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Medicinal Plant Research, 2026, Vol. 16, No. 4, 266-282

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Medicinal Plant Research, 2026, Vol. 16, No. 4, 283-295

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Medicinal Plant Research, 2026, Vol. 16, No. 4, 296-312

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Research Article

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Bulb Propagation Techniques and Large-scale Production Application of *Fritillaria thunbergii* Miq.Xiaoying Li¹, Jianhua Wang² ✉¹ Songyang Xiaoying Family Farm, Songyang, 323400, Zhejiang, China² Songyang Shuimoshicang Agricultural Products Co., Ltd, Songyang, 323499, Zhejiang, China✉ Corresponding author: wjianhua2009@vip.qq.comMedicinal Plant Research, 2026, Vol.16, No.4 doi: [10.5376/mpr.2026.16.0016](https://doi.org/10.5376/mpr.2026.16.0016)

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Abstract *Fritillaria thunbergii* Miq. is an important medicinal plant resource in China, and the quality of its bulbs directly affects medicinal yield and the accumulation of active compounds. With the expansion of the cultivation industry, traditional bulb propagation methods have shown limitations, including low propagation efficiency, unstable seed source quality, and insufficient capacity for large-scale supply, which restrict the sustainable development of the *F. thunbergii* industry. This review focuses on bulb propagation techniques and large-scale production applications of *F. thunbergii*. The biological characteristics, bulb formation patterns, and major factors affecting bulb quality were systematically summarized, and key propagation technologies, including conventional bulb division, bulb scale propagation, and tissue culture, were reviewed. Furthermore, methods for establishing standardized seed source systems were discussed from the perspectives of bulb morphological traits, nutrient accumulation, physiological indicators, and quality evaluation. The application of regionalized propagation models, integration of bulb propagation with storage and production technologies, and the role of high-quality bulbs in promoting industrial development were also analyzed. In response to current challenges, including insufficient propagation efficiency, incomplete quality evaluation systems, and limited application of digital management, future development strategies involving rapid multiplication technology optimization, standardized quality control, and precision production management were proposed. This study provides theoretical references and technical support for high-quality seed bulb production, large-scale cultivation, and sustainable development of the *F. thunbergii* industry.

Keywords *Fritillaria thunbergii*; Bulb propagation; Bulb reproduction; Tissue culture; Large-scale production**1 Introduction**

Fritillaria thunbergii Miq., the source plant of *Fritillariae Thunbergii* Bulbus (Zhebeimu), is a long-used traditional Chinese medicinal species whose dried bulbs are valued for antitussive, expectorant, anti-inflammatory, anti-ulcer, analgesic, and other pharmacological activities (Nile et al., 2021). It is one of the officially recognized medicinal *Fritillaria* sources in the Chinese Pharmacopoeia and is widely cultivated in southeastern and east-central China, especially in Zhejiang, Jiangsu, Anhui, Hunan, and major authentic-production areas such as Ningbo and Pan'an (He et al., 2021; Liu et al., 2025). Because its bulbs contain diverse bioactive constituents, particularly steroidal alkaloids such as peimine and peiminine, *F. thunbergii* has become one of the representative medicinal bulbs within the Beimu market and an important component of the "Zhejiang Eight Flavors" geo-authentic medicinal industry (Huang et al., 2024). At the same time, the broader *Fritillaria* market has substantial and persistent demand, and artificial cultivation has been recognized as a necessary strategy to protect wild resources and relieve the contradiction between supply and demand in medicinal *Fritillaria* industries. Although *F. thunbergii* itself has a long history of commercial bulb reproduction in China, with bulb propagation technology adopted centuries ago, the contemporary industry still faces unstable quality and yield, inefficient cultivation links, and market pressures that increasingly demand standardized, high-quality propagation materials for sustainable large-scale production (Qu et al., 2022).

The quality of propagation bulbs directly influences field establishment, vegetative growth, resistance performance, final yield, and the formation of medicinal quality in *F. thunbergii*. In medicinal production,

excessive pursuit of biomass or yield can reduce the accumulation of active ingredients and lower the proportion of bulbs meeting commercial standards, showing that productive performance and medicinal quality must be coordinated rather than treated separately (Liu et al., 2025). Recent cultivation studies further show that bulb yield and alkaloid quality are highly sensitive to agronomic conditions: organic fertilizer increased peimine and peiminine contents to 0.060 3% and 0.050 2%, respectively, while producing a yield of 2.70 kg/m², and potassium supply above 40 kg K₂O/hm² allowed bulb quality to meet Pharmacopoeia standards while 108.4~128.0 kg K₂O/hm² optimized yield. Shading likewise increased active ingredient accumulation by about 11.7% to 20.71%, but reduced bulb biomass by about 11.3% to 17.24%, whereas combined shading and potassium application partly alleviated the biomass penalty while improving medicinal constituent accumulation and pharmacological activity. These findings indicate that bulb quality is not merely a matter of size; it reflects a complex integration of physiological vigor, nutrient status, environmental adaptation, and secondary metabolite biosynthesis, including key pathways linked to ABA signaling and steroidal alkaloid accumulation. Consistent with this, variety differences also translate into propagation and production differences: the cultivar “Zhebei 3” showed a bulb proliferation rate of 261.2%, a propagation coefficient of about 1:2.6, higher yield, higher peimine plus peiminine content, and better resistance to bulb stem soft rot than controls (Jiang et al., 2019).

For *F. thunbergii*, securing high-quality propagation materials is especially important because conventional reproduction is inherently slow and faces biological and sanitary constraints. Across *Fritillaria*, bulb reproduction is the main domestication method and usually requires about 100 days to 3 years, whereas sexual reproduction by seed often takes more than five years, making rapid multiplication of elite materials difficult. In bulbous plants, natural propagation rates are generally low, only a few daughter bulbs are produced annually, and using limited mother-bulb material can increase the risk of transmitting viral and fungal infections to progeny bulbs (Marković et al., 2021). This has driven the development of rapid propagation and micropropagation technologies in *Fritillaria*, which are important not only for commercial multiplication but also for germplasm conservation and the production of healthy starting materials. For *F. thunbergii* specifically, high-frequency in vitro bulblet regeneration has already been achieved from bulb-scale explants, with an optimum of 13.7 bulblets per scale section on MS medium containing 1.62 µmol/L NAA and 4.65 µmol/L KN, leaf and root formation within 12 weeks, and 100% sprouting after transplanting when bulblets exceeded 10 mm following 5 weeks of cold treatment. Established tissue-culture systems for *F. thunbergii* and other medicinal *Fritillaria* species show that hormone composition, light, temperature, and dormancy release are key technical nodes, while regenerated bulbs may even accumulate more alkaloids than wild bulbs, though consistency in morphology and phytochemical profile remains a barrier to marketization (Qu et al., 2022).

Against this background, research on bulb propagation techniques of *F. thunbergii* should aim to integrate germplasm selection, healthy seed-bulb production, rapid multiplication, dormancy regulation, and quality-oriented cultivation into a scalable technical system for industrial application. Such research is significant because it can shorten propagation cycles, improve the multiplication coefficient of elite lines, stabilize field performance, and coordinate yield with medicinal quality, thereby addressing current bottlenecks in large-scale cultivation. It can also support sexual propagation and early seedling-bulb utilization, since seedling bulbs have been shown to reach the total alkaloid standard required by the Chinese Pharmacopoeia, providing a basis for expanding propagation pathways beyond traditional bulb splitting alone. In parallel, modern quality-evaluation tools, including HPLC fingerprinting and multicomponent quantification as well as hyperspectral imaging with deep learning, provide practical means for discriminating varieties, monitoring consistency, and strengthening standardized quality control of propagation materials and commercial bulbs. Therefore, systematic study of bulb propagation techniques and their large-scale production application is not only a technical need for improving the productivity and quality stability of *F. thunbergii*, but also a strategic requirement for safeguarding geo-authentic medicinal resources, enhancing industrial competitiveness, and promoting the sustainable development of the *F. thunbergii* industry.

2 Biological Characteristics and Foundation of Bulb Propagation in *Fritillaria thunbergii*

2.1 Growth and development characteristics and bulb formation patterns of *Fritillaria thunbergii*

Fritillaria thunbergii is a perennial bulbous medicinal plant whose commercial organ is the dried bulb, and artificial cultivation has long relied on the biology of bulb growth and renewal rather than on rapid seed-based turnover (He et al., 2021; Qu et al., 2022). In cultivated production, its growth cycle is distinctly seasonal: one field study reported planting in mid-September with sprouting the following season, while another experiment recorded October planting and emergence in February, indicating a clear autumn planting-winter dormancy-spring emergence rhythm (Liu et al., 2025). Variety traits modify this rhythm, as the cultivar “Zhebei 3” emerged early, senesced later, and showed an average growth period of about 100 days, longer than the comparison cultivars (Jiang et al., 2019). Bulb enlargement is concentrated in a relatively short developmental window, with rapid filling beginning 32 days after sprouting and full bulb growth requiring about 72 days, which helps explain why cultivation management during the expansion stage has disproportionate effects on final bulb size and propagation value.

Bulb formation in *F. thunbergii* follows the general geophyte pattern in which daughter bulbs arise from the mother bulb and then pass through dormancy before sprouting in the next cycle. Temperature is central to this pattern: high temperatures induce dormancy, whereas winter chilling breaks dormancy and promotes spring sprouting, and fritillary bulbs regenerated in vitro likewise fail to resume normal growth unless they receive low-temperature treatment (Marković et al., 2021). Evidence from *F. thunbergii* tissue culture matches this developmental requirement, because regenerated bulblets were cold-treated at 5°C for 5 weeks, and bulblets larger than 10 mm then achieved 100% sprouting after transplantation. At the molecular level, bulb development also appears to be linked to hormonal regulation, as ABA-related signaling was associated with bulb yield and the gene *FtGGPS* was implicated in coordinating GA and ABA levels during bulb development, providing a mechanistic basis for differences in bulb expansion and propagation coefficient among cultivars (Huang et al., 2024; Xu et al., 2026).

2.2 Propagation methods and bulb development processes of *Fritillaria thunbergii*

The propagation of *F. thunbergii* mainly includes vegetative bulb reproduction, seed reproduction, and in vitro rapid propagation, with bulb reproduction historically serving as the principal domestication method. Across *Fritillaria*, bulb reproduction generally requires about 100 days to 3 years, whereas seed reproduction usually takes more than five years, which is why bulbs are commonly used as planting material in production systems seeking faster turnover (Qu et al., 2022). Even so, seed-based pathways still matter for breeding and propagation diversification, and an early study showed that total alkaloid content in *F. thunbergii* seedling bulbs already met the Pharmacopoeia standard, supporting the practical value of sexual propagation for future production. Conventional vegetative propagation remains biologically constrained because only a few daughter bulbs can be produced from each mother bulb each year, and repeated use of mother bulbs can also transmit viral and fungal infections to progeny bulbs (Marković et al., 2021).

For these reasons, tissue culture has become a key supplementary route for large-scale propagation of *F. thunbergii* (Qu et al., 2022). In vitro morphogenesis in fritillaries can be induced from bulbs, bulb scales, inflorescence parts, and embryos, and whole plants can be regenerated through bulblet formation or somatic embryogenesis. For *F. thunbergii* specifically, bulb-scale sections cultured on MS medium with 1.62 µM NAA and 4.65 µmol/L KN produced an optimum of 13.7 bulblets per explant, and these bulblets formed leaves and roots within 12 weeks under a 16 h light/8 h dark regime at 25°C. Other culture work found that combinations of 2,4-D and kinetin were more effective than NAA and BA for bulblet induction, that most bulbs formed from axillary buds of nodal explants, and that light culture outperformed dark culture for bulb formation, shoot growth, callusing, and rooting. Taken together, the developmental process of propagated bulbs in *F. thunbergii* can be summarized as explant induction, bulblet differentiation, root and shoot formation, dormancy establishment, low-temperature dormancy release, and transplant establishment, after which field bulb expansion determines whether the propagated material becomes productive seed bulbs or commercial medicinal bulbs (Marković et al., 2021).

2.3 Main factors affecting bulb quality formation in *Fritillaria thunbergii*

Bulb quality formation in *F. thunbergii* depends on the interaction of genotype, cultivation year, nutrient supply, light environment, and rhizosphere ecology, and quality must be understood as both biomass performance and accumulation of steroidal alkaloids such as peimine and peiminine (Nile et al., 2021). Genotypic differences are already evident in elite materials: “Zhebei 3” had a bulb proliferation rate of 261.2%, a propagation coefficient of about 1:2.6, higher yield, higher combined peimine and peiminine content, and better resistance to bulb stem soft rot than controls (Jiang et al., 2019). Cultivation duration also changes bulb output, because yield increased by 88% at two years and 189% at three years relative to one year, although the proportion of bulbs heavier than 5 g declined from 89% at one year to 77% at three years, indicating a trade-off between cumulative yield and size structure. Quality control studies further show that production origin and cultivation environment can shift chemical profiles, since Zhejiang samples clustered together whereas Nantong, Jiangsu material separated from them in HPLC fingerprinting analyses (He et al., 2021).

Nutrient and ecological management have especially strong effects on medicinal quality formation. Fertilization influences both yield and quality, and organic fertilizer gave the best combined performance in one recent study, with peimine and peiminine contents of 0.060 3% and 0.050 2% and a yield of 2.70 kg/m² (Huang et al., 2024). Potassium is particularly important: bulb quality met Pharmacopoeia standards above 40 kg K₂O/hm², yield rose to a plateau above about 120 kg K₂O/hm², and the optimal K range for yield was 108.4~128.0 kg K₂O/hm². Shading increased active ingredient accumulation by about 11.7~20.71% but reduced bulb biomass by about 11.3~17.24%, whereas combining shading with potassium partly offset the biomass penalty and enhanced steroidal alkaloid accumulation and pharmacological activity (Liu et al., 2025). Soil-centered strategies also matter: compost and manure increased yield and marketable proportion in older fertilizer trials, while recent understory work showed that biochar plus organic fertilizer improved yield, total alkaloids, soil nutrients, beneficial microbes, and overall rhizosphere function (Liu et al., 2026). At the mechanistic level, bulb quality formation appears to involve both plant metabolic regulation and microecological mediation, including ABA signaling, FtFPS-linked steroidal alkaloid biosynthesis, and rhizosphere microbial groups positively associated with medicinal component accumulation (Huang et al., 2024).

3 Key Technologies for Bulb Propagation of *Fritillaria thunbergii*

3.1 Conventional bulb division propagation technology and its application characteristics

Conventional bulb division propagation of *Fritillaria thunbergii* is based on the natural renewal pattern of mother bulbs producing daughter bulbs, and this has long been the principal domestication and commercial reproduction route for the species (Li et al., 2019). In *Fritillaria* more broadly, vegetative multiplication through bulb splitting remains standard because seed propagation is slow and of limited practical value for production, with seedlings requiring many years to develop usable bulbs. Evidence from the related medicinal species *F. cirrhosa* provides a comparative example of in vitro bulblet regeneration (Figure 1) (Chang et al., 2020; Marković et al., 2021; Thakur et al., 2024). The main advantage of this method is that it is simple, field-adapted, and does not require specialized facilities, so it remains suitable for traditional production bases and routine nursery multiplication of locally adapted germplasm (Hasnain et al., 2022; Bhardwaj et al., 2025). Its practical application also depends strongly on varietal traits, because elite cultivars differ in multiplication coefficient, bulb vigor, and disease resistance, as shown by “Zhebei 3,” which had a bulb proliferation rate of 261.2%, a propagation coefficient of about 1:2.6, and better resistance to bulb stem soft rot than the controls.

The main limitation of conventional division is its inherently low propagation rate, since only a few daughter bulbs are produced from each mother bulb annually, making it difficult to meet the demand for rapid expansion of standardized planting materials (Chang et al., 2020). This method also carries a sanitary risk, because repeated use of mother bulbs can transfer viral and fungal infections to daughter bulbs and gradually reduce population health. In addition, conventional vegetative propagation in bulbous crops is often economically inefficient because development is slow and commercial profitability may require several years (Marković et al., 2021). For that reason, conventional division in *F. thunbergii* is best understood as a reliable but slow baseline technology, most

useful for maintaining elite field materials and supplying initial propagules, while large-scale industrial multiplication increasingly requires combination with scale propagation and tissue culture (Bhardwaj et al., 2025).

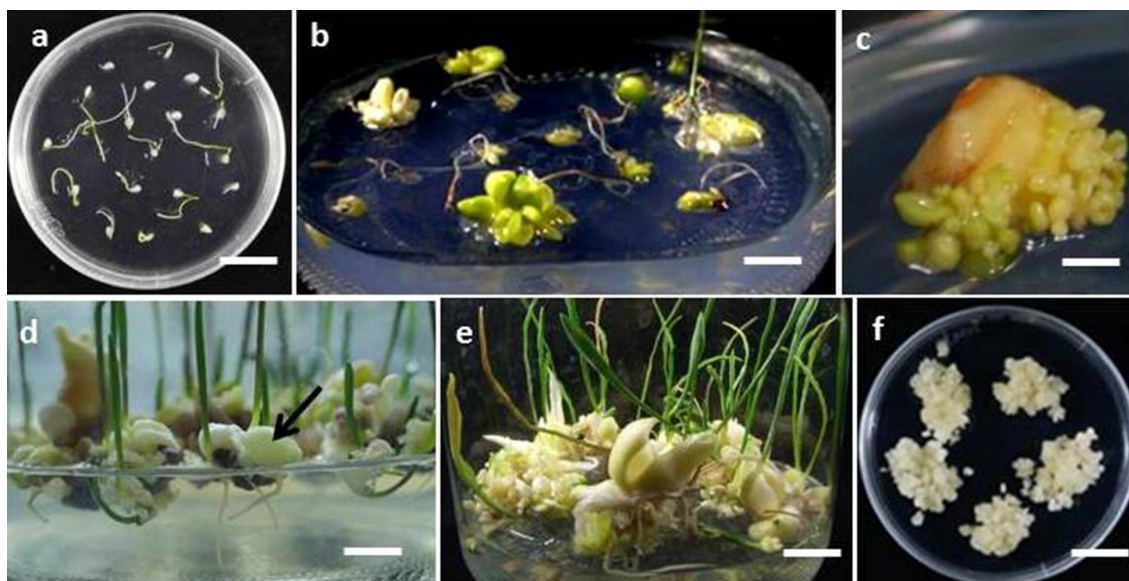


Figure 1 *F. cirrhosa* (Adopted from Chang et al., 2020)

Image caption: a: *In vitro* seed germination on MS basal medium supplemented with BA (1.0 mg/L), NAA (0.4 mg/L) after incubation for 20 days (bar=1.8 cm). b: Bulblet and callus formation in 4 month old seedlings growing on 1/2X MS basal medium supplemented with sucrose (2.5%), GPP (0.4%) (bar=1.24 cm). c, d, e: Bulblet regeneration from bulb sections after 2 months of culture (c, bar=0.25 cm); at the end of subculture 2 (6 months) (d, bar=0.9 cm, arrow showing a bulblet); and at the end of subculture 5 (12 months) (e, bar=1.5 cm); f: Callus growth under darkness (bar=1.8 cm) (Adopted from Chang et al., 2020)

3.2 Scale propagation and rapid multiplication technology using bulb scales and bulblets

Scale propagation uses bulb scales or scale sections as explants to induce direct bulblet formation, and it is one of the most important rapid multiplication routes developed for *F. thunbergii* (Chang et al., 2020). In a classic *F. thunbergii* study, bulb-scale sections cultured on MS medium produced a high frequency of bulblets, with an optimum of 13.7 bulblets per scale section on medium containing 1.62 μ M NAA and 4.65 μ mol/L KN (Marković et al., 2023). Light and temperature are key to this process, because a 16 h light/8 h dark regime at 25°C produced better bulblet formation than continuous darkness (Pasternak and Steinmacher, 2024). Earlier culture-method work in *F. thunbergii* also showed that solid MS medium with 1.0 mg/L kinetin and 0.3 mg/L NAA outperformed liquid and suspension culture for bulblet formation and propagation rate, while activated charcoal and 1~2% mannitol further promoted bulbing and subsequent bulblet growth.

