. In addition to its traditionally used tuberous roots, the leaves, stems, and other aboveground parts are also rich in flavonoids, polysaccharides, phenolic acids, and other bioactive constituents, showing potential for further development into functional foods and plant-derived products. Its shade-tolerant and moisture-preferring ecological characteristics are highly compatible with under-forest environments characterized by relatively low light intensity, stable temperature and humidity, and active soil microecology. Therefore, under suitable conditions, under-forest cultivation can support quality formation. Future local industrial development should fully integrate local germplasm resources, suitable forest stands, and ecological conditions to establish a characteristic industry system based on high-quality resources and ecological production.

At present, the *T. hemsleyanum* industry still faces several major challenges, including a fragile resource base, insufficient standardization, and a relatively short industrial chain. Wild resources have long been subjected to overharvesting, while the long growth cycle, low seed yield, and limited efficiency of conventional propagation continue to restrict the stable supply of elite germplasm and high-quality seedlings for large-scale production. Meanwhile, substantial differences in yield and quality occur among producing areas, habitats, and cultivation models, and standardized under-forest cultivation technologies with strong regional adaptability are still lacking, particularly for light, moisture, soil, and stand management. In the processing sector, problems such as limited product diversity, incomplete quality-control systems, insufficient industrial application of deep-processing technologies, and inadequate traceability of geographical origin and cultivation mode continue to hinder the transformation of local resource advantages into brand and market competitiveness.

Future development should promote the coordinated upgrading of the under-forest *T. hemsleyanum* industry through germplasm conservation, ecological cultivation, and industrial value addition. Upstream efforts should strengthen surveys of local germplasm resources, selection of elite germplasm, and rapid propagation technologies to establish a stable system for improved-variety breeding and seedling supply. At the production level, shading, water management, soil conditions, microbial regulation, and cultivation practices should be optimized according to germplasm and forest-site conditions to achieve standardized production and precise ecological regulation. Downstream development should emphasize comprehensive utilization of both tuberous roots and aboveground resources, promote high-value products such as polysaccharides, flavonoid extracts, and functional foods, and improve origin traceability, quality evaluation, and processing standards. By integrating resource conservation, standardized under-forest production, deep processing, and regional brand development, *T. hemsleyanum* can gradually shift from a traditional medicinal material resource toward an integrated under-forest industry with distinctive local characteristics.

Conflict of Interest Disclosure
The author affirms 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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Review and Progress Open Access

Effects of Organic Fertilizer Substitution for Chemical Fertilizers on Yield and Quality Formation of *Atractylodes macrocephala*

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Abstract This review examines the effects of organic fertilizer substitution for chemical fertilizers on the growth environment, yield formation, quality accumulation, stress resistance, and ecological benefits of *Atractylodes macrocephala* Koidz. The results indicate that organic fertilizer substitution provides favorable conditions for the growth and development of *A. macrocephala* by increasing soil organic matter content, improving soil physicochemical properties, optimizing nutrient supply, and regulating rhizosphere microbial community structure. Meanwhile, organic fertilizer substitution promotes rhizome yield by enhancing root development, increasing photosynthetic assimilate accumulation, and regulating dry matter allocation. In terms of quality formation, organic fertilizer substitution facilitates the accumulation of key active constituents, including atractylenolides, polysaccharides, and volatile oils, and its underlying mechanisms are closely associated with nutrient regulation, activation of secondary metabolic pathways, and rhizosphere microbial-mediated regulation. Furthermore, organic fertilizer substitution improves the stress resistance of *A. macrocephala*, reduces agricultural non-point source pollution, promotes resource recycling, and supports the sustainable development of the medicinal plant industry. However, suitable substitution ratios vary among different ecological regions and cultivation conditions, and the molecular mechanisms underlying quality formation and precision fertilization systems require further investigation. Future studies should integrate multi-omics approaches, precise soil monitoring, and intelligent management technologies to establish a quality-oriented, green, and efficient cultivation system for *Atractylodes macrocephala*.
Keywords *Atractylodes macrocephala*; Organic fertilizer substitution; Yield formation; Medicinal quality; Green cultivation

1 Introduction

Atractylodes macrocephala Koidz., commonly known as Baizhu, is one of the most important traditional Chinese medicinal plants in East Asia and has been used for more than 2 000 years. Its rhizome is widely employed in clinical and health-related applications, and modern studies attribute its medicinal value to multiple bioactive constituents, especially sesquiterpenoids such as atractylenolides and atractylone, as well as polysaccharides and other secondary metabolites (Cui et al., 2025). Pharmacological studies indicate that *A. macrocephala* has anti-inflammatory, antioxidant, neuroprotective, immunomodulatory, gastrointestinal regulatory, and other bioactivities, which has sustained strong clinical and market demand for this species (Zhu et al., 2018). At the same time, the medicinal quality of *A. macrocephala* depends not only on rhizome yield, but also on the accumulation of key active compounds, because atractylenolides, atractylone, and related constituents are widely used as quality markers for evaluating its pharmacological potential and consistency. Recent work further shows that both biomass and active component content are significantly higher in authentic production areas than in emerging production regions, while rhizome growth and phytochemical composition can respond differently to environmental conditions, indicating that the industry increasingly requires cultivation practices that can coordinate both yield and quality rather than pursuing output alone (Zhou et al., 2025; Lee et al., 2025).

With the expansion of artificial cultivation and rising demand for high-quality medicinal materials, *A. macrocephala* production faces increasingly strict requirements for stable yield, superior medicinal quality, and ecological sustainability. Wild resources have become scarce because of increasing demand, habitat degradation, and slow growth, which has made standardized cultivation the main pathway for ensuring supply (Cui et al., 2025). However, studies on *A. macrocephala* indicate that achieving consistent quality in cultivation remains difficult, and that soil properties and climate are closely associated with atractylenolide accumulation, while biomass and quality may be regulated by partly independent environmental networks (Lee et al., 2025). Regional comparison also shows that rhizosphere microbial structure, organic matter decomposition, pH, and enzyme-related soil characteristics are closely linked with the quality formation of *A. macrocephala* (Zhou et al., 2025). In medicinal plants more broadly, rhizosphere microecology directly or indirectly affects growth, metabolic regulation, and active ingredient accumulation, and medicinal plant production is especially sensitive to changes in soil fertility and biological properties because quality formation is inseparable from secondary metabolism (Wang et al., 2022; Rostaei et al., 2024). Therefore, for the Baizhu industry, fertilizer management must satisfy dual production goals: maintaining rhizome biomass while promoting the synthesis and accumulation of pharmacodynamically important compounds.