The application value of scale propagation lies in its ability to raise multiplication efficiency while using limited source material, and in fritillaries generally bulb scales are among the most effective explants for morphogenesis and rapid regeneration. This route also reduces pressure on whole mother bulbs, and *in vitro*-derived bulbs or bulb parts can lower contamination and reduce destructive harvesting of source populations (Chang et al., 2020). However, scale propagation remains sensitive to plant growth regulator combinations and explant source, because different auxin-cytokinin balances can shift cultures toward bulblet formation, shoot proliferation, or somatic embryogenesis rather than a single uniform response (Marković et al., 2023). As a result, scale-based rapid multiplication is highly useful for nursery expansion of seed bulbs and for bridging field production with laboratory propagation, but it still requires precise control of medium composition, explant physiological state, and dormancy management before it can be stably translated into year-round industrial production (Marković et al., 2021).

3.3 Tissue culture propagation and rapid expansion technology for high-quality planting materials

Tissue culture propagation provides the most promising route for rapid expansion of high-quality *F. thunbergii* planting materials because it enables aseptic, season-independent, and large-scale clonal multiplication from small

explants (Hamdeni et al., 2022; Mehbub et al., 2022; Thakur et al., 2024). More generally, high-quality planting material for horticultural production should be genetically uniform, physiologically vigorous, and pathogen-free, and tissue culture is valued precisely because it can reduce disease transmission while accelerating multiplication (Bhardwaj et al., 2025). In *F. thunbergii*, micropropagation systems have been established from bulblet scales, stems, node-buds, and shoot tips, and explant age strongly affects response. Node-bud and young stem tissues can outperform bulb-scale segments, with young tissues below 3 cm shoot length showing stronger regeneration and a maximum multiplication rate of about 20-fold. Organogenic routes are also explant-specific, because many bulbs in culture are formed directly from axillary buds, and favorable kinetin concentrations for bulblet induction vary by source tissue from 1.0 to 5.0 mg/L.

The industrialization of tissue-culture propagation depends not only on multiplication, but also on stable dormancy release, acclimatization, genetic fidelity, and cost control (Hamdeni et al., 2022; Bhardwaj et al., 2025). In fritillary bulbs, dormancy is a major bottleneck, and low-temperature pretreatment is often essential for sprouting; in *F. thunbergii*, bulblets chilled at 5°C for 5 weeks and larger than 10 mm achieved 100% sprouting after transplantation. Broader fritillary evidence shows that short cold treatments can markedly improve sprouting, whereas prolonged chilling may reduce sprouting percentage, underscoring the need for calibrated dormancy-breaking protocols (Marković et al., 2021). For large-scale production of high-quality seed bulbs, current research also emphasizes species-specific protocol optimization rather than uniform historical recipes, along with early monitoring of somaclonal variation and the use of improved systems such as low-cost media strategies, molecular diagnostics, and bioreactor-supported propagation (Pasternak and Steinmacher, 2024).

4 Bulb Quality Evaluation and Standardized Production System of *Fritillaria thunbergii*

4.1 Evaluation of bulb morphological characteristics and external quality

The external quality evaluation of *Fritillaria thunbergii* bulbs should begin with macroscopic observation, because raw-material assessment in herbal medicines routinely starts from organoleptic and visual inspection of identity, appearance, and abnormalities (Wang et al., 2023). For *Fritillaria* bulbs specifically, morphological traits differ significantly among cultivated species, and these differences are useful for source identification and medication safety control. Among measured external traits, the short diameter of the bulb was identified as the most important indicator for distinguishing species, indicating that bulb size and shape should be core descriptors in *F. thunbergii* grading. Recent work on *Fritillariae thunbergii* Bulbus further argues that traditional morphological assessment should not be discarded, but integrated with chemical profiling because external traits can correlate with intrinsic quality parameters (Zhang et al., 2026).

In practice, morphological evaluation of *F. thunbergii* bulbs should include size uniformity, transverse and longitudinal diameter, fullness, surface integrity, color, and freedom from visible rot or blight lesions. This is especially important because bulb diseases can rapidly destroy commercial quality: in Zhejiang fields, blight incidence reached 20~25%, with early browning of the stalk followed by complete bulb rot within days (Xu et al., 2022). External morphology also reflects internal structural differences in storage materials, since *Fritillaria* starch granules vary in size and shape across species, and *F. thunbergii* starch granules ranged from 5 to 30 µm, supporting the view that bulb appearance is linked to underlying compositional traits. Because production origin affects quality, morphological assessment should also be interpreted together with provenance information, as Zhejiang and non-Zhejiang materials can differ enough to require origin authentication in market standardization (Zhang et al., 2026).

4.2 Evaluation of nutrient accumulation and physiological indicators of bulbs

The internal quality of *F. thunbergii* bulbs is determined primarily by the accumulation of alkaloids, carbohydrates, amino acids, nucleosides, and related metabolites, with steroidal alkaloids remaining the most important medicinal components (Nile et al., 2021; Cheng et al., 2023). Quantitative analysis of peimine and peiminine is therefore central to bulb evaluation, and cultivation studies show that these compounds respond strongly to management conditions. Organic fertilizer produced bulbs with peimine and peiminine contents of 0.060 3% and 0.050 2%, together with a yield of 2.70 kg/m² (Huang et al., 2024). Potassium fertilization increased

bulb yield, peimine and peiminine content, and net income by 6.4~23.8%, 2.1~26.6%, and 47.7~205.4%, respectively, and both yield and quality were positively correlated with potassium accumulation in underground parts. These findings show that nutrient accumulation indicators should include not only active alkaloid content, but also mineral accumulation and biomass partitioning to bulbs (Sui et al., 2021).

Physiological evaluation should also recognize that bulb quality is spatially heterogeneous within the bulb and dynamically shaped by ecological regulation. Multi-omics analysis showed that the outer scale layers were enriched in total alkaloids, peimine, and flavonoids by about 1.18-fold, 1.28-fold, and 1.24-fold, whereas the inner layers accumulated more sucrose and starch, at 1.37-fold and 2.18-fold of the outer layers (Wang et al., 2026). Shading increased active ingredient content by about 20.71% but reduced biomass by about 17.24%, while potassium under shading improved both medicinal substance accumulation and pharmacological performance, with the K2S treatment giving the best antitussive, expectorant, and anti-inflammatory effects (Liu et al., 2025). Biocontrol-agent application likewise significantly enhanced plant growth and increased steroidal alkaloids, including peimine and peiminine, while metabolomic profiling identified 48 alkaloids in treated and control bulbs (Cheng et al., 2023). Taken together, nutrient and physiological evaluation of *F. thunbergii* bulbs should combine targeted alkaloid quantification, carbohydrate and starch assessment, and responsiveness to cultivation conditions that affect biosynthesis pathways such as ABA signaling, oxidative phosphorylation, and alkaloid-related genes (Huang et al., 2024; Liu et al., 2025).

4.3 Establishment of bulb grading standards and quality control systems

A standardized production system for *F. thunbergii* bulbs should extend from raw-material evaluation to finished-product control, because herbal medicine quality cannot be assured by end-point testing alone. Standardization in herbal medicines is fundamentally the assurance of identification, quality, and purity across the whole life cycle, and current guidance emphasizes pharmacopoeial criteria, WHO-style standardization parameters, and in-process controls rather than isolated appearance checks. For *F. thunbergii*, a practical bulb grading system should therefore combine external grade descriptors with internal quality markers. Morphological descriptors should include bulb diameter, mass, uniformity, integrity, and disease-free status, while chemical grade descriptors should include peimine, peiminine, and broader alkaloid fingerprints (He et al., 2021; Zhang et al., 2026). The concept of quality markers (Q-markers) is particularly useful here, because it provides a basis for linking raw bulbs, processing stages, and final medicinal efficacy in one traceable system.

The quality control system should also specify the methods used at each stage. Raw bulbs should undergo documental, organoleptic, physicochemical, and microbiological evaluation, supported by macroscopic and microscopic examination, chromatographic analysis, and contaminant testing for heavy metals and other hazards. For chemical authentication and consistency control, HPLC-ELSD fingerprinting with multicomponent quantification has already shown that Zhejiang samples cluster together while some Jiangsu materials separate, indicating that fingerprint analysis can discriminate origin-related quality variation (He et al., 2021). LC-MS combined with chemometrics can further differentiate Zhejiang from non-Zhejiang materials and identify 11 alkaloid markers significantly correlated with external morphology, which supports a more rigorous origin-specific grading framework (Zhang et al., 2026). At the production level, standardized protocols should be implemented under propagation and cultivation, with proper documentation, personnel training, hygiene, SOPs, and traceability from bulb propagation to processing, because only this full-chain approach can stabilize the composition, safety, and clinical consistency of *F. thunbergii* products (Wang et al., 2023).

5 Large-scale Production Models and Applications of *Fritillaria thunbergii* Bulbs

5.1 Regionalized bulb propagation production models based on cultivation conditions

Regionalized production models for *Fritillaria thunbergii* bulbs should be built around the species' established cultivation belt in southeastern and central-eastern China, especially Zhejiang, Jiangsu, and Anhui, because production origin and local cultivation environment measurably affect both bulb quality and industrial suitability (He et al., 2021). Zhejiang remains the core region for geo-authentic production, and elite cultivars such as "Zhebei 3" have shown stable characters, higher yield, stronger disease resistance, and suitability for planting in

Zhejiang Province, supporting a cultivar-by-region matching strategy rather than a uniform national model (Jiang et al., 2019). Field evidence also shows that cultivation models must be adjusted to local edaphic conditions, because the major coastal production regions are characterized by relatively high soil salinity, while understory systems face poor fertility constraints that require different soil-improvement strategies (Liu et al., 2025; Liu et al., 2026). More broadly, *Fritillaria* domestication research supports region-specific artificial cultivation, careful survey of growth environments, and integration of bulb and tissue-culture propagation with seed systems where appropriate (Figure 2) (Qu et al., 2022).



Figure 2 Artificial and imitating wild cultivation of *F. thunbergii* (Adopted from Qu et al., 2022)

Image caption: (A): The large-scale artificial cultivation of *F. thunbergii* in Zhangshui town of Ningbo in Zhejiang Province of China; (B): The imitating wild cultivation of *F. thunbergii* in Siming Mountain in Zhejiang Province of China; (C): The *F. thunbergii* Flos; (D): The bulb of *F. thunbergii* by artificial cultivation, Bar: 1 cm; (E): The bulb of *F. thunbergii* by the imitating wild cultivation; Bar: 1 cm (Adopted from Qu et al., 2022)

Within these regional models, production conditions should be optimized for the local balance between yield and medicinal quality rather than yield alone. In Pan'an, Zhejiang, organic fertilizer produced the best combined outcome, with peimine and peiminine contents of 0.060 3% and 0.050 2% and a yield of 2.70 kg/m², indicating that fertilization schemes can be regionally standardized around local soil conditions (Huang et al., 2024). Potassium management is another core regional variable, because field studies across two cultivars showed that potassium fertilization increased bulb yield, bulb quality, and net income, with 120 kg K₂ O/hm² emerging as the best overall rate when economic and environmental benefits were considered (Sui et al., 2021). In areas using ecological or understory cultivation, biochar plus organic fertilizer appears especially suitable, because it improved yield, total alkaloids, soil nutrient status, and rhizosphere microbial structure under forest conditions (Liu et al., 2026). In contrast, where light is excessive or medicinal quality is prioritized, regional ecological regulation by shading combined with potassium can increase active ingredients while partly offsetting the biomass penalty of shading alone, which supports differentiated production models for medicinal bulbs versus propagation bulbs (Liu et al., 2025).

5.2 Integration of bulb propagation, storage, and scalable production technologies

Large-scale production depends on linking rapid propagation with reliable storage and transplant establishment. Conventional bulb reproduction remains the main domestication method in *Fritillaria*, but its multiplication cycle ranges from about 100 days to 3 years, so industrial systems increasingly need to combine field bulb propagation with in vitro multiplication to supply enough healthy seed bulbs (Qu et al., 2022). In *F. thunbergii*, bulb-scale culture already provides a workable expansion route, producing an optimum of 13.7 bulblets per explant on solid MS medium, with leaf and root formation within 12 weeks. More generally across *Fritillaria*, bulb scales are among the most effective explants for large-scale morphogenesis, and tissue culture can provide many homogeneous plants year-round from small amounts of starting material (Marković et al., 2023). This propagation module can be paired with regional field nurseries, where elite bulbs are further enlarged under standardized fertilizer and spacing regimes before entering commercial production (Liu et al., 2025).

Storage and post-propagation handling are equally important because dormancy is a major bottleneck in bulb multiplication systems. Bulbs produced in vitro enter dormancy and must undergo controlled low-temperature treatment before uniform sprouting in the next vegetation cycle (Marković et al., 2021). For *F. thunbergii*, bulblets chilled at 5°C for 5 weeks and larger than 10 mm achieved 100% sprouting after transplantation, showing that storage protocols can be standardized around bulb size and chilling duration. Related *Fritillaria* studies also show that bulbs are often stored at 4°C before regeneration or acclimatization to improve regeneration capacity and dormancy breaking, while successful bulblet systems depend on low-temperature pretreatment, rooting, and ex vitro enlargement (Muraseva and Novikova, 2018; Marković et al., 2023). Direct evidence for mechanized production in *F. thunbergii* is limited in the supplied literature, but the available studies consistently support the technological logic of integrating standardized propagules, cold-chain dormancy management, uniform field planting, and scalable acclimatization, which are the biological prerequisites for later mechanized transplanting, harvesting, grading, and handling (Sharma et al., 2023).

5.3 Promoting the development of the *Fritillaria thunbergii* industry through the application of high-quality bulbs

Applying high-quality bulbs can directly strengthen the *F. thunbergii* industry because the crop faces high market demand but persistent production bottlenecks related to unstable yield, reduced medicinal quality under yield-oriented cultivation, and inefficient expansion systems (Sui et al., 2021; Liu et al., 2025). High-quality bulbs should be understood as bulbs that combine strong propagation performance, disease resistance, and high alkaloid accumulation, as exemplified by “Zhebei 3,” whose average yield reached 5 095.5 kg/hm², bulb proliferation rate 261.2%, propagation coefficient about 1:2.6, and peimine plus peiminine content 0.172 2% (Jiang et al., 2019). High-quality starting bulbs also support varietal upgrading and molecular breeding, because bulb development differs among cultivars and is associated with genes such as *FtGGPS*, which regulates bulb development through GA and ABA dynamics (Xu et al., 2026). At the germplasm level, breeding methods that shorten selection cycles and improve heat resistance, propagation coefficient, and absolute yield can further expand the supply base for industrial seed bulbs.

Industrial promotion also depends on proving and preserving product quality from bulb to market. *F. thunbergii* bulbs have broad pharmacological value and are used medicinally for cough, inflammation, bronchitis, and related disorders, so stable alkaloid quality is central to industry credibility and market expansion (Nile et al., 2021; Liu et al., 2025). Quality control systems based on HPLC-ELSD fingerprinting and multicomponent analysis can distinguish production origins and support standardized evaluation of commercial bulbs and propagation materials (He et al., 2021). Artificial cultivation and in vitro propagation also have strategic value beyond productivity, because they reduce pressure on wild *Fritillaria* resources, improve supply security, and fit the broader trend toward sustainable domestication of medicinal bulb crops (Qu et al., 2022). Therefore, the large-scale application of high-quality bulbs is not only a technical measure for raising yield and quality, but also a core pathway for strengthening regional brands, stabilizing medicinal standards, and promoting the sustainable modernization of the *F. thunbergii* industry.

6 Current Challenges and Future Development Directions

6.1 Improving bulb propagation efficiency and large-scale supply capacity

A central constraint on the large-scale supply of *Fritillaria thunbergii* bulbs is that conventional vegetative propagation remains inherently slow, while seed reproduction takes several years and therefore cannot rapidly expand elite planting material. This supply problem is economically important because market demand for dried *F. thunbergii* bulbs is high, yet production systems still struggle to deliver stable yield and quality at industrial scale (Sui et al., 2021; Cheng et al., 2023; Liu et al., 2025). The most immediate development direction is therefore to integrate conventional seed-bulb propagation with rapid multiplication systems based on bulb scales and tissue culture, which can greatly raise multiplication efficiency from limited source material (Marković et al., 2021). In *F. thunbergii*, bulb-scale culture already supports this transition, because scale sections on optimized MS medium produced 13.7 bulblets per explant and formed leaves and roots within 12 weeks.

Improving propagation efficiency also requires solving the linked bottlenecks of dormancy release, sanitary control, and field enlargement. In fritillaries, in vitro bulbs enter dormancy and cannot resume normal growth without low-temperature treatment, making dormancy management one of the main limiting steps in rapid multiplication (Marković et al., 2021). For *F. thunbergii*, cold treatment at 5°C for 5 weeks enabled 100% sprouting of bulblets larger than 10 mm, showing that post-culture handling can be standardized to improve transplant success. Sanitary risk is another obstacle, because repeated use of mother bulbs can transmit viral and fungal infection to daughter bulbs, while field blight caused by *Fusarium oxysporum* has already reached 20%~25% incidence in Zhejiang and can rot whole bulbs within days (Xu et al., 2022). Future large-scale supply systems should therefore combine pathogen-free micropropagation, resistant cultivar selection, and agronomic optimization, especially potassium and organic nutrient management, which increase yield, quality, and economic return while supporting more reliable bulb enlargement in the field (Sui et al., 2021; Huang et al., 2024).

6.2 Improving bulb quality evaluation and standardization systems

A major challenge in bulb standardization is that *F. thunbergii* quality varies with geographic origin, cultivation conditions, and post-harvest handling, which makes it difficult to define a single stable quality benchmark (Wang et al., 2023). Current evidence shows that origin authentication remains necessary: Zhejiang samples clustered together in HPLC-ELSD fingerprint analysis, whereas material from Nantong, Jiangsu separated from Zhejiang samples, likely because of different cultivation environments (He et al., 2021). A stronger future standardization system should therefore integrate external morphology with internal chemistry instead of relying on either alone (Zhang et al., 2026). This is feasible because bulb morphology and chemistry are both discriminative: among cultivated *Fritillaria* species, short bulb diameter was the most informative morphological identifier, while alkaloid and saponin contents helped distinguish morphologically similar materials.

Future quality evaluation should also move beyond a small number of marker compounds toward multicomponent and spatially resolved assessment. LC-MS chemometrics differentiated Zhejiang from non-Zhejiang *Fritillariae Thunbergii Bulbus* and identified 11 alkaloids as characteristic markers that correlated significantly with external morphological traits (Zhang et al., 2026). Processing studies further show that quality markers are not fixed across all product forms, because different processing methods altered steroidal alkaloid composition and revealed zhebeininolide and imperline-3-β-D-glucoside as new control indicators (Shi et al., 2022). Quality standards should also account for within-bulb heterogeneity, since the outer bulb layers are enriched in total alkaloids, peimine, and flavonoids, whereas the inner layers accumulate more sucrose and starch (Wang et al., 2026). The most useful standardization framework is therefore a full-chain system linking morphology, fingerprinting, multicomponent quantification, origin tracing, and process control, consistent with broader herbal-medicine guidance that calls for molecular authentication, real-time monitoring, and shared industry standards across cultivation, harvesting, processing, and quality control (Wang et al., 2023).

6.3 Prospects of digital management and precision production technologies

Digital management and precision production technologies offer a realistic next step for *F. thunbergii* because the crop's quality and yield respond strongly to local variation in nutrients, light, disease pressure, and soil microecology (Huang et al., 2024; Liu et al., 2026). Precision agriculture research shows that IoT and AI can support real-time monitoring and data-driven decision-making, with soil, optical, and stress sensors already being used to optimize irrigation, fertilization, and pest management in crop systems (Miller et al., 2025; Mansoor et al., 2025). For *F. thunbergii*, this approach is especially relevant because potassium status can already be diagnosed dynamically through a potassium nutrition index based on leaf K concentration, providing a clear entry point for sensor-assisted nutrition management. Digital management could also improve ecological cultivation strategies by enabling site-specific regulation of shading and fertilization, which is important because shading raises active ingredient content but reduces biomass, while potassium under shading partly restores yield and improves medicinal performance (Liu et al., 2025).

The main future direction is to connect sensing, modeling, and field operations into integrated production platforms. Remote sensing and UAV-based systems are already widely used in precision agriculture for crop

monitoring, nutrient management, disease detection, and yield prediction, although performance still depends on image resolution, growth stage, and environmental conditions (Sishodia et al., 2020). These tools could support *F. thunbergii* by enabling earlier disease detection, more reproducible field diagnosis, and simpler decision workflows for bulb fields, where current disease losses can be rapid and severe (Xu et al., 2022). Broader IoT work suggests that future systems will likely include digital twins, 5G or LPWAN-enabled connectivity, scalable sensor platforms, and AI-assisted prediction, but adoption will depend on lowering costs, improving usability, and addressing data ownership and cybersecurity concerns (Mansoor et al., 2025). In *F. thunbergii*, the long-term goal should be a precision production system that links propagation batches, storage conditions, nutrient diagnosis, disease warning, and quality fingerprint data, so that high-quality bulbs can be produced with greater consistency, lower waste, and stronger traceability across the full industrial chain (Wang et al., 2023; Liu et al., 2026; Zhang et al., 2026).

7 Conclusion

Bulb propagation remains the fundamental production pathway for *F. thunbergii*, because bulb reproduction has historically been the main domestication method in *Fritillaria*, has been commercially practiced in China for centuries, and is much faster than seed-based reproduction, which generally requires more than five years. At the same time, conventional vegetative propagation alone cannot meet modern industrial demand, because only a few daughter bulbs are produced annually from each mother bulb, conventional propagation is economically slow, and infected mother bulbs can transmit viral or fungal problems to progeny. The practical solution supported across studies is to combine field bulb propagation with rapid in vitro multiplication, since bulb-scale culture in *F. thunbergii* can produce an optimum of 13.7 bulblets per explant within 12 weeks, while young stem or node-bud explants can reach about 20-fold multiplication under suitable kinetin conditions. Stable production also depends on cultivar improvement and physiological regulation, as “Zhebei 3” showed higher yield, a bulb proliferation rate of 261.2%, a propagation coefficient of about 1:2.6, and stronger soft-rot resistance, while mechanistic work indicates that genes such as *FtGGPS* and ABA- and GA-related regulation are involved in bulb development and yield formation.

A standardized propagation system is necessary because *F. thunbergii* quality is highly sensitive to cultivation conditions, nutrient supply, geographic origin, and bulb developmental status. Fertilization studies show that standardization can improve both output and medicinal quality: organic fertilizer increased yield to 2.70 kg/m² while producing high peimine and peiminine contents, potassium fertilization increased bulb yield, quality, and net income, and an optimal K range of about 108.4–128.0 kg K₂ O/hm² or a practical target of 120 kg K₂ O/hm² was repeatedly supported. Standardization must also extend to quality evaluation, because HPLC-ELSD fingerprinting distinguished *F. thunbergii* from related species and showed clustering among Zhejiang samples, while LC-MS chemometric analysis identified 11 alkaloid markers and linked external morphology with internal chemical quality. Together, these findings support a propagation standardization framework that integrates elite cultivar selection, seed-bulb grading, nutrient diagnosis through leaf K-based indices, and coordinated morphological and chemical assessment so that propagation materials and medicinal bulbs can be managed under the same quality logic.

Future development of the *F. thunbergii* industry will depend on technological innovation that simultaneously expands bulb supply, protects wild resources, and improves ecological and economic sustainability. Tissue culture and morphogenesis technologies are central to this transition because they enable year-round multiplication from small explants, can use bulb scales as highly effective starting material, and are suitable for large-scale propagation when hormone balance, explant type, and dormancy management are optimized. Dormancy release remains a key technical bottleneck, but cold treatment at 5°C for 5 weeks enabled 100% sprouting of *F. thunbergii* bulblets larger than 10 mm, showing that propagation, storage, and transplant establishment can be linked into a controllable production chain. Sustainability-oriented innovations are also expanding beyond classical propagation, because biochar plus organic fertilizer improved understory yield, total alkaloids, soil nutrients, and rhizosphere microbial structure, shading plus potassium increased active ingredient accumulation while mitigating

biomass loss, and endophytic bacteria from *F. thunbergii* showed potential for nutrient promotion and biocontrol against *Fusarium* pathogens. Overall, the most promising path is an integrated system that combines rapid propagation, standardized quality evaluation, and ecological precision cultivation, thereby supporting the large-scale, high-quality, and sustainable modernization of *F. thunbergii* production.

Conflict of Interest Disclosure

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

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Review and Progress

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Evaluation of the Effects of Water and Fertilizer Management on Fruit Yield and Quality Formation in *Rubus chingii*

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Abstract This review evaluates the effects of water and fertilizer management on fruit yield and quality formation in *Rubus chingii* Hu, aiming to provide a theoretical basis for high-quality cultivation and industrial production of *R. chingii*. As an important medicinal and edible plant resource, *R. chingii* fruits contain abundant flavonoids, phenolic compounds, terpenoids, ellagic acid, kaempferol-3-O-rutinoside, and other bioactive constituents, exhibiting high medicinal value and development potential. However, current production still faces challenges including unstable yield, significant variation in fruit quality, and inconsistent accumulation of medicinal active compounds. This study systematically analyzed the effects of water supply, nitrogen-phosphorus-potassium nutrient management, and water-fertilizer coupling regulation on plant growth, fruit yield formation, fruit quality characteristics, and bioactive compound accumulation in *R. chingii*. Evidence from *R. chingii* and related fruit crops suggests that enhanced photosynthetic capacity and water-use efficiency, and provided sufficient material resources for fruit development. Balanced nitrogen, phosphorus, and potassium application optimized plant nutritional status, promoted biomass accumulation, and improved fruit-setting capacity and yield performance. Integrated water-fertilizer regulation coordinated yield and quality improvement by regulating carbon assimilation, nutrient uptake and transport, and secondary metabolic pathways. Meanwhile, water and fertilizer conditions played important roles in regulating fruit appearance quality, sugar-acid composition, nutritional quality, and the accumulation of medicinal active compounds such as flavonoids and phenolic compounds. Current research on *R. chingii* water-fertilizer management still faces limitations, including insufficient understanding of water and nutrient requirements at different growth stages, incomplete technical systems and production standards, and limited knowledge of the mechanisms underlying the coordinated improvement of yield and quality. Future studies should integrate cultivar characteristics, growth stages, and environmental conditions to establish precision water-fertilizer regulation models, promote integrated water-fertilizer technologies and smart agriculture approaches, and achieve coordinated improvements in yield, quality, and resource-use efficiency, thereby supporting standardized cultivation and sustainable industrial development of *R. chingii*.

Keywords *Rubus chingii*; Water and fertilizer management; Fruit yield; Quality formation; Precision regulation

1 Introduction

Rubus chingii Hu is a medicinal and edible plant with long-standing use in China and substantial potential for coordinated development of herbal medicine, functional foods, and fruit processing industries (Yu et al., 2019; He et al., 2023). Its dried unripe fruit is the official Rubi Fructus recorded in the Chinese Pharmacopoeia, while the ripe fruit is also consumed directly or processed into products such as juice, jam, wine, vinegar, beverages, and teas, reflecting its dual-use value in medicine and food (Liu et al., 2023; Xiong et al., 2024; Wu et al., 2024). Traditional records and modern reviews consistently describe *R. chingii* as useful for nourishing the kidney and liver, consolidating essence, reducing urination, and improving vision, and modern studies further attribute antioxidant, anti-inflammatory, antitumor, immunomodulatory, hypoglycemic, anti-aging, and neuroprotective activities to its diverse phytochemicals (Sheng et al., 2020). Chemically, the fruit is rich in terpenoids, flavonoids, phenolic compounds, organic acids, vitamins, amino acids, polysaccharides, and related secondary metabolites, with ellagic acid and kaempferol-3-O-rutinoside currently used as representative quality markers (Yu et al., 2019; Wu et al., 2024). Recent work also shows that the accumulation of these compounds varies markedly with genotype, tissue, origin, and fruit developmental stage, indicating that medicinal quality and edible quality are both dynamic traits rather than fixed characteristics (Li et al., 2025).

Despite this high value, the industrial development and standardized cultivation of *R. chingii* still lag behind its resource potential (He et al., 2023). Existing studies emphasize that the species has great development value in Zhejiang and other East China production areas, and it has been recognized as one of the representative “Zhe Bawei” medicinal materials, but current drug development remains relatively limited and the mechanistic understanding linking phytochemistry, pharmacology, and production practices is still not deep enough (Xiong et al., 2024). At the same time, fruit quality studies have identified large differences among genotypes in developmental period, soluble solids, acidity, vitamin C, anthocyanins, terpenoids, ellagic acid, and fruit firmness, and quality-marker studies across production origins have shown further differences in antioxidant activity, acidity, carbohydrates, volatiles, and candidate Q-markers. These findings show that improving the consistency of yield and quality in *R. chingii* requires not only germplasm selection and harvest-stage optimization, but also field management strategies capable of regulating vegetative growth, reproductive performance, and bioactive compound formation under production conditions (Li et al., 2025).

In medicinal and horticultural crops more broadly, water and fertilizer management is one of the main agronomic determinants of plant growth, yield formation, nutrient uptake, photosynthetic performance, and the synthesis of quality-related metabolites (Li et al., 2024; Chatzistathis et al., 2025; Sharma et al., 2025). Multiple studies show that irrigation and fertilization often act through a coupling effect rather than as isolated factors. In *Panax notoginseng*, combined water and soluble organic fertilizer treatments increased yield and improved saponin accumulation, with intermediate irrigation and fertilizer levels producing the best comprehensive performance (Mu et al., 2023). In wolfberry, irrigation, nitrogen, and their interaction significantly affected growth, chlorophyll, yield, and quality, and the optimized water-nitrogen regime improved both productivity and quality indices. In melon, irrigation, fertilization, and their interaction significantly affected fruit yield and quality, while structural equation analysis indicated that photosynthesis influenced quality and yield mainly through dry matter accumulation and plant growth. Similar patterns have been reported in capsicum, pear, kiwifruit, eggplant, bitter melon, aonla, and *Ophiopogon japonicus*, where moderate or optimized nutrient-water regimes improved biomass, fruit weight, soluble solids, phenolics, antioxidant activity, medicinal components, or water and fertilizer use efficiency, whereas excessive or poorly coordinated inputs reduced quality or created sustainability risks (Cai et al., 2025; Dolatmand-Shahri et al., 2025; Liu et al., 2025). These results also highlight an important constraint: excessive irrigation and chemical fertilizer use can degrade soil conditions, increase production costs, and undermine sustainable cultivation, making precise water-fertilizer management especially important for high-value medicinal crops (Yang et al., 2023).

This review investigates the regulatory effects and potential mechanisms of water and fertilizer management on fruit yield and quality formation in *Rubus chingii*. Although current studies on *R. chingii* have clarified its major bioactive compounds, developmental patterns, and potential quality markers, research on how cultivation practices regulate the coordinated formation of yield and quality traits under field conditions remains relatively limited. Since the medicinal value of *R. chingii* mainly depends on the accumulation of bioactive compounds such as ellagic acid, kaempferol derivatives, flavonoids, and terpenoids, and since the accumulation of these compounds is jointly influenced by growth stage, fruit tissue characteristics, and environmental conditions, optimizing water and nutrient supply to match plant growth, development, and fruit formation processes is essential for achieving high-yield, high-quality, and stable production of *R. chingii*. This review systematically summarizes the effects of different water and fertilizer management regimes on plant growth, fruit yield, external quality, nutritional quality, and accumulation of medicinal active compounds in *R. chingii*. Furthermore, the physiological mechanisms underlying water-fertilizer regulation of yield and quality formation will be analyzed, and optimized management strategies integrating production efficiency, stable medicinal quality, and sustainable industrial development will be proposed. This review provides a theoretical basis for establishing precision water-fertilizer management systems, implementing standardized cultivation practices, optimizing input management, and improving quality-oriented harvesting and processing, thereby promoting the efficient utilization of *R. chingii* medicinal resources and the high-quality development of its industry.

2 Effects of Water and Fertilizer Management on Growth and Development of *Rubus chingii*

2.1 Effects of water supply on vegetative growth and root development of *Rubus chingii*

Rubus chingii is a woody perennial medicinal and edible shrub whose field productivity depends on stable vegetative growth and effective root water uptake (He et al., 2023). Although direct irrigation studies in *R. chingii* are still limited, evidence from raspberry and other perennial fruit crops shows that water supply strongly regulates canopy expansion, branch growth, plant water status, and ultimately the root-shoot balance (Li et al., 2024; Venig and Teuşdea, 2026). In red raspberry, irrigation level significantly changed yield, fruit number, plant water status, and water productivity, and irrigation at 75% ET_c produced the highest yield while saving 20~28% of water relative to heavier irrigation, indicating that moderate water supply can outperform excessive irrigation. Likewise, pulse drip irrigation in raspberry improved soil water availability and increased later-season production, while also increasing canopy cover and cane diameter in one or both years, showing that irrigation pattern as well as irrigation amount can affect vegetative vigor (Carroll et al., 2024).

Water deficit generally suppresses aboveground growth first, but moderate deficit can redirect assimilates toward the root system and improve water-use efficiency. In jujube, mild deficit irrigation reduced plant height growth and leaf area index, yet helped optimize source-sink relations and improved water-use efficiency, whereas severe deficit caused persistent physiological damage and stronger growth inhibition (Qiang et al., 2025). Pear studies further show that roots are highly sensitive to local water and nutrient conditions, and suitable water-fertilizer treatments increased root area and root density in the 0~60 cm soil layer while sustaining a higher leaf area index (Li et al., 2024). In apricot nursery plants, moderate irrigation maintained higher soil moisture and produced vegetative growth comparable to higher irrigation depths, again suggesting that growth benefits plateau once water supply exceeds plant demand (Venig and Teuşdea, 2026). For *R. chingii*, these findings support the expectation that insufficient water will restrict shoot extension, leaf development, and root activity, while a moderate and well-timed water supply should favor coordinated vegetative growth and a more efficient root system.