In practice, however, the pursuit of higher yields in medicinal plant cultivation has often led to excessive dependence on chemical fertilizers, and this strategy is increasingly recognized as unsustainable. Across medicinal plant systems, long-term or excessive chemical fertilizer use causes soil compaction, acidification, nutrient imbalance, decline of soil organic matter, and deterioration of microbial diversity and abundance (Wang et al., 2022; Su et al., 2025). Excessive chemical fertilizer application has also been linked to soil degradation in *Pinellia ternata* cultivation, where yield reduction and disease pressure were associated with deteriorated physicochemical properties, nutrient imbalance, and unfavorable shifts in the soil microflora.

In *Salvia miltiorrhiza*, lack of scientific fertilization guidance and excessive chemical fertilizer use directly reduced the content of tanshinones in roots, demonstrating that fertilization can impair not only soil health but also medicinal quality (Ji et al., 2025). Similar concerns appear in other medicinal crops: overuse of agrochemicals in *Polygala tenuifolia* compromised both soil health and medicinal quality, while continuous chemical fertilizer use in Chinese herbal medicine systems has promoted disease occurrence and inferior quality compared with bio-organic alternatives (Huang et al., 2024). Although chemical fertilizer can contribute substantially to crop yield and provides rapid nutrient release, its low use efficiency, with more than 50% of applied nitrogen reportedly not absorbed by crops, means that high-input cultivation often brings ecological costs without proportionate gains in sustainable productivity (Rostaei et al., 2024).

This review examines the mechanisms underlying the effects of organic fertilizer substitution for chemical fertilizers on the growth environment, yield formation, and quality accumulation of *Atractylodes macrocephala*, aiming to provide a theoretical basis for sustainable and green cultivation of medicinal plants. Organic fertilizer substitution can improve soil conditions, enhance nutrient-use efficiency, promote microbial activity, and regulate the formation of medicinal quality. Previous studies have shown that in *Pinellia ternata* cultivation, replacing 75% of chemical fertilizer with organic fertilizer increased yield by 44.93% without reducing alkaloid content; in *Codonopsis pilosula* production, bio-organic fertilizer improved emergence rate and yield while reducing disease incidence; and in *Polygala tenuifolia* cultivation, partial substitution with microalgae fertilizer increased underground biomass and active compound content. In addition, organic fertilizer substitution has demonstrated beneficial effects on improving soil fertility, maintaining yield, and enhancing quality in crops such as maize, *Saposhnikovia divaricata*, senna, *Prangos ferulacea*, tea, and *Salvia miltiorrhiza*.

However, the effectiveness of organic fertilizer substitution is influenced by crop species, soil conditions, fertilizer sources, and application methods, and it does not always outperform chemical fertilization under all conditions. Therefore, this review systematically analyzes the effects of organic fertilizer substitution for chemical fertilizers on soil environment, yield formation, quality accumulation, and ecological benefits of *Atractylodes macrocephala*, aiming to clarify its underlying mechanisms and provide a theoretical foundation for the development of green cultivation practices and scientific fertilization strategies for *Atractylodes macrocephala*.

2 Effects of Organic Fertilizer Substitution for Chemical Fertilizers on the Growth Environment of *Atractylodes macrocephala*

2.1 Improvement effects on soil physical and chemical properties

Organic fertilizer substitution improves soil structure mainly by increasing soil organic matter and aggregate stability, which then enhances aeration and water retention. In a long-term field experiment, manure and compost increased soil organic matter by 1.86~2.47% and also increased water-stable aggregates and air permeability at two soil depths (Acar et al., 2025). The same study found that organic fertilizer treatments increased field capacity and available water content in surface soil and improved bulk density and total porosity in deeper soil layers, indicating broad physical improvement beyond short-term nutrient input. A review of organic amendments similarly concluded that they lower bulk density by more than 5% relative to sole urea fertilization and increase water-holding capacity as soil organic matter rises (Aytenew and Bore, 2020). Under drought- and salinity-prone conditions, organic-input systems also maintained higher maximum water-holding capacity and lower bulk density than chemical-based systems, showing that the structural benefits of organic matter can strengthen soil resilience under stress (Sharma, 2022).

Organic substitution also tends to moderate adverse chemical conditions created by fertilizer overuse, although the exact direction of pH change depends on the starting soil condition and organic material used. Excessive chemical fertilizer application has been associated with soil compaction and acidification in medicinal-plant cultivation systems (Wang et al., 2022; Huang et al., 2024). In short-term substitution experiments, organic manure reduced soil bulk density, pH, and electrical conductivity while increasing nutrient status and enzyme activity (Ren et al., 2021). In strongly acidic soils, organic fertilizer compost ameliorated soil quality and shifted microbial communities toward structures closer to native soils. In other systems, alkaline organic inputs moved soil pH toward neutral conditions and significantly altered bacterial richness, showing that pH regulation is context dependent but agronomically important (Shang et al., 2020). For *A. macrocephala*, this matters because regional differences in organic matter, electrical conductivity, and pH are part of the soil factor set associated with quality formation and fungal network structure.

2.2 Regulation of soil nutrient supply capacity

Organic fertilizer substitution regulates soil nutrient supply by increasing organic matter inputs, broadening nutrient pools, and stimulating enzyme-mediated nutrient transformation. A three-year substitution experiment found that partial organic fertilizer replacement significantly increased alkali-hydrolyzable nitrogen, available phosphorus, available potassium, and soil organic matter, with especially strong effects at 30-50% substitution ratios (Lu et al., 2025). In tea plantations, organic-only treatments produced the highest total nitrogen, available nitrogen, organic matter, and pH, while mixed organic-chemical regimes improved overall growth and soil function more effectively than chemical fertilizer alone (Miao et al., 2024). Organic inputs in cotton also increased total nitrogen, hydrolyzed nitrogen, available phosphorus, and available potassium across the 0-40 cm soil layer while reducing salinity (Zhao et al., 2025). In degraded grassland soil, vermicompost and mushroom residue particularly increased available phosphorus and available potassium, confirming that organic materials can selectively enhance the readily available nutrient fractions most relevant to plant uptake (Shang et al., 2020).

The nutrient-regulation effect of organic substitution is not limited to nutrient stocks; it also changes nutrient form, cycling rate, and use efficiency through enzyme activity and decomposition pathways. In *Fritillaria thunbergii*, both organic and inorganic fertilization lowered the NH^{4+}/NO^{3-} ratio by 64%, increased bulb yield 6.8-fold, and showed that a lower ratio favored yield, while organic fertilizer uniquely maintained urease activity relative to inorganic fertilizer (Du et al., 2024). In maize rhizosphere soil, partial substitution increased urease, invertase, and alkaline phosphatase activities, and path analysis showed that soil physicochemical changes influenced enzyme activity through shifts in microbial communities (Ren et al., 2021). Repeated application of organic amendments has been reported to increase microbial biomass by up to 100% and enzymatic activity by up to 30%, providing a broader mechanism for improved nutrient mineralization and cycling (Aytenew and Bore, 2020). Because the synthesis of active constituents in medicinal plants depends on nutrient status and rhizosphere ecology, this stronger and more buffered nutrient supply is likely to be important for coordinating rhizome growth with quality formation in *A. macrocephala* (Wang et al., 2022; Zhou et al., 2025).