2.2 Effects of nitrogen, phosphorus, and potassium supply on plant growth and biomass accumulation

Nitrogen, phosphorus, and potassium are the primary macronutrients controlling plant growth, biomass formation, and nutrient metabolism, and their effects are especially important in medicinal plants because biomass production and active compound accumulation often respond differently to fertilization intensity (Fang et al., 2024; Chrysargyris and Tzortzakis, 2025a). In *Ophiopogon japonicus*, nitrogen source, P+K fertilization, and micronutrient supply all significantly affected agronomic traits and biomass production; P+K promoted plant height and fibrous root growth, and all three fertilization factors significantly affected tuber biomass, the main determinant of medicinal yield (Cai et al., 2025). This pattern is consistent with the broader evidence that balanced NPK supply, rather than single-nutrient maximization, is required to regulate root development, biomass accumulation, and whole-plant health. A global meta-analysis further found that aboveground biomass increased with N, P, and K additions individually, but increased more strongly with combined nutrient additions, especially NP and NPK treatments, supporting widespread nutrient co-limitation of plant growth.

The response to N, P, and K supply is not linear, and moderate or balanced rates often outperform deficiency and excess. In *Sideritis cypria*, an intermediate NPK scheme increased phenols, flavonoids, and antioxidant activity, whereas low nitrogen reduced fresh weight and chlorophyll, and very high potassium induced oxidative stress (Chrysargyris and Tzortzakis, 2025a). In *Origanum dubium*, intermediate NPK levels improved tissue potassium status, low potassium reduced biomass and increased oxidative stress, and higher nitrogen increased N accumulation and flavonoids but altered essential-oil composition (Chrysargyris and Tzortzakis, 2025b). Field evidence from *Vitex negundo* also shows that phosphorus supply can substantially increase biomass and essential-oil yield, with 200 kg P/ha producing the highest biomass and bioactive ingredient content (Peng and Ng, 2022). Because *R. chingii* fruit quality depends on flavonoids, phenolics, terpenoids, and related metabolites, balanced N, P, and K nutrition likely supports not only shoot and root biomass accumulation but also the material basis for later fruit yield and medicinal quality formation (Figure 1) (Yu et al., 2019; He et al., 2023; Wu et al., 2024).



Figure 1 Plant, flowers, dried fruitlet of *R. chingii* Hu (Fu-Pen-Zi) and related Chinese medicines (Adopted from He et al., 2023)
Image caption: (A) Plant of *R. chingii* Hu, (B) Flowers, (C) WuziYanzong Pill, and (D) Dried fruitlet (Fu-Pen-Zi) (Adopted from He et al., 2023)

2.3 Effects of integrated water and fertilizer regulation on plant growth performance and stress resistance

Integrated water and fertilizer regulation usually has a stronger effect on plant performance than changing either factor alone because growth, nutrient absorption, and photosynthesis are jointly controlled by soil moisture and nutrient availability (Kazemalilou et al., 2021). In melon, irrigation, fertilization, and their interaction all significantly affected yield and quality, and the W2F2 treatment most effectively promoted total dry mass, while structural equation analysis showed that photosynthesis influenced yield and quality mainly through dry matter accumulation and growth (Yang et al., 2023). In capsicum, moderate irrigation and nitrogen supply produced the highest plant height, branch number, fruit weight, and nitrogen-use efficiency, with the I2N2 treatment giving the best overall performance (Sharma et al., 2025). Pear studies similarly found that suitable coupling treatments improved root growth, leaf area index, fruit development, and yield, indicating that coordinated supply better supports whole-plant growth than single-factor adjustment (Li et al., 2024).

Integrated regulation is also important for stress resistance, especially under water deficit. In bitter melon, reduced irrigation decreased fruit number, fruit weight, chlorophyll, and leaf phosphorus, while increasing electrolyte leakage and malondialdehyde, but AMF inoculation and phosphorus fertilizer reduced membrane damage and improved fruit weight under all irrigation levels (Dolatmand-Shahri et al., 2025). In lemon balm, combining compost, biochar, NPK fertilizer, and beneficial microbes significantly improved chlorophyll content, photosynthesis, stomatal conductance, antioxidant activity, and biomass under moderate drought, with integrated treatments increasing biomass by 2.31~2.76 times relative to the stressed control (Bolhassani et al., 2024). Tomato

studies likewise show that compost, PGPR, and AMF alleviated drought-induced growth inhibition and increased shoot biomass and fruit yield, while broader synthesis indicates that integrated organic and inorganic fertilization improves water and nutrient uptake and enhances drought tolerance in a cost-effective way (Kazemalilou et al., 2021). For *R. chingii*, this evidence supports testing integrated water-fertilizer schemes as a practical route to improve vegetative growth, biomass accumulation, and resilience, thereby laying the physiological foundation for stable fruit yield and quality.

3 Water-Fertilizer Effects on *Rubus chingii* Yield Formation

3.1 Effects of irrigation methods and water supply on fruit yield formation

Irrigation method and water supply level directly affect fruit yield formation by changing fruit number, single-fruit mass, and the duration of effective fruit filling. In red raspberry, irrigation at 75% ETc produced the highest yield and fruit number, exceeding both the farmer's higher irrigation level and the more severe deficit treatment, which shows that moderate irrigation can support stronger reproductive output than excessive watering. The same raspberry study found that 50% ETc gave the highest water productivity but not the highest yield, indicating that maximizing yield and maximizing water productivity are not identical goals. A later raspberry field study similarly showed that full irrigation at 100% ETc maximized yield per florican and per meter of trellis, while stronger deficits reduced productivity, especially in cultivars sensitive to water shortage (Andelić et al., 2025).

Irrigation pattern also matters, not only total water volume. In red raspberry under drip irrigation, pulse irrigation improved soil water availability and increased fruit production by 1 210~1 230 kg/ha in later harvest periods, with the gain arising mainly from larger fruit in one season and more berries per plant in another (Carroll et al., 2024). In strawberry, fixed partial root-zone drying generally outperformed traditional deficit irrigation, and F-PRD80 maintained yields statistically similar to full irrigation while using less water, whereas stronger water deficits clearly reduced yield and yield-related traits (Kaman et al., 2023). Mango showed the same overall pattern: irrigation amount was the most important factor affecting fruit yield and water-use efficiency, and severe drought constrained production, whereas a moderate deficit could improve comprehensive benefit when aligned with stage-specific fertilization (Sun et al., 2022). For *R. chingii*, these results support the view that fruit yield formation is favored by moderate, stable, and development-matched water supply, while both over-irrigation and excessive deficit can weaken fruit set or limit fruit enlargement.

3.2 Effects of different fertilization strategies on fruit-setting capacity and yield components

Different fertilization strategies influence yield mainly through their effects on fruit-setting rate, fruit number, and single-fruit weight, and the response is usually strongest under balanced rather than maximal NPK input. In Chinese cherry, NPK fertilization increased vegetative growth and positively affected fruit weight, fruit size, internal quality, and fruit set rate, with one intermediate combination giving the best overall fruit set and size rather than the highest nutrient dose. Fruit set rate in cherry was also positively correlated with fruit weight, vertical diameter, and soluble sugars, indicating that reproductive success and fruit filling were regulated together (Guo et al., 2022). In blueberry, fertilization significantly increased yield relative to the unfertilized control, and the best treatment raised yield per plant by 79.26%, while phosphorus and potassium showed particularly strong influence on fruit weight and yield ranking (Zhang et al., 2023).

Fertilizer timing is as important as fertilizer ratio. In peach, NPK supply from 95-65-76 to 165-84-103 kg/ha produced the highest yields, especially when nitrogen supply was high during flowering and fruit set, while higher N and K during fruit development and ripening improved fruit weight and size. In custard apple, split application of N, P, and K across basal, fruit-set, fruit-enlargement, and pre-harvest stages increased fruit yield by 23% and also gave the highest fruit number and fruit weight (Palepad et al., 2025). More broadly, farmers manage water and fertilization because they are the main levers for obtaining economic yield and fruit quality, but the evidence across fruit crops shows that excessive or poorly staged fertilization is less effective than balanced, growth-stage-specific nutrient supply (Maatallah et al., 2024). For *R. chingii*, whose fruits are valued for both medicinal and edible uses, this implies that rational N, P, and K scheduling should improve fruit-setting capacity and yield components while avoiding nutrient waste (Sheng et al., 2020; He et al., 2023; Wu et al., 2024).

3.3 Effects of water-fertilizer coupling management on yield performance and production efficiency

Water-fertilizer coupling management affects not only total yield but also yield performance and production efficiency because synchronized resource supply better matches crop demand across reproductive stages. In pear, appropriate coupling treatments promoted root and leaf growth and produced the highest yield, single-fruit weight, and primary fruit rate, showing that coordinated water, nitrogen, and phosphorus inputs improve the structural basis for stable fruit production (Li et al., 2024). In capsicum, moderate irrigation and nitrogen supply produced the highest fruit weight and fruit number per plant, and the I2N2 combination also maximized irrigation water productivity and fertilizer nitrogen use efficiency (Sharma et al., 2025). In jujube, increasing irrigation and nitrogen significantly increased fruit yield, and integrated water-fertilizer regulation improved economic efficiency by reducing mismatches between water and nutrient supply (Zhang et al., 2024).

Meta-analyses show that these responses are general rather than crop-specific. Across China, drip fertigation increased yield by 12.0%, water productivity by 26.4%, and nitrogen use efficiency by 34.3% compared with traditional irrigation and broadcast fertilization, with fruit crops showing especially large gains in nitrogen use efficiency (Li et al., 2021). A second meta-analysis found that water-fertilizer integration with drip irrigation improved yield by 12.5%, NUE by 31.3%, and WUE by 34.5%, and recommended lower-flow drip systems with nitrogen rates reduced by 10~25% from traditional practice. Stage-specific coupling studies in mango and watermelon add an important nuance: the treatment with the highest yield is not always the one with the highest comprehensive efficiency score, because moderate water deficit can reduce input costs and improve WUE while maintaining strong production (Sun et al., 2022; Wu et al., 2026). For *R. chingii*, the practical implication is that water-fertilizer coupling should aim at coordinated and stage-adapted input management to secure stable fruit yield, higher resource-use efficiency, and lower production risk rather than simply maximizing irrigation or fertilizer application.

4 Fruit Quality Formation in *Rubus chingii*

4.1 Effects of water and fertilizer conditions on fruit appearance quality and commercial value

Fruit appearance quality is a core component of the commercial value of *Rubus chingii* because size, firmness, color, and uniformity directly affect market acceptance for both fresh fruit and processed raw material, and these traits are highly responsive to preharvest water and fertilizer management (Jezek et al., 2018; He et al., 2023). Across fruit crops, suitable water and fertilizer supply improves fruit growth and marketable appearance, whereas insufficient or excessive inputs reduce quality by disturbing assimilate allocation and fruit development (Yang et al., 2023). In pear, water and fertilizer control within an appropriate range improved fruit growth and quality, and the best coupling treatment produced the highest fruit shape index, indicating a direct effect on appearance traits linked to commodity value (Li et al., 2024). In blackberry, nitrogen form strongly altered appearance quality, and $\text{NH}_4^+\text{-N}$ improved fruit size, firmness, and color more than other treatments, showing that not only fertilizer amount but also nutrient form can shape the external quality of berry fruit (Duan et al., 2023).

Water regulation also changes visible fruit traits in ways that can either improve appearance or sacrifice yield-related attributes, depending on stress intensity and timing. In table grape, a deficit irrigation program reduced water input by 30% without reducing total yield and promoted berry growth, higher maturity index, and earlier harvest, while biostimulation further increased berry size, berry weight, and the proportion of commercially colored berries (Zapata-García et al., 2025). In Crimson Seedless grape, reducing irrigation from 100% ETc to 40% ETc enhanced berry color, but the highest berry diameter and firmness occurred under full irrigation, and 60% ETc was judged the best compromise for pigmentation and quality with only slight yield penalties. Strawberry studies likewise show that fertilizer regime significantly changes color parameters and firmness, with organic fertilization producing more intensely colored fruit and higher soluble solids but lower firmness than conventional fertilizer (Kılıç et al., 2021). For *R. chingii*, these findings support the expectation that moderate water supply and balanced nutrient management will improve fruit size, color development, and marketability, whereas severe water deficit or unbalanced fertilization will tend to create trade-offs between appearance quality and production stability (Yu et al., 2019; He et al., 2023; Wu et al., 2024).

4.2 Effects of water and fertilizer regulation on sugar-acid composition and nutritional quality of fruits

Sugar-acid composition is one of the main determinants of fruit flavor and eating quality, and water-fertilizer management consistently changes soluble solids, soluble sugars, titratable acidity, and sugar-acid ratio across fruit crops (Kılıç et al., 2021; Yang et al., 2023). In mango, irrigation amount was the strongest factor affecting soluble solids and total sugar content, and the treatment with 75% ETc plus stage-specific fertilization produced the highest total sugar content and the lowest titratable acid content, while a different full-irrigation treatment gave the best soluble solids, vitamin C, and carotenoid contents (Sun et al., 2022). In wine grape, moderate irrigation reduced titratable acid by 3.3% and increased sugar-acid ratio by 12.2%, while lower irrigation reduced acid further and increased sugar-acid ratio by 20.0%, showing that water deficit often improves flavor balance up to a point (Han et al., 2023). Strawberry responds similarly: as soil moisture decreases, soluble sugar rises, titratable acidity falls, and the sugar-acid ratio increases markedly, although stronger stress also reduces yield, so the recommended irrigation level is about 70~80% of field capacity when balancing flavor and production (Yang et al., 2025).

Fertilizer strategy also affects nutritional quality beyond sugars and acids. In strawberry, fertilizer application significantly changed soluble solids, total acidity, vitamin C, and individual sugars, and organic fertilizer increased SSC and glucose but reduced vitamin C relative to conventional chemical fertilizer (Kılıç et al., 2021). In loquat, humic-acid water-soluble fertilizer increased single-fruit weight, raised total soluble sugar by 18.58~21.25%, reduced total organic acid by 13.73~21.50%, and increased sweetness value and sugar/acid ratio, although vitamin C declined at one concentration and total phenols and carotenoids were unchanged (Xing et al., 2026). In melon and tomato, irrigation amount remained the primary determinant of fruit quality indices, including soluble solids, vitamin C, soluble sugars, lycopene, and titratable acidity, while fertilizer timing at later reproductive stages contributed strongly to quality optimization (Yang et al., 2023). For *R. chingii*, whose ripe fruit is consumed directly and processed into multiple food products, these results indicate that regulating water deficit within a moderate range and coordinating fertilizer supply by developmental stage should help improve sweetness, acid balance, and nutritional value, but excessive stress or overfertilization could impair stability of quality formation (Yu et al., 2019; He et al., 2023; Wu et al., 2024).

4.3 Effects of water and fertilizer management on the accumulation of medicinal active compounds

For *Rubus chingii*, fruit quality is not defined only by sensory quality but also by the accumulation of medicinally active compounds, especially ellagic acid, kaempferol-3-O-rutinoside, flavonoids, terpenoids, phenolic acids, and related metabolites (Sheng et al., 2020; Wu et al., 2024). The Chinese Pharmacopoeia uses ellagic acid and kaempferol-3-O-rutinoside as index components, with minimum contents specified for quality control, which makes agronomic regulation of these compounds directly relevant to medicinal raw-material quality (Figure 2) (He et al., 2023). Evidence from broader fruit and medicinal-plant research shows that plant nutrient status strongly affects anthocyanins and other polyphenols, and finely tuned fertilization in amount and timing can improve fruit quality by regulating anthocyanin accumulation (Jezek et al., 2018). A general review of fertilization and plant polyphenols further shows that lower fertilization levels can increase flavonols and ellagic acid in strawberry, that high nitrogen often lowers polyphenol accumulation, and that the effect of NPK depends strongly on combination and crop context (Heimler et al., 2017).

The interaction between water stress and fertilization is especially important for secondary-metabolite formation because moderate stress can stimulate protective metabolism, whereas severe stress tends to damage protein status and membrane integrity. In medicinal plants, mild to moderate drought increased phenolics, flavonoids, and anthocyanins, while organic fertilizers such as vermicompost and azocompost stabilized antioxidant activity, reduced oxidative damage, and produced the strongest biochemical enhancement under moderate stress. Meta-analysis of medicinal plants shows that both organic and inorganic fertilizers can increase active constituents, while combined fertilization often gives the best balance between compound accumulation and soil sustainability. In blackberry, $\text{NH}_4^+\text{-N}$ promoted anthocyanin, ellagic acid, and vitamin C accumulation, and polyphenols, ellagic acid, and anthocyanins were positively correlated with sugar content and fruit weight,

indicating that quality improvement in berry crops can align sensory and functional quality under suitable nutrition (Duan et al., 2023). Therefore, for *R. chingii*, moderate water control and balanced fertilizer management, especially schemes that avoid excessive nitrogen and integrate organic and inorganic nutrient sources, are likely to favor the coordinated accumulation of medicinal actives and support higher-value production for both food and medicinal uses (Wu et al., 2024).