2.3 Effects on soil microbial community structure

Organic fertilizer substitution markedly alters soil microbial community structure, usually with stronger effects on bacteria than fungi and with consequences for disease suppression, nutrient cycling, and crop performance. In maize rhizosphere soil, partial substitution changed both bacterial and fungal community composition, but the effect was stronger on bacterial alpha diversity, and community shifts were closely related to soil water, organic carbon, nitrate, and total nitrogen (Ren et al., 2021). Long-term organic fertilization in medicinal-plant systems has also been reported to promote microbial diversity and soil enzyme activity, whereas excessive chemical fertilizer can reduce microbial diversity and soil fertility. In acidified soils, organic fertilizer enhanced bacterial network complexity, increased microbial abundance, and improved network stability, indicating that substitution can reorganize microbial interactions rather than only changing taxonomic composition. Oilseed rape experiments further showed that a 25% chemical plus 75% organic treatment increased bacterial abundance, species diversity, and ecological network complexity, although it also increased potential plant pathogenicity risk.

Evidence from medicinal plants suggests that these microbial shifts can translate into better soil health and may influence medicinal quality, but the effects are not uniformly positive across all systems. In *Codonopsis pilosula*, bio-organic fertilizer produced stronger and more stable microbial networks than chemical fertilizer and reduced root-rot disease index by 76.60% while increasing emergence rate and yield by 21.12% and 33.65%, respectively (Huang et al., 2024). In *Fritillaria thunbergii*, organic fertilization increased saprotrophic fungi, enhanced Pezizales abundance tenfold, reduced Hypocreales by 51%, and was considered favorable for maintaining soil health and high yield (Du et al., 2024). For *A. macrocephala*, authentic production areas showed the most complex rhizosphere fungal networks, and fungi involved in organic matter decomposition, including *Mortierella* and Basidiomycota-related groups, were linked to medicinal quality. However, long-term work in Huajuhong found that organic fertilizer was not inherently superior to chemical fertilizer and could increase pathogenic fungi abundance, so the value of substitution in *A. macrocephala* likely depends on substitution ratio, fertilizer maturity, and local soil conditions.

3 Effects of Organic Fertilizer Substitution for Chemical Fertilizers on Growth Development and Yield Formation of *Atractylodes macrocephala*

3.1 Effects on vegetative growth characteristics of *Atractylodes macrocephala*

Organic fertilizer substitution generally promotes the vegetative growth of *Atractylodes macrocephala* by improving the rhizosphere conditions that support aboveground development and root activity. In a direct study on *A. macrocephala*, several organic fertilizers produced yields comparable to customary fertilization under basal application, and suitable dosage ranges were identified, indicating that organic nutrient supply can sustain normal plant growth in this species (Kim et al., 2016). Evidence from other medicinal plants shows the same growth-promoting direction: in *Polygonum cuspidatum*, organic residue amendment significantly increased plant height, stem diameter, leaf number, node number, and both aboveground and root biomass, with the intermediate rate performing best. In soybean, moderate organic-inorganic fertilization increased plant height, root length, biomass, nodulation, nitrogenase activity, and photosynthetic capacity relative to full chemical fertilization and full organic fertilization, showing that balanced substitution often supports stronger vegetative vigor than either extreme (Zhang et al., 2026).

The growth-promoting effect appears to depend on improved photosynthesis, hormone balance, and rhizosphere biological activity rather than nutrient input alone. In *P. cuspidatum*, organic amendment increased SPAD value, net photosynthetic rate, transpiration rate, and intercellular CO_2 concentration, while root IAA and zeatin riboside rose by 11.0~41.7% and 17.8~46.0%, respectively, and both hormones were positively correlated with root biomass. In white lupin, a PGPB-enriched organic fertilizer increased shoot weight by 70%-88%, total biomass by about 80%, and shoot elongation by up to 36%, supporting the view that organic matrices combined with beneficial microbes can directly stimulate plant growth (Robas-Mora et al., 2026). More broadly, biofertilizer-associated microorganisms can enhance nutrient acquisition, stress tolerance, and pathogen suppression, all of which contribute to improved vegetative development (Fasusi et al., 2021). For *A. macrocephala*, this suggests that partial replacement of chemical fertilizer with well-matured organic inputs is likely to favor seedling establishment, canopy growth, and root system activity when nutrient release is matched to crop demand.

3.2 Effects on rhizome expansion and yield formation

For a rhizome medicinal plant such as *A. macrocephala*, the central agronomic question is whether organic substitution promotes assimilate accumulation into the underground organ. Direct evidence indicates that organic fertilizer can do so. In *A. macrocephala*, application of organic fertilizer 1 at 2.0 times the standard amount increased yield to 203.0 kg per 10 a, compared with 134.0 kg under conventional fertilization, and this difference was statistically significant (Kim et al., 2016). In Rhizoma atractylodis, vermicompost bio-organic fertilizer increased yield by 70% compared with the control while also increasing key sesquiterpenoid constituents, showing that organic fertilization can simultaneously support underground biomass accumulation and medicinal-quality formation in *Atractylodes* species. Similar rhizome responses were observed in *Paris polyphylla* var. *yunnanensis*, where inoculation with organophosphate-degrading bacteria increased rhizome biomass by 134.58% in the best treatment and raised steroidal saponins together with soil available phosphorus.

Yield formation under organic substitution is closely tied to better phosphorus activation, carbon turnover, and beneficial microbial recruitment in the rhizosphere. In *Polygala tenuifolia*, substituting 40% of chemical fertilizer with microalgae increased underground biomass by 29.30%, and the abundance of *Chloroflexi* was positively correlated with both underground biomass and active-compound content (Su et al., 2025). A global meta-analysis found that replacing chemical fertilizers with organic fertilizers increased crop yield by 10.89%, and yield gains were positively related to increases in total nitrogen, available phosphorus, AM fungal richness, and soil health index (Figure 1) (Wang et al., 2025). Long-term greenhouse vegetable data further showed that organic substitution increased enzyme activity, microbial PLFAs, and soil nitrogen transformation, and these changes improved soil nitrogen supply capacity and yield (Yuan et al., 2024). Taken together, these findings indicate that rhizome expansion in *A. macrocephala* under organic substitution likely results from a coordinated improvement in nutrient activation, root-microbe interactions, and sustained assimilate supply to the underground storage organ.