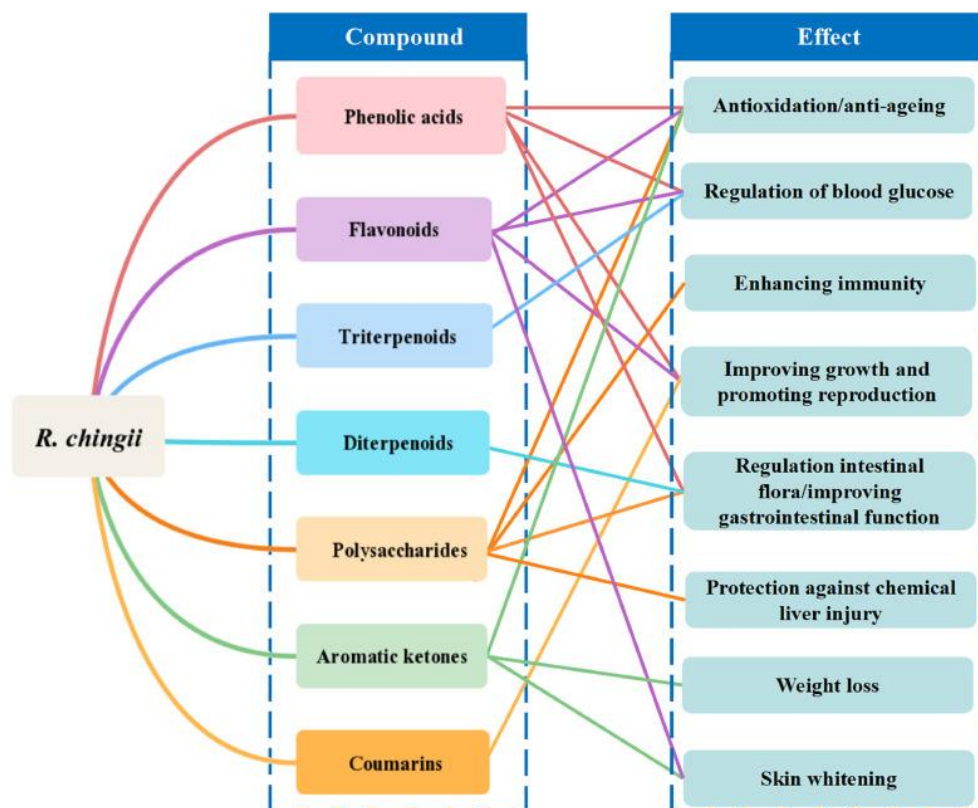


Figure 2 Correlation diagram of chemical components and efficacy of Rubi fructus (Adopted from Wu et al., 2024)

5 Mechanisms of Water-Fertilizer Regulation in *Rubus chingii*

5.1 Regulatory effects of water and fertilizer conditions on photosynthesis and carbon assimilation

Water and fertilizer conditions regulate yield and quality formation first by controlling leaf photosynthesis, stomatal behavior, canopy carbon gain, and the subsequent distribution of assimilates among vegetative organs and fruits. In fruit-tree models, carbon assimilation is explicitly linked to leaf area, canopy radiation interception, and organ growth demand, while carbohydrate allocation depends on source supply, sink demand, and root-shoot functional balance (Rahmati et al., 2018). Under water deficit, peach vegetative growth declines first through a direct reduction in sink strength and then through an indirect reduction in photosynthesis, showing that drought limits both carbon acquisition and the capacity of shoots to use assimilates (Rahmati et al., 2018). In bell pepper, elevated CO₂ increased biomass under mild and moderate water stress by boosting leaf photosynthesis, increasing stomatal number and openness, and improving leaf-level water-use efficiency, but this benefit weakened as soil water deficit became severe (Fan et al., 2020). These results indicate that carbon assimilation in *R. chingii* should depend on maintaining a water supply sufficient to preserve stomatal conductance, photosynthetic capacity, and active vegetative sinks, while avoiding excessive vegetative consumption that competes with fruit growth.

Fertilizer supply modifies this process by affecting photosynthetic enzymes, sugar metabolism, and the partitioning of photoassimilates to reproductive organs. In cotton, drought sharply reduced net photosynthesis, stomatal conductance, intercellular CO₂, and Rubisco activity when potassium was absent, whereas potassium application alleviated these declines and improved biomass accumulation and assimilate partitioning. Potassium also maintained higher leaf sucrose under drought by regulating sucrose phosphate synthase, sucrose synthase, and acid invertase activities, indicating that nutrient supply affects not only carbon fixation but also carbon

conversion and export (Zahoor et al., 2017). In tomato, fruit fresh weight, dry weight, and carbon allocation were highly sensitive to irrigation amount under potassium supply, and the activities of sucrose synthase, sucrose phosphate synthase, acid invertase, and AGPase responded strongly to water regime, showing that water-potassium interactions directly shape fruit carbon metabolism (Wu et al., 2023). In red raspberry, moderate irrigation at 75% ETc produced the highest yield, implying that carbon gain and reproductive allocation are optimized under moderate rather than excessive irrigation. For *R. chingii*, these findings support a mechanism in which suitable water-fertilizer management enhances photosynthetic carbon assimilation, stabilizes sucrose metabolism, and improves the transfer of assimilates from leaves to developing fruits.

5.2 Regulatory mechanisms of water and fertilizer supply on nutrient uptake, transport, and allocation

Water and fertilizer management also regulates yield and quality through its effects on nutrient release in soil, root absorption, xylem-phloem transport, and allocation among leaves, stems, roots, and fruits. Water availability strongly governs nutrient mobility in soil and transpiration-driven mass flow, so drought often creates simultaneous water and nitrogen limitation and restricts nutrient entry into the vascular system (Plett et al., 2020). In alpine plants, drought restricted rhizospheric nitrogen release, limited root growth, reduced root surface area, root length, and root volume, and decreased both aboveground and belowground fertilizer utilization rates. Soybean showed the same overall pattern: water deficit and no nitrogen fertilization reduced the accumulation and partitioning of N, P, K, Ca, Mg, S, and micronutrients, and water limitation impaired biomass and nutrient accumulation even when nitrogen was supplied (Setubal et al., 2023). These mechanisms are highly relevant to *R. chingii* because stable fruiting requires continuous nutrient supply to both vegetative tissues and reproductive sinks, and any reduction in root uptake or long-distance transport can weaken fruit set, fruit growth, and quality formation.

The effect of fertilizer depends on both dose and coordination with water supply. In substrate-grown tomato, an appropriate potassium level promoted coordinated uptake of K, N, P, Ca, and Mg during the reproductive stage, while insufficient potassium restricted root-mediated water and nutrient flux and excessive potassium reduced physiological efficiency because of luxury consumption and salt stress. In winter wheat, NPK uptake in aboveground biomass decreased as water stress intensified, but mild deficit did not differ significantly from full irrigation, and moderate fertigation promoted nutrient transfer to grains without significantly reducing yield or protein (Yan et al., 2022). In greenhouse grape, bacterial fertilizer under mild water stress increased available phosphorus, dissolved organic carbon, microbial biomass carbon and nitrogen, and soil enzyme activities, indicating that rhizosphere biological processes can improve nutrient availability and production efficiency under constrained water supply (Gao et al., 2025). Together, these studies indicate that *R. chingii* likely responds best to moderate, coordinated water-fertilizer supply that sustains root activity, preserves ionic balance, and directs more nutrients toward fruit-bearing organs rather than inefficient vegetative accumulation.

5.3 Effects of water and fertilizer conditions on secondary metabolite biosynthesis and accumulation

Water and fertilizer conditions affect fruit quality further by regulating the biosynthesis and accumulation of secondary metabolites, which are central to the medicinal and nutritional value of *R. chingii*. *Rubus chingii* fruit contains abundant flavonoids, phenolic compounds, terpenoids, phenolic acids, organic acids, and related metabolites, and ellagic acid and kaempferol-3-O-rutinoside are currently used as representative quality markers (He et al., 2023). In fruit crops more broadly, secondary metabolism is highly sensitive to abiotic cues, and these compounds influence pigmentation, flavor, antioxidant capacity, and economic value (Savoi et al., 2016). Grape studies show that water deficit directly modulates the flavonoid pathway: early or moderate deficit can increase anthocyanin accumulation by upregulating *PAL*, *C4H*, *4CL*, *CHS*, *F3H*, *F3'5'H*, *UFGT*, *GST*, and related transcriptional regulators, whereas severe or poorly timed deficit can downregulate pathway genes or shift composition in less favorable directions (Palai et al., 2022). Water deficit can also accelerate sugar accumulation and ripening, thereby interacting with developmental signals that promote anthocyanin synthesis.

These metabolic responses arise through both concentration effects and true biosynthetic regulation, and fertilizer status modifies them further. In Shiraz grape, water deficit reduced berry size, increased the skin-to-pulp ratio, and thereby increased phenolic concentration indirectly, but it also exerted a direct effect on biosynthesis that varied with stress timing and severity. In white grape, prolonged drought altered 4 889 genes, increased phenylpropanoids, monoterpenes, and tocopherols, and modulated 18 phenylpropanoid, 16 flavonoid, 9 carotenoid, and 16 terpenoid structural genes, showing that drought broadly reprograms secondary metabolism beyond anthocyanins alone (Savoi et al., 2016). Nutrient status interacts with these pathways because potassium improved anthocyanin, ellagic acid, and vitamin C accumulation in blackberry under ammonium nutrition, and strategic nutrient supply is recognized as a tool for modifying anthocyanin biosynthesis and fruit quality (Duan et al., 2023). For *R. chingii*, this supports a mechanism in which moderate water regulation and balanced fertilization not only maintain yield, but also reshape phenylpropanoid, flavonoid, terpenoid, and related pathways to determine the accumulation of medicinally active compounds and the final quality of the fruit.

6 Current Research Problems in *Rubus chingii* Water-Fertilizer Management

6.1 Insufficient understanding of water and fertilizer requirements at different growth stages

A primary problem in current *Rubus chingii* research is the lack of precise knowledge about water and fertilizer requirements across different growth stages, even though evidence from other fruit crops shows that the sensitivity of yield and quality traits changes sharply with phenology. In mango, irrigation amount and fertilizer rates at flowering, fruit expansion, and ripening contributed differently to yield, WUE, sugar, vitamin C, and carotenoids, and the recommended schedule required different fertilizer inputs at each stage rather than a single fixed regime (Sun et al., 2022). Tomato studies likewise show that irrigation amount is the primary determinant of yield and WUE, but fruit quality traits are affected differently by fertilizer applications in early, middle, and late reproductive stages, indicating that static fertilizer ratios cannot fully meet dynamic crop demand. Kiwifruit provides especially direct evidence that water-fertilizer deficit thresholds vary by stage: stage II and III deficits mainly changed physical quality, whereas stage III and IV deficits more strongly improved chemical quality, with different optimal deficit thresholds for water and fertilizer (Zha et al., 2023).

This gap is important for *Rubus chingii* because stage-specific regulation likely determines not only fruit yield but also medicinal-quality formation, yet current evidence is still too sparse to define critical windows for irrigation and fertilization. Melon experiments show that fertilization significantly affected net photosynthesis during flowering and fruiting, while growth then became the strongest direct driver of yield and quality, indicating that stage-specific water-fertilizer effects operate through changing physiological bottlenecks over time (Yang et al., 2023). Raspberry production research also shows that fruiting responses differ by fertilization system, and biologically supported mineral systems increased fruiting laterals, fruits per lateral, fruit weight, and soluble solids, suggesting that reproductive-stage nutrient demand is not captured well by conventional uniform fertilization schemes (Pešaković et al., 2026). Even in controlled strawberry systems, most water management strategies still rely on rigid schedules rather than variable plant requirements over time, and comprehensive comparisons remain limited, which underscores how underdeveloped dynamic demand-based management remains across berry crops (Hutchinson et al., 2025).

6.2 Need for improvement in water and fertilizer management systems and production standards

A second major problem is that water-fertilizer management systems and production standards for *Rubus chingii* are still insufficiently standardized, especially for precise irrigation, fertigation, and sustainability-oriented input control. Kiwifruit research states this problem explicitly: orchard water and fertilizer management lacked quantitative standards, and this seriously affected yield and quality, making regulated drip irrigation and fertilization necessary for green and efficient production (Zha et al., 2023). The broader fruit-crop literature shows that drip fertigation can synchronize water and nutrient delivery with crop demand and often serves as the basis for benchmark management schedules, yet its performance depends strongly on local climate, soil, and managerial conditions (Han et al., 2023). In China-wide meta-analysis, drip fertigation increased crop yield by 12.0%, water

productivity by 26.4%, and NUE by 34.3% relative to traditional practices, with fruit crops showing the greatest NUE gain, which supports the need for *Rubus chingii* production standards built around precise fertigation rather than empirical watering and fertilization (Li et al., 2021).

The problem is not only the absence of standards, but also the lack of intelligent and adaptive management tools that can support those standards in production. In greenhouse strawberry, sensor-based fertigation outperformed empiric timer-based management by saving 38% of nutrient solution and 26% of water while increasing WUE and nutrient productivity without compromising fruit quality, showing that real-time monitoring can replace coarse scheduling rules (Bonelli et al., 2024). A second strawberry study reached a similar conclusion: drier sensor-controlled thresholds and leaching-fraction approaches gave the best combined yield and resource-use performance, whereas common rigid scheduling did not track variable plant demand well (Hutchinson et al., 2025). Current tomato work also argues for dynamic fertilization models, plant physiological indicators such as leaf N and K, and soil sensors for real-time nutrient monitoring, which highlights the direction *Rubus chingii* management standards still need to move toward.

6.3 Limited research on the coordinated improvement mechanisms of yield and quality

A third problem is the limited mechanistic understanding of how water and fertilizer management can improve yield and quality together, rather than improving one at the expense of the other. Many studies show that the best treatment for yield is not the best for fruit quality. In mango, one regime produced the highest yield and PFP, while another produced the highest total sugar and lowest titratable acidity, and the final recommendation required multi-objective evaluation rather than a single agronomic index (Sun et al., 2022). Tomato showed the same pattern: one treatment achieved the highest integrated score for yield, WUE, and PFP, while another performed best for vitamin C, lycopene, SSC, and soluble protein. Wine grape likewise required moderate water and fertilizer to balance yield, berry quality, and resource-use efficiency, while moderate fertilization specifically produced the richest anthocyanin and tannin accumulation (Han et al., 2023).

For *Rubus chingii*, this unresolved coordination problem is even more critical because target quality includes not only edible traits but also medicinally active compounds. Bitter melon under irrigation deficit showed a typical trade-off: reduced irrigation lowered fruit number and weight but increased flavonoids, anthocyanins, and medicinal secondary metabolites, while AMF and phosphorus partly buffered yield loss and enhanced phytochemicals (Dolatmand-Shahri et al., 2025). Red raspberry studies similarly show that some fertilizers improve berry weight, sugars, and bioactive compounds, while unfertilized control can still produce a better sweetness index, indicating that different quality dimensions do not move together automatically (Stojanov et al., 2019). Emerging work in raspberry and pear suggests that microbial or bio-organic inputs may help bridge this gap by improving fruiting traits, phenolics, antioxidant activity, soil fertility, and yield through rhizosphere-mediated mechanisms, but the exact causal links remain disputed and insufficiently resolved for standardized field application in *Rubus chingii* (Wang et al., 2022; Pešaković et al., 2026).

7 Development Directions for Precision Water-Fertilizer Management

7.1 Establishment of precision water and fertilizer regulation models based on cultivar characteristics and growth stages

A key development direction for *Rubus chingii* is the establishment of precision regulation models that explicitly incorporate cultivar characteristics, phenological stage, and multi-objective production targets. Current precision water-fertilizer research shows that different crops require nutrient ratios and irrigation schedules that are scientifically matched to crop characteristics and growth stages rather than applied uniformly (Xing and Wang, 2024). In mango, irrigation amount and fertilizer rates at flowering, fruit expansion, and fruit ripening affected yield, water-use efficiency, sugars, vitamin C, and carotenoids differently, and the recommended schedule was stage-specific rather than fixed across the season (Sun et al., 2022). Tomato studies reached the same conclusion: irrigation amount was the primary determinant of yield and WUE, but fruit quality responded differently to fertilizer inputs at seedling, flowering/fruit-set, and peak-fruit stages, so optimization required a multi-objective framework rather than a single yield criterion.

Future *Rubus chingii* models should therefore be dynamic rather than static, using growth and physiological indicators to update recommended water and nutrient inputs over time. In industrial strawberry, a closed-loop framework quantified stage-specific responses of growth and photosynthetic traits across seedling, flowering, and harvest stages, achieved a model error of only 0.60%, and identified optimal ranges of water, nitrogen, and potassium that balanced high yield, high efficiency, and low pollution (Li et al., 2026). Kiwifruit likewise showed that the critical periods and thresholds for improving physical quality differed from those for chemical quality, with stage II-III deficits favoring physical traits and stage III-IV deficits more strongly improving chemical quality (Zha et al., 2023). Because perennial berry crops also show strong stage dependence in dry matter accumulation and nutrient uptake, *Rubus chingii* regulation models should be built around phenology-specific demand curves and then calibrated for cultivar-specific yield and medicinal-quality targets (Bao et al., 2023).

7.2 Promotion of integrated water and fertilizer technologies and green efficient cultivation practices

A second major direction is the promotion of integrated water-fertilizer technologies, especially drip fertigation and deficit-based coupling strategies that raise production efficiency while lowering resource losses. Large meta-analyses show that water-fertilizer integration with drip irrigation increased yield by 12.5%, WUE by 34.5%, and NUE by 31.3%, and was particularly suitable for fruit trees in medium-textured soils. A second China-wide meta-analysis similarly found that drip fertigation increased yield by 12.0%, water productivity by 26.4%, and NUE by 34.3%, with fruit crops showing the largest NUE gains (Li et al., 2021). Reviews of drip fertigation further show that targeted delivery to the root zone reduces evaporation, runoff, and deep percolation while enabling stage-specific nutrition and better economic returns, which makes it a strong candidate technology for green and efficient *Rubus chingii* cultivation (Kaviyazhagan et al., 2025).

For *Rubus chingii*, integrated systems should emphasize spatiotemporal coupling of irrigation and fertilization, moderate deficit control, and reduced conventional fertilizer input rather than simply increasing supply intensity. In watermelon, intelligent drip fertigation tailored irrigation thresholds and fertilizer allocation to crop stage, reduced irrigation, N, P₂O₅, and K₂O inputs by 33%, 46%, 72%, and 57%, respectively, without compromising yield or fruit quality (Bao et al., 2023). In pear, suitable coupling treatments improved fruit shape, yield, primary fruit rate, and fruit quality, indicating that integrated management can simultaneously strengthen productivity and commodity traits (Li et al., 2024). Grape studies further show that optimal irrigation and fertilization intervals differ between wet and dry years, so future *Rubus chingii* systems should include climate-responsive adjustment rules rather than one fixed annual formula (Peng et al., 2024).

7.3 Application of smart agriculture technologies for precision water and fertilizer management and quality regulation

A third development direction is the application of smart agriculture technologies to support real-time diagnosis, automated control, and quality-oriented regulation. Precision water-fertilizer systems increasingly rely on sensors, remote sensing, GIS, IoT communication, and AI-assisted decision support to monitor soil moisture, fertility, and crop growth in real time (Xing and Wang, 2024). Reviews of smart sensing in specialty crops show that proximal sensors, UAV hyperspectral imaging, and data-fusion models can diagnose crop nutritional and water status non-destructively and replace uniform input strategies with crop-responsive management (Khoddamzadeh et al., 2026). More general IoT reviews reach the same conclusion: soil moisture, pH, temperature, and nutrient sensors provide real-time field data, while variable-rate application and predictive analytics allow inputs to be delivered only where and when needed (Mansoor et al., 2025).