3.3 Regulation effects of different organic fertilizer substitution modes on *Atractylodes macrocephala* yield

Different organic fertilizer substitution modes do not produce the same yield response, and moderate substitution usually outperforms both sole chemical fertilization and excessive organic replacement. In *Polygala tenuifolia*, 40% chemical fertilizer substitution with microalgae gave the strongest growth-promoting effect, whereas microbial inoculant treatments with reduced chemical fertilizer showed no significant difference from full chemical fertilizer in underground growth (Su et al., 2025). In muskmelon, 15% and 30% organic substitution increased yield by 5.60~11.9% compared with conventional chemical fertilization and also improved economic returns (Yu et al., 2025). In rice, long-term green manure substitution improved yield sustainability only within a moderate range, with 0~40% substitution in early rice and 0~20% in late rice improving both soil quality and yield stability, whereas further increases reduced the sustainability yield index (Zhang et al., 2023).

This pattern is reinforced across broader substitution experiments. In soybean, 30% organic plus 70% inorganic fertilization was identified as the optimal strategy, outperforming both full chemical and full organic treatments for growth and yield (Zhang et al., 2026). In maize dryland production, a relatively low substitution rate of 12.5% increased grain yield by 6.60% and biomass by 4.59% compared with chemical fertilizer, and 12.5~37.5% substitution improved key carbon fractions linked to yield (Chen et al., 2025). In double-rice systems, substituting 20% of phosphorus fertilizer with organic manure increased grain yield by 4.59% and soil Olsen-P by 25.48%, while reduced-phosphorus substitution maintained yields comparable to conventional fertilization (Jin et al., 2025). However, evidence from Huajuhong shows that organic fertilizer is not inherently superior in all cases and may increase pathogenic fungi abundance under long-term use, so complete substitution is not always the best option.

Therefore, for *A. macrocephala*, the most reasonable expectation is that yield can be optimized by a moderate substitution strategy that combines chemical fertilizer with organic fertilizer or bio-organic inputs, rather than by absolute replacement.

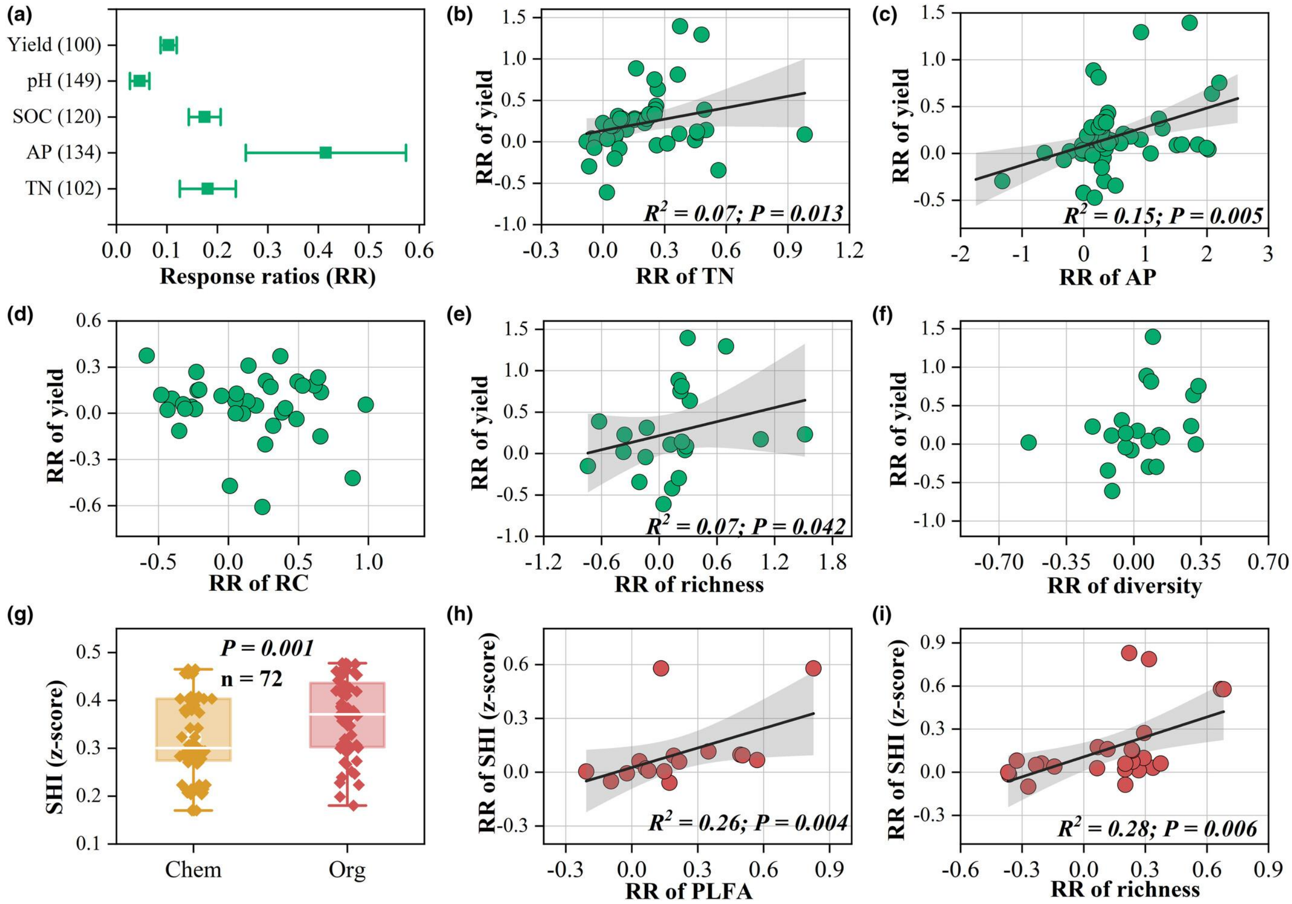

Figure 1 Regulatory factors of the impact of organic fertilizer replacing chemical fertilizer on crop yield and soil health (Adopted from Wang et al., 2025)

Image caption: Effects of organic fertilizers replacing chemical fertilizers on crop yield, soil physicochemical properties (a) and soil health (g). Linear regression analysis between response rate (RR) of total nitrogen (TN) (b), available phosphorus (AP) (c), arbuscular mycorrhizal fungal root colonization (d), richness (e) and diversity (f) and crop yield. Linear regression and analysis between RR of phospholipid fatty acid (PLFA) (h), richness (i) and soil health. Solid points and open points represent significant (95% confidence interval [CI] not overlapping with zero) and non-significant effect sizes, respectively. The numbers in parentheses represent the sample size of observations. The shaded bands with grey colour show 95% pointwise CIs. The soil health index in meta-analysis is calculated by normalizing soil organic carbon, TN, AP and pH values through z-score to obtain the average value. Chem, chemical fertilizer application; Org, organic fertilizer application; PLFA, phospholipid fatty acid; RR, response rate; SHI, soil health index (Adopted from Wang et al., 2025)