For *Rubus chingii*, the practical value of smart agriculture will depend on translating these tools into closed-loop fertigation and quality-regulation platforms. In greenhouse tomato, an intelligent drip irrigation and fertigation system combined automatic control with flow-meter monitoring to ensure treatment-specific water delivery. In tomato and watermelon, FDR sensor-linked intelligent fertigation increased dry matter accumulation, nutrient uptake, root growth, yield, and quality while markedly reducing irrigation inputs and nutrient leakage. Broader smart-irrigation studies show that machine-learning systems can integrate sensor and weather data, achieve high

predictive accuracy, and provide web-based supervision for low-cost deployment, although infrastructure cost, interoperability, and rural connectivity remain important implementation constraints (Tace et al., 2022; Miller et al., 2025).

8 Conclusions and Perspectives

Water and fertilizer management plays an important role in fruit yield formation of *Rubus chingii*. Appropriate irrigation and balanced nutrient supply can regulate photosynthesis, reproductive development, fruit set, fruit enlargement, and resource-use efficiency, thereby improving yield performance. Studies in fruit crops show that moderate water and fertilizer inputs generally achieve better production performance than excessive application, while balanced fertilization promotes photosynthetic capacity and assimilate supply, providing a physiological basis for stable fruit development. For *R. chingii*, rational water-fertilizer management is therefore a key strategy for achieving efficient and sustainable yield formation.

Water-fertilizer regulation also has great potential for improving fruit quality and medicinal value in *R. chingii*. By optimizing water supply and nutrient allocation, it can regulate sugar-acid balance, nutritional characteristics, and the accumulation of bioactive compounds such as flavonoids, phenolics, ellagic acid, and kaempferol-3-O-rutinoside. Moderate water regulation and balanced fertilization may promote the coordinated improvement of edible quality and medicinal quality, providing an effective approach for producing high-value raw materials for both food and traditional medicine applications.

Future *R. chingii* production should focus on developing precision water-fertilizer management systems based on cultivar characteristics, growth stages, environmental conditions, and intelligent monitoring technologies. Precision drip fertigation, sensor-based regulation, and data-driven models are promising approaches for improving water and nutrient use efficiency. Further studies should establish region-specific management thresholds, evaluate economic and ecological benefits, and integrate genotype selection, stage-based fertigation, biological inputs, and smart sensing technologies to achieve simultaneous improvements in yield, fruit quality, medicinal value, and sustainable production efficiency.

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

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Comparative Analysis of Wild-Simulated and Facility Cultivation Modes of *Dendrobium officinale*

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Abstract This article analyzes and compared the differences between the two cultivation modes in terms of ecological environment regulation, production management, growth performance, yield formation, active compound accumulation, and industrial applications. The results showed that wild-simulated cultivation promotes secondary metabolite accumulation through the reconstruction of natural epiphytic environments, ecological adaptation, microbial interactions, and moderate environmental stress, demonstrating advantages in plant morphology, metabolite richness, and overall medicinal quality. In contrast, facility cultivation relies on greenhouse environmental control, standardized seedlings, and precise water-fertilizer management to improve production stability, yield performance, and large-scale supply capacity. The two cultivation modes exhibit distinct characteristics in yield formation and quality development: facility cultivation is more suitable for large-scale and standardized production, whereas wild-simulated cultivation is more appropriate for the development of high-quality medicinal materials and ecological products. Future development of the *Dendrobium officinale* industry should promote the integration of advantages from both cultivation modes by establishing a combined production system of “facility-based seedling propagation-ecological cultivation-quality improvement,” strengthening precision environmental regulation, green cultivation technologies, and intelligent management, and developing a comprehensive quality evaluation system incorporating polysaccharides, flavonoids, alkaloids, metabolomic characteristics, and bioactivity-related indicators. These efforts promote the development of the *Dendrobium officinale* industry toward high quality, high efficiency, and sustainability.

Keywords *Dendrobium officinale*; wild-simulated cultivation; facility cultivation; active compounds; quality evaluation

1 Introduction

Dendrobium officinale is a precious perennial orchid medicinal plant that has long been used in China as both a traditional medicine and a functional food. It is recorded in early materia medica and is officially included in the Chinese Pharmacopoeia, and its dried stems are widely consumed directly or processed into “Tiepi Fengdou” products (Yuan et al., 2020; Xu et al., 2022). Modern phytochemical studies show that *D. officinale* contains abundant polysaccharides, alkaloids, flavonoids, phenolic acids, amino acids, bibenzyls, phenanthrenes, and other constituents, among which polysaccharides are generally regarded as the principal active components and an important quality indicator (Tan et al., 2023; Lai et al., 2024). These compounds underpin a broad range of reported bioactivities, including immunomodulatory, antioxidant, anti-inflammatory, hypoglycemic, gastrointestinal protective, hepatoprotective, cardiovascular protective, anti-osteoporosis, and neuroprotective effects, giving *D. officinale* substantial medicinal, nutritional, and commercial value (Chen et al., 2021; Duan et al., 2022). In recent years, this species has attracted increasing attention from the medicine, health food, and cosmetics sectors, and its stems, leaves, and flowers are all being explored for diversified product development and higher-value utilization (Li et al., 2025; Wang et al., 2025).

Despite its high resource value, the industrial development of *D. officinale* has long been constrained by the scarcity of wild resources, low natural reproduction rate, slow growth, and historically heavy dependence on natural habitats. Wild populations are limited, and increasing market demand has intensified the contradiction between resource protection and industrial supply (Cheng et al., 2026). To address this problem, artificial rapid propagation based on tissue culture has been widely adopted and has become an essential foundation of the

modern *Dendrobium* industry, while new varieties, technical procedures, and standardized cultivation systems have gradually improved industrial capacity (Cheng et al., 2026). Since the beginning of the new century, artificial cultivation of *D. officinale* has made major progress, and greenhouse cultivation, semi-wild cultivation, bionic-facility cultivation, original ecological cultivation, pot cultivation, and epiphytic cultivation have all been developed in response to different production goals (Tan et al., 2023). However, as industrial expansion has shifted supply from wild collection to artificial production, ensuring that cultivated material retains desirable medicinal quality has become a central scientific and practical issue (Yuan et al., 2020; Yang et al., 2023; Yang et al., 2026).

Against this background, wild-simulated and facility cultivation have emerged as two representative development paths for *D. officinale*. Facility cultivation emphasizes controllable environmental conditions, efficient seedling establishment, and relatively high yield, making it an important mode for stable large-scale production. By contrast, wild-simulated cultivation seeks to reconstruct natural or near-natural habitat conditions, so that the ecological environment, plant morphology, and quality traits are closer to those of wild materials. Existing studies indicate that cultivation mode substantially affects the accumulation of active ingredients and the overall metabolite profile. Environmental variables such as temperature, humidity, sunshine duration, pH, and soil nutrients are key drivers of medicinal quality, while light, water, and nutrient supply also influence growth and secondary metabolite accumulation (Yuan et al., 2020; Zhang et al., 2024). Comparative studies further show that wild or wild-simulated materials often contain higher levels of some major active constituents than greenhouse-grown materials, although the pattern is not uniform across all compounds or cultivation settings: one *D. officinale* study found wild plants had the highest polysaccharide content, whereas another found stone epiphytic and greenhouse cultivation exceeded live-tree epiphytic cultivation in polysaccharides, while stone epiphytic plants showed the richest differential metabolite accumulation and strongest antioxidant activity (Yang et al., 2023). Greenhouse cultivation also reshapes environmental drivers and biological interactions, including shifts in high-quality production zones and differences in root fungal endophyte communities that correlate with polysaccharide accumulation. In addition, evidence from related *Dendrobium* species suggests that wild-simulated cultivation can provide better quality and economic returns, and may also offer lower carbon emissions and global warming potential than facility cultivation (Yi et al., 2021).

This study investigates the differences between wild-simulated and facility cultivation modes of *Dendrobium officinale* and their effects on plant growth, quality formation, and industrial development. By systematically comparing the two cultivation modes in terms of growth environment, morphological characteristics, yield formation, active compound accumulation, and quality evaluation, this study aims to clarify the impacts of different cultivation strategies on the medicinal value and industrial attributes of *D. officinale*. Available evidence indicates that with efficient utilization. Furthermore, this study will contribute to the transition of *D. officinale* production from a yield-oriented approach toward quality improvement, ecological coordination, and sustainable development, thereby providing theoretical support for the modernization of the *D. officinale* industry and the high-value utilization of medicinal plant resources.

2 Biological Characteristics and Cultivation Basis of *Dendrobium officinale*

2.1 Growth characteristics and ecological adaptability

Dendrobium officinale is a perennial epiphytic orchid with slow growth and high environmental sensitivity, which helps explain both its rarity in nature and the need for protected or semi-natural cultivation (Ding et al., 2018; Jia et al., 2022; Hou et al., 2025). Wild populations are limited not only by overexploitation but also by biological constraints, including low seed-setting rates, lack of seed endosperm, and dependence on symbiosis with endophytic fungi for natural germination (Liu et al., 2025b; Luo et al., 2024). As an epiphyte, *D. officinale* is adapted to growing on trees, rocks, or other well-aerated supports rather than in compact agricultural soils, and this ecological background remains the biological basis for current stone- and tree-attached production systems (Tan et al., 2023). Current industrial cultivation therefore relies heavily on tissue culture propagation and artificial seedling production to compensate for its low natural reproductive efficiency and endangered status.

Its ecological adaptability is notable but conditional. *D. officinale* shows physiological flexibility in carbon assimilation, functioning as a facultative CAM plant in which the balance between C3 and CAM photosynthesis shifts with environmental conditions. Decreasing substrate water content induces a more typical CAM pattern, while rewatering promotes a return toward mixed C3-CAM behavior, indicating an adaptive response to intermittent water deficit common in epiphytic habitats. This plasticity supports survival under drought, heat, and nutrient limitation, but adaptation is not unlimited: karst forest cultivation often faces severe water shortage, slow growth, and low yield, and recent work shows that combined high temperature and drought stress can markedly impair morphology, antioxidative status, yield, and polysaccharide accumulation, with clear differences among germplasm types (Luo et al., 2024; Gao et al., 2026). Endophytic and mycorrhizal fungi are therefore not incidental associates but part of its adaptive strategy, because they can improve growth, drought tolerance, disease resistance, and overall stress resilience (Li et al., 2021).

2.2 Requirements for light, temperature, humidity, and substrate

The growth and quality formation of *D. officinale* depend strongly on coordinated regulation of light, temperature, humidity, and water status. Multiple studies identify light, temperature, and water as major environmental cues affecting photosynthesis, growth rate, and active-compound synthesis (Zhang et al., 2024). *D. officinale* is a photosensitive plant, and inappropriate shading leads to unstable yield and quality. Evidence from light-gradient experiments indicates that moderate light is preferable to either extreme: under 11 000 lx, plants achieved peak biomass, maximal bioactive compound yield, superior fresh-consumption quality, and lower oxidative stress, whereas excessive light increased antioxidant enzyme activity and structural carbohydrate accumulation but suppressed plant height and edible quality. Greenhouse trials likewise found that 50~70% shade improved growth and biomass, while red light favored biomass production and increased polysaccharide and alkaloid contents (Nguyen et al., 2023).

Temperature and humidity must also be controlled within a relatively narrow ecological window. *D. officinale* has strict climatic requirements, and quality-related components are significantly associated with ecological variables such as maximum and minimum relative humidity, maximum temperature, and sunshine duration (Yuan et al., 2020). Recent synthesis further suggests that breaking the coupling of high temperature and high humidity is important for preventing southern blight, highlighting that warm and moist conditions are beneficial only when they do not cross the threshold for disease outbreaks (Liu et al., 2025b). Substrate conditions are equally important because this species is epiphytic and requires a loose, breathable rooting environment rather than dense field soil (Ding et al., 2018). Pine bark-based substrates appear especially suitable: one study reported high flavonoid accumulation in pine bark substrate (Zhang et al., 2024), while greenhouse-grown plants in physiological experiments were maintained successfully in a mixed substrate of pine bark fractions, perlite, and composted sawdust. Nutrient supply also shapes quality traits, as potassium treatment significantly increased anthocyanin accumulation and flavonoid-related metabolic responses, indicating that substrate fertility management is part of quality-oriented cultivation rather than merely biomass production (Jia et al., 2022).

2.3 Environmental regulation under different cultivation modes

The two main artificial production pathways for *D. officinale* are facility cultivation and wild-simulated or semi-wild cultivation, and the environmental regulation logic of these systems differs fundamentally (Yang et al., 2026). Facility cultivation emphasizes controllability, using greenhouse structures and monitoring systems to stabilize light, humidity, substrate moisture, and temperature. In related greenhouse control work, real-time monitoring and intelligent prediction based on soil temperature, soil moisture, humidity, and light achieved prediction error below 2.5%, showing that facility systems can support precise microclimate management. Wild-simulated cultivation, by contrast, relies on shade, breathable substrates, open ecological planting (Ding et al., 2018). This mode places greater emphasis on matching the original habitat and maintaining ecological interactions, including microbial and fungal symbioses (Liu et al., 2025b).

These different regulatory strategies lead to different biological and quality outcomes. Greenhouse cultivation can increase production stability, but it also changes growth patterns relative to wild plants and shifts the dominant

environmental drivers of quality from rainfall and temperature toward altitude and sunlight. Wild-simulated systems generally reproduce an ecological environment closer to natural habitat, and in related *Dendrobium* comparisons they produced plant form more similar to wild material, higher active-ingredient content, and stronger overall quality performance than facility cultivation (Yi et al., 2021). Evidence in *D. officinale* itself also indicates that cultivation environment substantially affects metabolite accumulation and medicinal quality: wild material showed the highest polysaccharide content in one large analysis, 3~4 year-old plants outperformed younger plants, and stone or tree epiphytic environments produced distinct metabolite profiles and therapeutic differences relative to greenhouse conditions (Hou et al., 2025). Overall, facility cultivation is better suited to standardized, high-efficiency production, whereas wild-simulated cultivation better aligns with the ecological habits of *D. officinale* and often favors quality-oriented production, making comparative evaluation of the two modes essential for optimizing both yield and medicinal value.

3 Wild-Simulated Cultivation Analysis of *Dendrobium officinale*

3.1 Environmental selection and key technical characteristics

Wild-simulated cultivation of *Dendrobium officinale* is designed to preserve medicinal quality by reconstructing the plant's original habitat as closely as possible rather than maximizing environmental control (Zhang et al., 2020; Yi et al., 2021). This logic fits the biological habit of *D. officinale* as an epiphytic orchid that naturally grows on rocks or tree trunks in well-aerated niches (Tan et al., 2023; Hou et al., 2025). Site selection therefore emphasizes forest or mountainous environments with appropriate shade, ventilation, and humidity, while avoiding prolonged coupling of high temperature and high humidity that favors southern blight (Liu et al., 2025b). In *D. officinale*, key quality-related ecological variables include maximum and minimum relative humidity, maximum temperature, sunshine duration, soil pH, and substrate nitrogen and phosphorus status, indicating that wild-simulated bases must be selected for both microclimate and nutrient conditions (Yuan et al., 2020; Wang et al., 2025).

Technically, wild-simulated cultivation usually relies on tissue-culture seedlings transplanted onto stone or tree-attached substrates, with the aim of restoring natural epiphytic growth conditions while maintaining production feasibility (Figure 1) (Hou et al., 2025; Liu et al., 2025b). Reported field designs include lithophytic cultivation on vertical rock walls under natural light and tree epiphytic cultivation under 70~80% canopy shade or comparable artificial shading. Core technical steps commonly include base cleaning, disinfection, construction of breathable woody or bark-based media, mist or spray irrigation, water-fertilizer management, and ecological pest control, while some systems use biogas slurry, organic amendments, or interplanting for low-residue management. Current evidence also highlights the importance of integrating mycorrhizal or endophytic fungi, because fungal co-culture supports germination, seedling establishment, stress resistance, and quality stability in restoration-friendly epiphytic cultivation (Zhang et al., 2020; Wang et al., 2021).

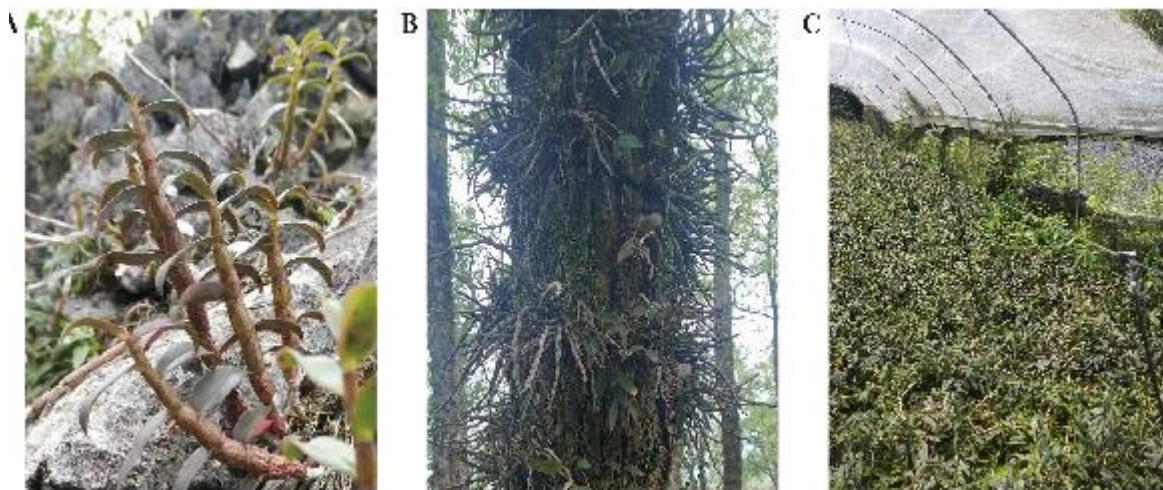


Figure 1 The three growth environments of *D. officinale* (Adopted from Hou et al., 2025)

Image caption: (A) Stone epiphytic culture environment in the wild; (B) Tree epiphytic culture environment in the wild; (C) Greenhouse culture environment (Adopted from Hou et al., 2025)

3.2 Growth performance and quality formation

Under wild-simulated conditions, *D. officinale* generally shows growth patterns closer to wild plants than those observed under greenhouse production (Lan et al., 2022). This mode does not always maximize biomass or total yield, but it better matches the species' ecological habit and often improves structural and sensory characteristics associated with traditional high-quality material (Yi et al., 2021). Growth performance in such systems remains strongly constrained by water availability and climate stress, especially in karst forest environments where drought and high temperature can slow growth and reduce yield. For this reason, strain screening for drought adaptation and physiological resilience has become an important support technology for wild-simulated production (Luo et al., 2024).