4 Mechanisms of Organic Fertilizer Substitution for Chemical Fertilizers in Quality Formation of *Atractylodes macrocephala*

4.1 Effects on accumulation of main active components in *Atractylodes macrocephala*

Organic fertilizer substitution can promote the accumulation of the main active components of *Atractylodes macrocephala*, but the effect is selective and depends on the fertilization mode and the physiological pathway being regulated. In a direct fertilization study on *A. macrocephala*, the HA organic fertilizer treatment produced a significantly higher atractylenolide I content than bacterial filtrate or conventional fertilization, and the highest atractylone-related index also appeared under HA treatment (Kim et al., 2016). This indicates that organic substitution can improve medicinal quality not only through biomass increase but also through enhancement of sesquiterpene lactone accumulation, which is one of the core quality targets in *A. macrocephala* (Lee et al., 2025).

Independent reviews further show that the major active constituents of *A. macrocephala* include volatile oils, polysaccharides, and lactones, and that polysaccharides themselves are important pharmacodynamic substances rather than only reserve carbohydrates. Therefore, any fertilization practice that simultaneously favors lactone and polysaccharide accumulation is directly relevant to medicinal quality formation in this crop (Figure 2) (Liu et al., 2022; Li et al., 2022).

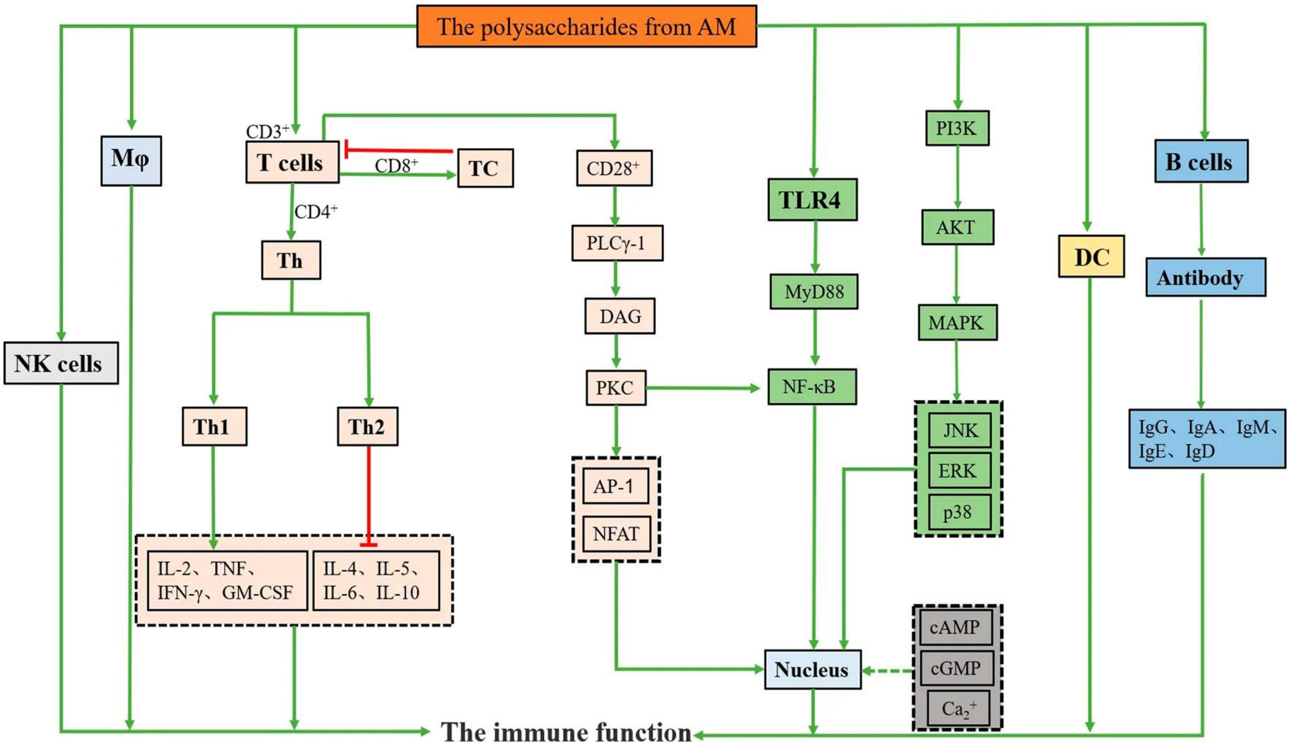

Figure 2 Immunomodulation activity mechanisms of polysaccharides from *A. macrocephala* (Adopted from Liu et al., 2022)

The likely mechanism is that organic substitution enhances secondary metabolism through rhizosphere signaling, carbon supply, and regulation of terpenoid biosynthesis pathways. In *A. macrocephala*, elicitation with exogenous plant polysaccharides significantly increased biomass, atractylenolides, and polysaccharides, and RT-qPCR showed that the induced terpenoid increase mainly depended on the mevalonate pathway (Zhou et al., 2021). Rhizosphere evidence also supports this interpretation: multiple bacterial and fungal genera in *A. macrocephala* soils were positively or negatively correlated with the accumulation of polysaccharides, atractylone, and lactones I-III, indicating that active-component formation is tightly linked to microbial community structure (Song et al., 2023). Similar organic-input responses have been reported in other medicinal plants: bio-organic fertilizer increased lignans, flavonoids, polysaccharides, and polyphenols in *Schisandra chinensis*, while integrated organic and inorganic fertilization improved rhizome bioactive content in *Kaempferia galanga* (Saitama et al., 2025; Xu et al., 2025). Together, these findings suggest that organic fertilizer substitution promotes quality formation in *A. macrocephala* by coordinating nutrient availability with secondary-metabolite biosynthesis and rhizosphere biological activation.

4.2 Effects on volatile components and quality evaluation of medicinal materials

The quality of *A. macrocephala* medicinal materials is strongly associated with its volatile components, especially atractylone and related sesquiterpenes, so the effect of organic substitution on volatile profiles is a central quality issue. Comparative metabolomic and GC/MS studies show that *A. macrocephala* is chemically characterized by volatile oils dominated by atractylone, while atractylolactones also serve as distinguishing constituents among *Atractylodes* species (Zhang et al., 2025). A GC/MS chemometric study of 59 batches identified 50 volatile components and proposed five characteristic markers for *Atractylodes* quality evaluation, including atractylone and atractylenolide I. More broadly, volatile oils are recognized as important active constituents and characteristic quality indicators in Chinese medicinal materials, including *A. macrocephala* (Zhu et al., 2019). Since organic fertilizer can increase atractylone- and lactone-related indices in *A. macrocephala* cultivation, it likely acts on precisely the fraction most relevant to medicinal-grade evaluation (Kim et al., 2016).

Volatile quality formation is mechanistically sensitive to both environment and post-accumulation transformation. For *A. macrocephala*, precipitation during the early growth season had an important effect on volatile-oil accumulation, showing that water and nutrient environment during vegetative and early rhizome development can shape the final volatile profile (Zhu et al., 2019). Environmental analysis also showed that atractylenolide content was robustly associated with soil texture, cation exchange capacity, temperature, and humidity, whereas growth and phytochemical quality were regulated by partly independent environmental networks (Lee et al., 2025). Processing studies add an important quality-evaluation perspective: raw essential oil is rich in atractylon, whereas processing significantly depletes atractylon and increases atractylenolides I, II, and III through time-dependent chemical conversion (Li et al., 2025). Because crude and processed *A. macrocephala* also differ in the number of detected volatile components and in bioactivity profiles, quality evaluation should consider not only total oil yield but also the balance among key volatile markers and their transformation products (Gu et al., 2019).

4.3 Mechanisms of nutrient regulation promoting quality formation of *Atractylodes macrocephala*

The nutrient-regulation mechanism by which organic fertilizer substitution promotes quality formation appears to involve both improved nutrient supply and activation of key biosynthetic enzymes and genes. Studies on medicinal plants consistently show that the biosynthesis of secondary metabolites is sensitive to nutrient status, especially nitrogen and phosphorus, and that fertilization method and application rate must be matched to the target compounds. In *Atractylodes chinensis*, high-phosphorus fertilization promoted the accumulation of volatile-oil components and increased the expression of *ACC* and *FPPS*, while *HMGR* also contributed to sesquiterpene regulation. This is mechanistically relevant to *A. macrocephala* because sesquiterpenes such as atractylone and atractylenolides are key quality constituents, and terpenoid synthesis in *Atractylodes* depends on precursor supply and pathway activity (Sun et al., 2022). Nutrient effects on volatile quality are also seen in other medicinal plants: increasing phosphorus significantly increased essential-oil production in *Vitex negundo*, plausibly because phosphorus supports acetyl-CoA-dependent terpenoid biosynthesis (Peng and Ng, 2022).

Organic substitution adds another layer by reshaping microbial nutrient cycling and root-zone signaling, which can stabilize nutrient release and improve metabolic efficiency. Organic fertilizer increased soil organic matter, total nitrogen, total phosphorus, alkali-hydrolyzable nitrogen, and available phosphorus in rubber rhizosphere, while upregulating microbial genes involved in organic N metabolism, nitrate transport, nitrification, denitrification, and organic P mineralization (Geng et al., 2026). In *Schisandra chinensis*, bio-organic fertilizer altered transcriptomic and metabolomic pathways associated with plant growth and nutrient accumulation, consistent with higher levels of multiple quality compounds (Xu et al., 2025). Nutrient interaction studies further show that N and P coordination can remodel root structure, transporter activity, organic-acid metabolism, and hormone signaling, thereby improving nutrient uptake efficiency rather than simply increasing fertilizer input (Tang et al., 2025). Accordingly, the quality-promoting effect of organic fertilizer substitution in *A. macrocephala* likely arises from a coupled process in which slower but more buffered nutrient release, stronger rhizosphere microbial function, and enhanced terpenoid-biosynthetic signaling together promote the accumulation of lactones, polysaccharides, and volatile oils.

5 Effects of Organic Fertilizer Substitution for Chemical Fertilizers on Stress Resistance and Ecological Benefits of *Atractylodes macrocephala*

5.1 Enhancement of stress resistance in *Atractylodes macrocephala*

Organic fertilizer substitution can enhance the stress resistance of *Atractylodes macrocephala* mainly by improving soil water retention, nutrient buffering, antioxidant capacity, and rhizosphere biological stability. A recent review concluded that organic fertilizers improve tolerance to drought, salinity, heat, and heavy metal stress by improving leaf water status, nutrient homeostasis, chlorophyll synthesis, osmolyte accumulation, antioxidant activity, and stress-related gene expression (Liu et al., 2024). Integrated organic-inorganic nutrition also tends to improve water and nutrient uptake and strengthen drought tolerance while reducing dependence on sole chemical fertilization (Kazemalilou et al., 2021). In medicinal and field crops under drought, organic amendments increased photosynthesis, membrane stability, proline and sugar accumulation, and the activities of antioxidant enzymes such as SOD, POD, CAT, APX, GR, and GPX, thereby mitigating oxidative damage (Ahanger et al., 2021; Najafi et al., 2021). Similar responses were reported in maize, where poultry manure and farmyard manure improved growth and yield under severe drought and enhanced antioxidant defense through SOD, POD, and CAT (Shah et al., 2023).

For medicinal plants, this stress-mitigation effect is especially important because resistance traits and secondary-metabolite accumulation are closely linked. In *Dracocephalum kotschyi*, organic and microbial fertilizers under mild to moderate drought increased CAT, POD, PPO, and APX activity together with proline, phenolics, flavonoids, and anthocyanins, indicating coordinated improvement in oxidative stress mitigation and phytochemical accumulation (Heidarzadeh et al., 2026). Biofertilizer treatments also improved biochemical stress indicators and increased flavonoid and anthocyanin contents under drought, while generally outperforming chemical fertilizer for stress tolerance and phytochemical enrichment (Heidarzadeh et al., 2026). In *Atractylodes* systems, vermicompost increased fungal diversity, available phosphorus, and enzyme activities, and humic substances in vermicompost can promote phenolic synthesis while enhancing root growth, soil structure, aeration, and water-holding capacity. Microbial fertilizers also help plants resist stress by recruiting beneficial rhizosphere organisms that compete with pathogens and induce systemic resistance, which provides a plausible mechanism for improved resilience in *A. macrocephala* under reduced chemical fertilizer input (Xing et al., 2025).