The main strength of wild-simulated cultivation lies in quality formation. Studies in *D. officinale* show that wild stone-epiphytic material contains higher polysaccharide, flavonoid, and alkaloid levels than greenhouse material, and stone epiphytic stems can accumulate substantially more up-regulated metabolites, especially flavonoids, than tree-epiphytic or greenhouse stems. In one comparative study, stone-epiphytic stems also showed stronger protective effects in chronic atrophic gastritis cell models, linking metabolite differences to functional differences (Hou et al., 2025). Related evidence across *Dendrobium* species is consistent: wild-simulated cultivation often yields higher levels of polysaccharides, flavonoids, alkaloids, amino acids, or non-starch polysaccharides than greenhouse cultivation, even though some individual studies report higher total polysaccharides in greenhouse-grown samples, showing that quality differences depend on the compound measured and the cultivation context (Hu et al., 2024). Mechanistically, this likely reflects the combined effects of habitat-like stress, niche-specific light and water regimes, and richer microbial interactions, all of which promote secondary metabolite accumulation and alter biosynthetic gene expression (Zhang et al., 2020).

3.3 Advantages, limitations, and application value

Compared with facility cultivation, wild-simulated cultivation offers several clear advantages. It restores the wild habitat more faithfully, produces plant morphology closer to traditional medicinal standards, and often increases the content of major active constituents and overall medicinal quality (Hou et al., 2025). Semi-wild systems are also associated with lower planting density, greater resistance to pests and diseases, reduced chemical residues, and stronger ecological compatibility. At the industry level, this mode fits the transition from purely sheltered mass production toward diversified ecologically friendly cultivation and helps connect commercial production with biodiversity conservation (Cheng et al., 2019; Wang et al., 2021). It is therefore valuable not only for medicinal quality control, but also for sustainable branding of high-end medicinal, edible, and health products derived from *D. officinale* (Liu et al., 2025b; Wang et al., 2025).

Its limitations are equally clear. Wild-simulated cultivation usually has lower yield, slower growth, and higher labor dependence than facility cultivation, and its outcomes are more vulnerable to drought, abnormal temperature, and site heterogeneity (Luo et al., 2024). Quality is often better, but not uniformly so across all indicators; for example, some studies found greenhouse or lithophytic systems superior to tree-epiphytic systems for polysaccharide content, and greenhouse-grown *D. huoshanense* showed higher total polysaccharides than imitation wild plants in one dataset (Hu et al., 2024). These mixed findings indicate that wild-simulated cultivation is not simply a high-quality shortcut, but a mode whose value depends on correct site selection, suitable germplasm, fungal support, and targeted quality indicators (Lan et al., 2022). Overall, wild-simulated cultivation is best understood as a quality-oriented and conservation-compatible production pathway with strong application value for premium *D. officinale*, especially when combined with standardized seedlings, ecological regulation, and modern quality evaluation methods (Yang et al., 2026).

4 Facility Cultivation Mode of *Dendrobium officinale*

4.1 Environmental regulation and standardized production technologies

Facility cultivation of *Dendrobium officinale* is a production mode centered on artificial environmental control, standardized seedling use, and integrated cultivation management to achieve stable and large-scale supply (Cheng et al., 2019). In recent years, greenhouse cultivation has become one of the main artificial cultivation modes

developed to relieve pressure on wild resources and meet expanding market demand (Yang et al., 2023). Its technical logic is to create a controllable microenvironment around this epiphytic orchid, because the accumulation of medicinal components is strongly affected by light, temperature, humidity, water, and nutrient conditions (Yuan et al., 2020; Jia et al., 2022). Greenhouse systems therefore regulate shade, irrigation, ventilation, humidity, and substrate conditions more intensively than wild-simulated systems, so that plants grow under relatively suitable and less fluctuating conditions while disease risk is reduced as much as possible (Liu et al., 2025b).

Standardized production in facility cultivation begins with industrial tube seedlings and high-quality transplant material, because seedling quality directly affects survival, vigor, and later yield (Cheng et al., 2019). Existing standards and technical procedures already provide guidance for cultivation, but national-level production standards are still incomplete, so further unification of germplasm, nursery, and production specifications remains necessary. Facility cultivation also supports precision regulation through monitored parameters such as soil or substrate temperature, moisture, air humidity, and light, and intelligent control models have been developed with prediction error below 2.5%, showing the feasibility of data-based environmental management (Ding et al., 2018). At the cultivation-operation level, standardized facility production usually includes seedling propagation, substrate optimization, disinfection, transplantation, shade management, water-fertilizer regulation, and eco-friendly pest control, with substrate, fertilization, and harvest timing all recognized as important determinants of final medicinal quality.

4.2 Yield formation and quality regulation

Under facility conditions, yield formation is shaped by the interaction of seedling quality, cultivation structure, environmental regulation, and growth duration. Greenhouse cultivation is widely adopted because it can provide a more stable production environment and generally higher biomass and stem yield than less protected systems (Yang et al., 2023). High-quality seedlings show higher survival, stronger growth vigor, and higher stem yield after transplantation, indicating that yield improvement begins at the nursery stage rather than only in field management. Growth duration also matters: dendrobine content increased with planting years in one cultivation study, but nutrient-accumulation comparisons under artificial-sheltered cultivation found the best harvest time in the third year in both southern and northern sites, indicating that the optimal harvest stage depends on the target quality trait rather than on biomass alone (Guo et al., 2021). Expanding facility cultivation northward further links yield to varietal adaptation, because low temperature is a major limitation in new production areas and cold-resistant strains can improve transplantation success, survival, and economic returns.

Quality regulation under facility cultivation depends on deliberate manipulation of environmental and nutritional signals. Light is one of the strongest regulators: moderate light intensity improved multifunctional traits, while red light promoted expression of a key polysaccharide-synthesis gene and also improved growth, biomass, and polysaccharide and alkaloid accumulation in greenhouse experiments (Wang et al., 2024). Light and potassium treatments significantly increased anthocyanin accumulation and shifted metabolite and transcript profiles toward flavonoid and phenylpropanoid biosynthesis, showing that facility quality control can act through coordinated metabolic regulation rather than simple stress avoidance (Jia et al., 2022). Temperature regime is likewise regulatable in protected production: a day-night temperature difference of 25/13°C was more favorable than constant-temperature treatments for chlorophyll, polysaccharides, and total flavonoids in protocorm-like bodies, with corresponding changes in genes related to sugar and flavonol metabolism (Chen et al., 2024). Substrate and growth regulators also affect quality, as pine bark substrate favored flavonoid accumulation, and field application of 2,4-epibrassinolide increased stem and leaf polysaccharide-related sugars, with dried-stem polysaccharide rising by as much as 61% after 35 days in one study (Lu et al., 2025).

4.3 Advantages, challenges, and industrial application prospects

The main advantage of facility cultivation is its suitability for standardized, large-scale production. It has been a core driver of the transition from wild collection to massive commercial artificial-sheltered cultivation and has effectively alleviated the historical supply-demand imbalance of *D. officinale*. Facility production supports stable

raw-material supply, scalable seedling propagation, expansion of cultivation areas, and the formation of complete industrial chains from cultivation to processing and health-product manufacture (Figure 2) (Cheng et al., 2019). It also offers practical residue-control advantages when managed well: one standardized comparison found no organophosphorus pesticide residues in growth-chamber cultivation, whereas residues were detected in bedstead production. These features make facility cultivation especially important for supplying medicinal, food, and health-product markets that require stable volume, traceability, and manageable production schedules.

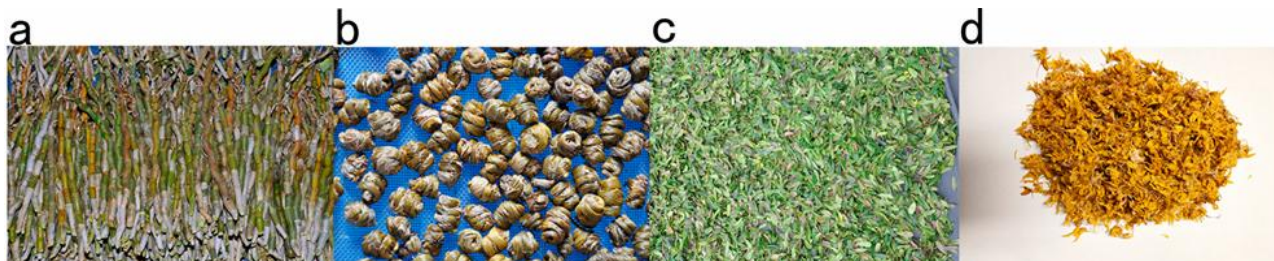


Figure 2 The usable parts and forms of *Dendrobium officinale* (Adopted from Cheng et al., 2019)

Image caption: (a) Stems; (b) Tiepi Fengdou; (c) Leaves; (d) Dry flowers (Adopted from Cheng et al., 2019)

Its challenges are equally clear. Evidence across comparative studies shows that artificial-sheltered or greenhouse cultivation can alter phenotype, metabolite composition, and sometimes medicinal efficacy relative to more natural cultivation environments, so higher controllability does not automatically mean higher medicinal quality (Jia et al., 2022; Yi et al., 2026). The industry also faces germplasm mixing, uneven quality and yield, incomplete national standards, and a still-low level of deep product development (Cheng et al., 2019). In addition, some comparative evidence suggests that greenhouse-grown material can be inferior to stone-epiphytic material for broad metabolite richness and some functional outcomes, even though greenhouse samples may equal or exceed other modes for specific indicators such as polysaccharides (Yang et al., 2023; Hou et al., 2025). Even with these limitations, facility cultivation has strong industrial prospects because *D. officinale* is now embedded in the expanding food-medicine homology sector, provincial standards for leaves and flowers are emerging, ISO-related standardization is advancing, and the genus already has broad economic value in medicinal, food, ornamental, and cosmetic applications. Overall, facility cultivation is best positioned as the scale and standardization platform of the *D. officinale* industry, while future progress depends on better varieties, tighter standards, lower chemical inputs, and more precise quality-oriented environmental regulation.

5 Comprehensive Comparison of Wild-Simulated and Facility Cultivation Modes

5.1 Differences in ecological environment and production management between the two modes

Wild-simulated cultivation and facility cultivation differ first in their basic ecological logic. Wild-simulated cultivation aims to restore the original habitat and site conditions of *Dendrobium officinale* as much as possible, typically through stone or tree epiphytic planting in forested or mountainous settings with more natural light, airflow, microbial communities, and environmental fluctuation (Zhang et al., 2020; Lan et al., 2022). Facility cultivation instead relies on greenhouse or other sheltered systems that create a controllable microenvironment through artificial shade, irrigation, ventilation, and substrate management. This ecological contrast matters because the main medicinal components of *D. officinale* are tightly linked to growing conditions, including relative humidity, maximum temperature, sunshine duration, soil pH, and substrate nitrogen and phosphorus status (Wang et al., 2025). Recent predictive work also suggests that greenhouse cultivation changes the environmental drivers of polysaccharide accumulation, shifting key influences from rainfall and temperature toward altitude and sunlight and moving high-quality production zones away from the pattern seen in wild habitats (Yang et al., 2026).

The two modes also differ substantially in production management. Wild-simulated systems usually emphasize ecological base selection, breathable epiphytic substrates, moderate shade, lower planting density, and the preservation of symbioses with endophytic or mycorrhizal fungi, because fungal interactions contribute to growth, stress resistance, and quality stability (Zhang et al., 2024; Liu et al., 2025b). Facility cultivation emphasizes

standardized seedlings, intensive water-fertilizer regulation, substrate optimization, and real-time environmental monitoring, which makes production more uniform and easier to schedule at large scale (Cheng et al., 2019). The two systems therefore differ not only in openness versus controllability, but also in biological regulation: wild-simulated cultivation uses niche matching and moderate stress to guide plant development, whereas facility cultivation uses technical intervention to reduce environmental variability and stabilize growth (Zhang et al., 2020). In practical terms, wild-simulated cultivation is closer to the ecological habit of an epiphytic orchid, while facility cultivation is closer to a standardized industrial production platform (Tan et al., 2023; Hou et al., 2025).

5.2 Comparative effects on yield, quality, and accumulation of active compounds

Across studies, facility cultivation tends to perform better for yield stability and production efficiency, while wild-simulated cultivation more often favors medicinal quality and the accumulation of diverse active compounds. Reviews of the industry consistently note that semi-wild systems usually have lower yields and higher labor costs, whereas greenhouse systems are used precisely because they can alleviate supply shortages and support stable large-scale output (Cheng et al., 2019). Comparative work in *Dendrobium huoshanense* likewise found that greenhouse cultivation had higher productivity and was more suitable for daily functional-food or health-product use (Hu et al., 2024). Facility systems can also be optimized further through standardized seedling production, strain selection, and controlled additive or nutritional treatments, all of which improve biomass or transplant survival (Liu et al., 2025a). Even so, yield advantage does not consistently translate into superior medicinal quality, because greenhouse conditions often reshape growth patterns and metabolite allocation relative to more natural environments (Yang et al., 2026; Yi et al., 2026).

Across *D. officinale* and related *Dendrobium* species, the available evidence tends to favor, especially when multiple compound classes or functional outcomes are considered. Simulative habitat cultivation produced morphology closer to wild material and higher quality than facility cultivation in *D. huoshanense* (Yi et al., 2021), and wild-simulated material showed higher levels of polysaccharides, flavonoids, alkaloids, amino acids, and other nutritional constituents in several comparative studies. In *D. officinale*, stone-epiphytic material showed 58 up-regulated metabolites relative to tree-epiphytic and greenhouse material, including seven amino-acid derivatives and eighteen flavonoids, and it also showed stronger protective effects in a chronic atrophic gastritis cell model (Hou et al., 2025). Wild-simulated or epiphytic systems also produced higher non-starch polysaccharide ratios and stronger antioxidant activity than facility cultivation in *D. catenatum*. However, this pattern is not absolute: one *D. huoshanense* study found higher total polysaccharide content in greenhouse-grown samples (Hu et al., 2024), and one *D. officinale* comparison reported that greenhouse and lithophytic cultivation both exceeded living-tree epiphytic cultivation in polysaccharide content. The strongest conclusion is therefore that facility cultivation can perform well for selected indicators, especially bulk polysaccharide production, but wild-simulated cultivation more consistently improves composite quality, metabolite richness, and some bioactivity-related outcomes.

5.3 Comparison of economic benefits and industrial applicability

From an economic perspective, the two modes serve different market positions. Facility cultivation is more suitable for scale, standardization, and stable supply, which is why it has become a major foundation of the modern *D. officinale* industry and of the transition from wild collection to commercial cultivation (Cheng et al., 2019). It supports expansion of planting areas, integration with seedling factories and processing chains, and the reliable supply of raw materials for pharmaceuticals, dietary supplements, foods, and related products (Liu et al., 2025a). Facility cultivation also fits precision agriculture and standardized production goals, especially as technical procedures, improved substrates, and environmental regulation systems continue to advance (Yang et al., 2026). For these reasons, facility cultivation has the broader industrial applicability in mass-market contexts, particularly where output consistency, traceability, and scalable processing matter most (Wang et al., 2025).

Wild-simulated cultivation has a different economic logic: it is less advantageous for maximum output, but often more advantageous for premium positioning, ecological value, and high-end medicinal use. One direct comparison in *D. huoshanense* reported that simulated habitat cultivation had high income, the lowest

input-output ratio, and significant economic benefit overall. One study reported prices approximately 5~10 times higher than greenhouse products, even though greenhouse cultivation had higher yield (Hu et al., 2024). Wild-simulated systems also align better with conservation-compatible and ecologically friendly industry development, because they connect medicinal-material production with habitat restoration, biodiversity protection, and lower chemical-residue expectations (Cheng et al., 2019). Their limitations remain clear: they are more labor-intensive, more dependent on suitable sites and microclimates, and less suited to rapid volume expansion. Overall, facility cultivation is the main route for large-scale industrial supply, whereas wild-simulated cultivation is better suited to quality-oriented, high-value, and ecological segments of the *D. officinale* industry (Zhang et al., 2020).

6 Optimization and Future Development of *Dendrobium officinale* Cultivation Modes

6.1 Promoting integrated cultivation systems combining the advantages of wild-simulated and facility modes

The future direction of *D. officinale* cultivation is not a simple replacement of one mode by another, but the construction of integrated systems that combine the stability of facility cultivation with the quality advantages of wild-simulated cultivation. Earlier work had already identified bionic-facility cultivation, original ecological cultivation, and pot cultivation as parallel technical routes, indicating that hybridized mode design is a recognized development path in *D. officinale* production (Yuan et al., 2020). This integrated logic is biologically reasonable because *D. officinale* depends on strict environmental conditions, while its quality remains tightly linked to ecological factors such as humidity, temperature, sunshine duration, pH, and substrate nutrient status (Ding et al., 2018). At the same time, simulated habitat systems more closely reproduce the wild environment and often deliver better plant form, higher medicinal-component accumulation, and stronger overall quality performance in related *Dendrobium* comparisons (Yi et al., 2021).

An optimized integrated system should therefore use facility conditions mainly for seedling propagation, transplantation buffering, and early-stage growth stabilization, then guide plants toward bionic, epiphytic, or understory production environments during quality-formation stages (Hou et al., 2025). Such a system can be further strengthened by matching variety breeding, site selection, and co-culture with endophytic fungi, which recent synthesis identifies as a key route for efficient cultivation. Wild-mimic integrated techniques already show that tissue-culture seedlings can be transplanted into breathable understory substrates with survival rates above 95%, while maintaining high effective-component content, low residue, and relatively convenient management. Under carbon-neutrality goals, this integration also has ecological significance, because simulative habitat cultivation in related *Dendrobium* systems produced far lower CO₂ emissions and global warming potential than facility cultivation, supporting the value of shifting at least part of production toward carbon-friendly hybrid systems (Tian et al., 2025).