5.2 Reduction of agricultural non-point source pollution

Organic fertilizer substitution can reduce agricultural non-point source pollution, especially nitrogen leaching and runoff, when it replaces rather than simply adds to chemical fertilizer. A global meta-analysis of 129 studies found that organic inputs reduced overall nitrogen leaching by 15% and runoff by 29% without compromising yield, and substitution based on equal total nitrogen reduced both leaching and runoff by more than 30%. The same analysis showed lower loss ratios for organic fertilizer than chemical fertilizer and identified optimal substitution ranges of 40~60% for leaching control and 60~100% for runoff control under equal-total-N substitution (Wei et al., 2021). Field evidence is broadly consistent: in tobacco systems, combined organic-inorganic fertilization improved nutrient uptake while reducing runoff and leaching losses of both N and P compared with farmers' organic practice. In paddy fields, substituting more than 30% of chemical N with organic N significantly lowered TN concentrations in ponded water while maintaining rice yield at comparable levels (Zhou, 2023).

The ecological advantage, however, depends on management details. Partial organic substitution in vegetable production reduced N_2O emission, N leaching, and runoff, likely because it lowered inorganic nitrogen surplus, and it also prevented soil acidification (Tang et al., 2022). A short-term Tibetan incubation study found that 40% substitution with compost, straw, or sheep dung reduced cumulative N_2O emissions by 16.64~53.43%, but nitrate tended to accumulate, indicating possible leaching risk if nitrogen transformation is not synchronized with crop uptake. Another study reported that organic fertilizers can be more easily washed out because of their soluble components, but combining fertilizer reduction with biochar and microbial agents reduced nutrient concentrations in infiltration and runoff waters by 5~10% while maintaining yield similar to full fertilization. Therefore, for *A. macrocephala*, organic substitution appears most effective for reducing non-point source pollution when used at moderate substitution rates and in combination with practices that stabilize nitrogen and phosphorus in the soil-plant system.

5.3 Promotion of sustainable development of the *Atractylodes macrocephala* industry

For the *Atractylodes macrocephala* industry, organic fertilizer substitution supports sustainable development by linking medicinal-material quality, soil restoration, waste recycling, and long-term input efficiency. Excessive chemical fertilizer use is associated with soil degradation, declining fertility, nutrient-use inefficiency, and broader environmental crisis, with only 30~50% nitrogen-use efficiency in major cereal systems and large fractions of applied nutrients lost through volatilization or leaching (Xing et al., 2025). Balanced mineral-organic fertilization instead improves soil structure, boosts water and nutrient retention, increases microbial biomass, and mitigates greenhouse-gas emissions and nutrient leaching while sustaining yields. In *Atractylodes* cultivation itself, suitable organic fertilizers increased rhizome yield and atractylenolide I content, showing that ecological fertilization can serve both production and medicinal-quality goals (Kim et al., 2016). Vermicompost studies in *Atractylodes* also demonstrate the value of converting agricultural wastes into high-value organic fertilizer, which broadens the utilization of organic residues while improving medicinal-herb yield and quality.

Sustainable industrial development also depends on profitability and risk control, not only on ecological outcomes. Partial substitution of chemical fertilizer with organic forms increased economic benefit per unit area by 37~46% in vegetable production and reduced agricultural inputs and environmental impacts per unit product by 22~44%, with 50% pig-manure substitution the most profitable strategy (Tang et al., 2022). Bio-organic fertilizer strategies in medicinal plants likewise provide an eco-friendly basis for reducing chemical fertilizer use while maintaining or improving medicinal-plant productivity and quality (Su et al., 2025). Microalgae-based biofertilizers offer an additional sustainability route because they improve nutrient cycling, reduce reliance on synthetic fertilizers, support beneficial soil microbiota, and can contribute to carbon sequestration (Gonçalves et al., 2023). Overall, organic fertilizer substitution appears to be a practical pathway for the sustainable development of the *A. macrocephala* industry, but the strongest evidence supports balanced substitution, not unconditional replacement, because some systems still show risks of nitrate accumulation, phosphorus mobilization, or pollutant wash-off under poorly matched organic inputs (Zhou, 2023; Xing et al., 2025).

6 Current Research Challenges and Future Development Directions

6.1 Optimization of organic fertilizer substitution ratios and application methods

At present, one major challenge is that the optimal substitution ratio of organic fertilizer for chemical fertilizer is not fixed, but varies with crop species, target traits, and local soil conditions. In *Epimedium pubescens*, 25% organic substitution produced the highest comprehensive score and was recommended for first-year production, even though fully or highly substituted treatments improved some soil indices or enzyme activities (Lai et al., 2024). In yam, the 25% organic plus 75% chemical treatment achieved the highest yield, commodity rate, and nitrogen use efficiency, while higher organic ratios reduced some yield traits. In contrast, *Euryales Semen* performed best at a 7:3 organic-to-chemical ratio, and tea responded most favorably to a 25% partial substitution treatment rather than complete replacement. These differences show that a single uniform substitution ratio cannot be directly transferred to *A. macrocephala* production.

Application method is another unresolved issue. Evidence across crops shows that substitution effects depend not only on proportion, but also on nutrient-equivalent design, fertilizer type, timing, and auxiliary amendments. The yam study maintained equal nitrogen input across treatments, which allowed a clearer comparison of substitution effects. In *Saposhnikovia divaricata*, the highest comprehensive scores came from a mode combining organic fertilizer, reduced chemical fertilizer, and biochar as a soil conditioner, indicating that optimization should include amendment combinations rather than ratio alone. A 20% commercial organic fertilizer substitution increased wheat yield and soil quality, but the authors emphasized that continued application requires monitoring soil organic matter and available nutrients to adjust fertilization over time (He et al., 2022). For *A. macrocephala*, future work should therefore move from simple ratio screening to multi-factor optimization that integrates substitution proportion, nutrient equivalence, fertilizer source, topdressing schedule, and soil-improving co-inputs under different production regions.

6.2 Insufficient research on the mechanisms of quality formation in *Atractylodes macrocephala*

A second major challenge is that the quality-formation mechanism of *A. macrocephala* remains insufficiently resolved. Environmental evidence shows that the factors regulating rhizome growth and those regulating atractylenolide accumulation are largely independent, and that optimizing yield and phytochemical quality may require different cultivation strategies. The same work argued that future cultivation should consider not only external conditions but also internal physiological mechanisms such as sink-source dynamics and storage-capacity development (Lee et al., 2025). This means that current fertilizer studies on *A. macrocephala* still explain outcomes mainly through correlations with soil properties, while the causal chain linking nutrient regulation to rhizome metabolite accumulation remains incomplete.

Mechanistic gaps also exist at the levels of microbiome, metabolism, and molecular regulation. Rhizosphere studies showed that 16 bacterial and 10 fungal genera were correlated with the accumulation of polysaccharides, atractylone, and lactones, but these results remain largely associative rather than functional (Song et al., 2023). Regional analysis further showed that authentic production areas had higher biomass and active-component levels, and that decomposer-associated fungi such as *Mortierella* and Basidiomycota were linked to quality formation (Zhou et al., 2025). At the plant level, *A. macrocephala* quality involves volatile oils, polysaccharides, and lactones (Liu et al., 2022; Yu et al., 2023); older rhizomes accumulate more sesquiterpenoids and phenolic acids, with upregulation of terpenoid and phenylpropanoid biosynthetic genes such as *HMGR, DXS, idi, GPS,* and *GGPS* (Cui et al., 2025). However, there is still no integrated framework showing how organic fertilizer substitution alters nutrient transformation, microbial networks, carbon allocation, and biosynthetic gene expression to jointly determine medicinal quality. Future research should combine controlled fertilization experiments with metabolomics, transcriptomics, enzyme assays, and rhizosphere microbiome manipulation to identify the key regulatory nodes of quality formation.

6.3 Establishment of green and precision fertilization technology systems

A third challenge is the lack of a green and precision fertilization technology system specifically tailored to *A. macrocephala*. Precision fertilization is increasingly recognized as a core pathway for optimizing nutrient application, improving productivity, and minimizing environmental harm through site-specific management, real-time monitoring, and variable-rate application. Reviews of specialty crops similarly show that precision systems should integrate crop and soil diagnostics, variable-rate fertilizer and irrigation management, and decision-support tools, while also incorporating organic and bio-based fertilizers into adaptive management frameworks (Khoddamzadeh et al., 2026). For *A. macrocephala*, this is especially relevant because soil texture, cation exchange capacity, humidity, and temperature all affect active-component accumulation, so fertilization should eventually be linked to fine-scale environmental diagnosis rather than uniform field application (Lee et al., 2025).

The future direction is to establish a fertilization system that combines soil testing, sensor monitoring, decision models, and organic substitution strategies. Site-specific nutrient management aims to match nutrient supply with spatial and temporal crop demand using tools such as remote sensing, GPS, GIS, and variable-rate technology, thereby improving nutrient-use efficiency and economic return rather than simply increasing inputs (Akhil et al., 2025). Precision water-fertilizer reviews further emphasize the need to couple nutrient management with irrigation, improve soil testing, refine predictive models, and build standardized indicator systems that account for soil heterogeneity and nutrient transformation processes (Xing and Wang, 2024). Practical experience from SSNM decision-support systems also shows that precision fertilization can improve productivity, soil fertility, microbial activity, and nutrient-use efficiency while remaining operational for extension and farm use (Pooniya et al., 2015). Accordingly, future *A. macrocephala* research should build region-specific green fertilization models for authentic and emerging production areas, develop quality-oriented nutrient recommendation standards, and integrate organic fertilizer substitution into digital, scalable precision management systems.

7 Conclusions and Prospects

Organic fertilizer substitution for chemical fertilizers should be regarded as an important approach for improving the production quality of *Atractylodes macrocephala*, but the evidence supports balanced substitution more strongly than complete replacement. In *A. macrocephala* itself, HA organic fertilizer maintained or exceeded conventional yield and significantly increased atractylenolide I content from 0.023% under customary fertilization to 0.036%, while the highest yield reached 203.0 kg per 10 a at the appropriate HA application rate. In related *Atractylodes* research, vermicompost increased yield by 70% and raised atractylenolide II, β-eudesmol, atractylenol, and atractylenolone by 34%, 175%, 72%, and 24%, respectively, while also increasing available phosphorus and lowering nitrate nitrogen. Across medicinal and field crops, partial substitution often performs best: 40% microalgae substitution increased underground biomass and active components in *Polygala tenuifolia* 25% partial substitution improved tea soil quality and amino acid quality traits while raising nitrogen use efficiency, and 20~40% mineral replacement is repeatedly associated with lower environmental risk while sustaining productivity. Because long-term chemical-fertilizer dependence reduces soil organic matter and disrupts soil biological activity, whereas organic inputs improve soil structure, nutrient retention, and microbial function, organic substitution should be treated as a core pathway for coordinating rhizome yield, medicinal quality, and ecological safety in *A. macrocephala* production.

Nutrient regulation is the key driver connecting fertilization mode with quality formation in *A. macrocephala*, because active-component accumulation depends not simply on nutrient quantity but on the balance among nutrient supply, rhizosphere transformation, and secondary-metabolite biosynthesis. In *Atractylodes chinensis*, precise NPK regulation showed that high-phosphorus fertilization increased yield and promoted sesquiterpene and polyacetylene accumulation by increasing ACC and FPPS expression, while HMGR responded more strongly under a different formula, indicating that different nutrient ratios regulate different biosynthetic branches (Sun et al., 2022). More broadly, medicinal-plant studies show that appropriate N and P improve biomass, essential oils, and bioactive compounds, but species differ in their optimal ratios and excessive or imbalanced fertilization can reduce target metabolites. Nitrogen also changes metabolic allocation: low N increased phenolic acids and flavonoids in *Artemisia argyi*, whereas high N increased volatile oil and terpene-related gene expression. At the system level, organic substitution improves soil organic matter, available nutrients, microbial diversity, and nutrient-use efficiency, while compost optimization with biochar can reduce nitrogen loss by 28.1% and preserve phosphorus availability before the fertilizer even reaches the field. Future work on *A. macrocephala* should therefore focus on how nitrogen, phosphorus, potassium, organic carbon, and rhizosphere microbes jointly regulate lactones, volatile oils, and polysaccharides rather than evaluating fertilizer treatments only by yield response.

The future prospect for *A. macrocephala* is the construction of a green and efficient cultivation technology system that integrates organic substitution, formula fertilization, soil testing, and precision management. Precision agriculture in medicinal plants is defined by site-specific monitoring and response, using tools such as GIS, GPS, crop scouting, remote sensing, and variable-rate technology to optimize output with lower resource use. Smart-farming reviews further show that data-driven irrigation and nutrient management can improve medicinal-plant yield, phytochemical consistency, and sustainability by directly regulating photosynthesis, nutrient uptake, stress response, and secondary-metabolite biosynthesis, although cost and scalability remain constraints. For fertilization practice, soil testing and formula-based nutrient management are recommended because proper fertilization improves bioactive compounds, whereas excess or imbalance can have the opposite effect. Organic-inorganic integration also improves drought tolerance and resource-use efficiency, and nano-organic fertilizer has been shown to enhance antioxidant metabolism, osmolyte accumulation, mineral nutrition, photosynthesis, and membrane stability under drought stress. Accordingly, future *A. macrocephala* cultivation should establish region-specific nutrient recommendation models for authentic and emerging production areas, dynamically monitor soil organic matter and available nutrients during long-term substitution, and combine ecological fertilization with digital decision support so that high yield, stable quality, stress resistance, and environmental protection can be achieved simultaneously.

Conflict of Interest Disclosure

The author affirms 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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