6.2 Strengthening precision environmental regulation and green cultivation technologies

Precision environmental regulation should become the technical core of future facility and semi-facility cultivation, because the main medicinal components of *D. officinale* are strongly shaped by environmental variables rather than by cultivation mode label alone (Yuan et al., 2020). Greenhouse control research shows that soil temperature, soil moisture, air humidity, and light can be monitored and modeled for real-time regulation, with average prediction error below 2.5%, providing a workable basis for precision cultivation (Ding et al., 2018). More recent intelligent agriculture work goes further: an IoT edge-computing and digital-twin control system improved temperature-control precision to $\pm 0.7^{\circ}\text{C}$, increased production by 23.6%, and reduced energy use by 42.6% across climates. Data-driven rule mining from greenhouse climate sensors also replicated about 80% of the climatic conditions associated with successful past cultivation, indicating that knowledge-based environmental replication can help maintain more consistent quality (Sun et al., 2018).

Future green cultivation should not pursue high inputs alone, because increased planting density and greater use of fertilizers, growth regulators, and pesticides in greenhouse systems can raise toxic and hazardous residues (Yuan et al., 2020). Recent industrial reviews therefore emphasize reducing chemical fertilizer and pesticide use,

improving disease and pest management, and establishing economically and environmentally sustainable production systems. Practical green technologies already supported in the literature include pine-bark or woody breathable substrates, organic nutrient inputs, understory shading, mist irrigation, and ecological pest-control designs, as well as mycorrhizal or endophytic-fungal application to improve drought resistance, disease resistance, and quality stability (Zhang et al., 2024). In addition, precision cultivation should shift from post-harvest correction to pre-plantation zoning, because machine-learning evidence shows that facility agriculture changes the key environmental drivers of polysaccharide accumulation and shifts high-quality production areas geographically (Yang et al., 2026).

6.3 Improving quality evaluation systems and standardized production systems

A major bottleneck in future development is that current quality evaluation still relies too heavily on polysaccharide content alone. Multiple studies state that polysaccharides are the main or even sole pharmacopoeial quality marker now in use (Tan et al., 2023), but metabolomics evidence shows that this standard is incomplete because secondary-metabolite patterns can move in the opposite direction from polysaccharide rankings across regions and cultivation environments (He et al., 2022). Recent multidimensional work strengthens this point by identifying 1 929 metabolites in stems from different cultivation environments and showing that stone-epiphytic samples had 58 up-regulated metabolites, especially flavonoids, along with stronger cell-level protective effects (Hou et al., 2025). Future quality evaluation should therefore move toward multi-index systems that jointly consider polysaccharides, flavonoids, alkaloids, polyphenols, oligosaccharide markers, and bioactivity-linked fingerprints (Wong et al., 2019).

Analytical technology for this transition is already available. Near-infrared spectroscopy combined with chemometrics can rapidly predict polysaccharides, polyphenols, total flavonoids, and total alkaloids and can identify geographical origin with very high accuracy (Yang et al., 2022). Oligosaccharide-marker methods and spectrum-effect approaches also provide rapid, validated, and functionally meaningful routes for polysaccharide-related quality control (Wong et al., 2019). Standardized production must advance in parallel, because the mixing of germplasm has already caused major variation in yield and quality, while national production standards are still lacking despite existing technical procedures, provincial food standards, and ongoing ISO alignment. Accordingly, future development should build a full-chain standardized system covering germplasm identification, seedling production, cultivation-mode matching, harvest timing, processing, and rapid quality verification, so that *D. officinale* can develop toward high-quality, green, and industrially consistent production (Gu et al., 2017; Hou et al., 2025).

7 Conclusion of Cultivation Modes

Wild-simulated cultivation and facility cultivation represent the two major production modes of *Dendrobium officinale* in current industrial development. Wild-simulated cultivation reconstructs the natural habitat and epiphytic environment of *D. officinale* through forest, rock, or tree-attached cultivation, allowing plants to grow under ecological conditions closer to the wild state. This mode promotes secondary metabolism through environmental adaptation, microbial interactions, and moderate ecological stress, and generally contributes to the formation of wild-like morphological characteristics and improved comprehensive quality. Facility cultivation, in contrast, relies on greenhouse-based environmental regulation, standardized seedlings, and precise water-fertilizer management to achieve stable and large-scale production. It has clear advantages in yield stability, production efficiency, and industrial supply capacity. However, artificial environments may alter plant metabolic characteristics and quality formation processes, and further optimization of quality regulation technologies is still required.

The selection of cultivation mode should be determined according to specific production objectives rather than based on a single evaluation criterion. For large-scale raw material supply, standardized production, and integration with pharmaceutical, food, and health-product industries, facility cultivation is more suitable due to its stable yield, standardized management, and high production efficiency. In contrast, wild-simulated cultivation has greater potential for premium medicinal materials, ecological branding, and high-value products, owing to its

advantages in active compound accumulation and ecological characteristics. However, neither mode has absolute superiority, as quality formation is influenced by cultivation environment, evaluation indicators, and plant developmental stage. Therefore, differentiated development strategies should be adopted: facility cultivation should focus on large-scale, standardized, and functional-product supply, whereas wild-simulated cultivation should target quality-oriented, high-value, and ecologically distinctive products.

Future development of the *D. officinale* industry should emphasize the integration of advantages from both cultivation modes rather than expanding either system independently. A composite production strategy, such as “facility-based seedling propagation combined with ecological cultivation for quality improvement,” can effectively combine production efficiency with medicinal quality enhancement. Meanwhile, precision environmental regulation, green cultivation technologies, and intelligent management should be further applied to improve production stability and quality consistency. In addition, quality evaluation systems should move beyond reliance on a single polysaccharide indicator and develop comprehensive evaluation frameworks incorporating polysaccharides, flavonoids, alkaloids, metabolomic characteristics, and bioactivity-related parameters. By improving germplasm management, production standards, and quality traceability systems, the *D. officinale* industry can achieve sustainable development characterized by high quality, high efficiency, and ecological compatibility.

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

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Construction of a Standardized Cutting Propagation and Seedling Production System for *Tetrastigma hemsleyanum*

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Abstract *Tetrastigma hemsleyanum* Diels et Gilg is an important medicinal plant resource in China with considerable medicinal value and development potential. However, the decline of wild resources, its relatively long growth cycle, and the insufficient supply of high-quality seedlings have constrained large-scale cultivation and industrial development. Cutting propagation offers several advantages, including the preservation of elite germplasm traits, a relatively short propagation cycle, simple operation, and suitability for large-scale seedling production, making it an important approach for producing high-quality *T. hemsleyanum* planting material. This article focuses on the construction of a standardized cutting propagation and seedling production system for *T. hemsleyanum*. It analyzes shoot regenerative characteristics, adventitious root formation, and the major factors affecting rooting, and systematically summarizes key techniques involving elite mother-plant selection, cutting type and specification, collection and rooting pretreatment, rooting substrate optimization, plant growth regulator application, cutting season, and planting density regulation. Seedling management measures involving temperature, humidity, water supply, light, shading, ventilation, nutrient supply, and pest and disease control are further discussed. On this basis, a standardized seedling production framework is proposed covering hardening and transplanting of rooted cuttings, seedling quality evaluation and grading, nursery release standards, and whole-process quality traceability. In view of current limitations, including insufficient screening of elite mother plants and high-rooting materials, inconsistent technical parameters and seedling quality standards, and relatively low levels of facility-based and digitalized production, future priorities should include strengthening elite germplasm selection, improving standardized operating procedures, and promoting facility-based, large-scale, and intelligent seedling production. This article provides a reference for improving cutting propagation efficiency, ensuring a stable supply of high-quality seedlings, and promoting the sustainable utilization of *T. hemsleyanum* medicinal resources.

Keywords *Tetrastigma hemsleyanum*; Cutting propagation; Adventitious root; Standardized seedling production; Seedling quality

1 Introduction

Tetrastigma hemsleyanum Diels et Gilg, commonly known as Sanyeqing, is a perennial climbing vine in the Vitaceae that has long been used in Chinese folk medicine and is widely recognized as a valuable traditional medicinal plant (Ji et al., 2021). Traditional and contemporary uses center on the tuberous roots and, in some contexts, the whole herb or aerial parts, which are used to clear heat, detoxify, reduce swelling and pain, promote blood circulation, and treat conditions such as high fever, pneumonia, hepatitis, pharyngeal disorders, convulsions, and inflammatory diseases (Zhu et al., 2020; Xia et al., 2023). Modern phytochemical studies show that the species contains a wide range of bioactive constituents, including flavonoids, phenolic acids, polysaccharides, triterpenoids, steroids, and organic acids, with flavonoids and polysaccharides regarded as the representative active components. These compounds underpin broad pharmacological activities, including anti-tumor, anti-inflammatory, antioxidant, antiviral, antibacterial, antipyretic, analgesic, hepatoprotective, and immunomodulatory effects (Wang et al., 2025). Mechanistic and spectrum-effect studies further indicate that *T. hemsleyanum* extracts can inhibit inflammatory signaling and tumor cell proliferation, while recent work on polysaccharides suggests additional antitumor activity through immune enhancement and gut microbiota regulation (Zhou et al., 2022). Because of this combination of long-standing medicinal use and expanding modern pharmacological evidence, *T. hemsleyanum* is increasingly regarded as a resource plant with high economic, social, and drug-development value (Hu et al., 2021; Pang et al., 2024).

At the same time, the industrial development of *T. hemsleyanum* remains constrained by resource scarcity, biological characteristics, and unstable production systems. Wild resources have been heavily overexploited and are now scarce or close to extinction in some regions, and the species has been described as endangered, rare, and precious because of its medicinal value and strict ecological requirements (Ji et al., 2021; Pang et al., 2024). The plant usually needs 3-5 years to form medicinally usable true roots, grows slowly, and is sensitive to habitat conditions such as shade and temperature, all of which limit rapid supply expansion (Zhu et al., 2020; Wang et al., 2023). Demand, however, continues to increase because the tuberous roots is the most valuable medicinal organ and the plant is already cultivated on a large scale in some areas, although its current planting modes are described as chaotic or inconsistent and the industry still lacks a scientific and measurable quality-control basis (Xia et al., 2023). Artificial cultivation has progressed over the past two decades, and greenhouse plus stereoscopic planting has been reported to improve biomass, flavonoid accumulation, yield, and overall herb quality relative to less optimized systems (Hu et al., 2023; Wang et al., 2025). Even so, the industry still faces the basic problem of producing enough uniform, high-quality planting material, which is a common bottleneck in medicinal crops and directly affects later yield, quality consistency, and resource conservation (Manohar et al., 2022; Muniandi et al., 2025).

The main propagation routes currently available for *T. hemsleyanum* include seed propagation, stem cutting, and tissue-culture-based rapid propagation, each with distinct practical advantages and limitations. Seed propagation offers a sexual route for population establishment, but in many medicinal plants it often produces heterogeneous offspring, and in *T. hemsleyanum* seed yield is already reported to be low, which limits its value for rapid industrial multiplication (Muniandi et al., 2025). Tissue culture and organogenesis can achieve high multiplication efficiency and disease-free material; for *T. hemsleyanum*, adventitious shoots have been regenerated from leaves and petioles, 100% rooting was achieved on media containing NAA or IBA, and acclimatized plantlets showed over 98% survival in peat:sand substrate (Pang et al., 2024). Axillary-bud rapid propagation and hairy-root systems also show strong biotechnological potential for mass propagation, conservation, and secondary metabolite production (Wang et al., 2023). However, tissue culture often requires specialized facilities, sterile operation, and higher costs, and in other medicinal plants it remains less accessible at farm level despite technical promise (Ioannidis et al., 2022). By contrast, cutting propagation preserves superior genotypes, enables relatively rapid and true-to-type multiplication, and is more compatible with nursery-scale and field-linked production systems. Species-specific evidence in *T. hemsleyanum* already shows that rooting reagent and cutting age significantly affect rooting, and that 2-3-year-old cuttings treated with 1 000 mg/L IBA for 10 s gave the best tested response, providing a direct technical basis for protocol development. More broadly, studies in medicinal species show that cutting success depends on mother-stock quality, cutting position, leaf retention, season, substrate, hormone treatment, and environmental regulation, which means that the value of cuttings lies not only in the method itself but in the possibility of standardizing it into a reproducible production chain (Zhang et al., 2025; Dumani et al., 2026; Vuong et al., 2026).

This article examines the construction of a standardized cutting propagation and seedling production system for *Tetrastigma hemsleyanum* by integrating research findings on elite mother-plant selection, cutting material selection and specification, rooting induction, environmental regulation, seedling quality grading, and whole-process quality traceability. On this basis, the effects of mother-plant and cutting quality, rooting substrates, plant growth regulators, temperature, humidity, and light conditions on rooting and seedling establishment will be systematically analyzed, and a standardized technical pathway covering propagation material selection, rooting regulation, seedling-stage management, quality grading, and nursery release will be developed. Establishing a relatively complete cutting-based seedling production system is expected to improve propagation efficiency and seedling uniformity, reduce nursery losses, and provide high-quality planting material for the stable multiplication of elite medicinal germplasm and large-scale artificial cultivation. In addition, this article address current problems such as inconsistent propagation parameters and the lack of unified seedling quality standards, and will propose future directions toward facility-based, standardized, and digitalized nursery production. These efforts will strengthen whole-process quality control from mother-plant origin to commercial seedlings, promote

coordination among germplasm conservation, standardized cultivation, and medicinal-material quality stability, and provide technical support for the sustainable utilization and high-quality industrial development of *T. hemsleyanum* resources.

2 Biological Basis of Cutting Propagation in *Tetrastigma hemsleyanum*

2.1 Shoot growth characteristics and regenerative capacity of cuttings

Tetrastigma hemsleyanum has clear regenerative potential, but current production still indicates that conventional cutting propagation yields are limited and require optimization for commercial multiplication (Pang et al., 2024). Evidence from in vitro regeneration shows that its vegetative organs retain strong organogenic competence, since leaves and petioles can regenerate adventitious shoots efficiently and axillary buds can be induced to proliferate rapidly under suitable culture conditions. This broad regenerative capacity supports the biological feasibility of building a cutting-based seedling system, because the species is not regeneration-deficient in principle but instead appears sensitive to the specification of propagule type and culture conditions.

The regenerative performance of cuttings depends strongly on the physiological status of the shoot segment, especially its age, maturity, reserve status, and nodal activity (Wei et al., 2019; Liu et al., 2025). In *T. hemsleyanum*, the strongest direct evidence is that 2-3-year-old cuttings rooted better than other ages, indicating that propagation material must balance juvenility with sufficient tissue maturity. Studies in other medicinal and woody species show similar positional and maturity effects: apical cuttings performed best in *Chrysanthemum indicum* (Ghimire et al., 2022), young apical shoots rooted better than old apical shoots in *Andrographis paniculata* (Hossain et al., 2021), whereas basal or middle segments in moringa often produced stronger shoots, thicker roots, or higher rooting percentages because of greater carbohydrate reserves and different endogenous hormone gradients (Muniandi et al., 2024).

2.2 Adventitious root initiation and formation in cuttings

Adventitious root formation is the developmental prerequisite for survival of detached cuttings and is therefore the core biological event in clonal propagation (Druege et al., 2019; Liu et al., 2025). In mechanistic terms, adventitious rooting is a strictly regulated process that generally proceeds through cell specification and reprogramming, primordium initiation through cell division, and primordium emergence and outgrowth (Wei et al., 2019). Tomato cutting studies further show that founder cells in basal pericycle-associated tissues first form disordered cell clusters, then dome-shaped primordia, and finally mature roots that emerge through the epidermis (Guan et al., 2019). This sequence explains why rooting speed and uniformity often vary among species and genotypes, since each stage depends on the successful completion of a distinct cellular program.

Within this program, auxin is the central regulator of adventitious rooting, while jasmonic acid, ethylene, cytokinins, and other signals modify the response (Wei et al., 2019; Liu et al., 2025). After excision, wound signaling rapidly alters hormone homeostasis, and tomato cuttings showed increased auxin and ethylene in the basal stem within 1 h, followed by auxin accumulation in meristematic founder regions and increased expression of auxin transporter genes during defined rooting phases (Guan et al., 2019). Tea and general rooting reviews likewise identify auxin as the leading hormone controlling root induction, while recent work in grape indicates that auxin and cytokinin are prominent in bud germination and leaf expansion, salicylic acid is associated with callus and root formation, and jasmonic acid and gibberellins are more closely linked to direct rooting (Wei et al., 2019; Zheng et al., 2025). In *T. hemsleyanum*, high rooting competence is also evident in tissue culture, where regenerated shoots formed roots at 100% frequency on media containing NAA or IBA, confirming that the species is highly auxin-responsive once suitable physiological conditions are established (Pang et al., 2024).

2.3 Major factors affecting rooting of cuttings

The main factors affecting rooting of *T. hemsleyanum* cuttings can be grouped into propagule traits, hormonal regulation, and environmental conditions, and this multifactorial control is consistent across diverse cutting systems (Campbell et al., 2021; Liu et al., 2025). For *T. hemsleyanum* specifically, rooting reagent and cutting age significantly affected rooting rate, whereas the tested cutting medium had no obvious effect in one study, and the

best combination was 2-3-year-old cuttings treated with 1 000 mg/L IBA for 10 s. More broadly, auxin type and concentration are repeatedly decisive: IBA is widely recognized as an effective rooting auxin, concentration often has the strongest effect among hormone variables (Sun et al., 2023), and excessively high levels can damage tissues and impair rooting. Species-level optima still differ, with 2 000 ppm IBA performing best in chrysanthemum (Ghimire et al., 2022), 50 ppm NAA for 30 min in *Valeriana jatamansi* (Gautam et al., 2021), and 3.0 mmol/L IBA accelerating rooting in young *Andrographis* cuttings (Hossain et al., 2021).

Environmental control is equally important because light, temperature, water status, substrate aeration, and mineral nutrition modify auxin activity, carbohydrate supply, and tissue competence for root initiation (De Almeida et al., 2017). Rooting improves when carbohydrate status is maintained, and higher light during early cultivation can offset carbohydrate depletion in cuttings, whereas low light and poor photosynthetic recovery restrict root formation (Druege et al., 2019). Light quality also matters: far-red promoted rooting in medicinal cannabis when supplied during the initial 7 d, while blue had no significant effect in that experiment. Temperature interacts strongly with auxin responses, with 25°C repeatedly supporting better root number and length than cooler or warmer conditions in chrysanthemum and tomato experimental systems (Guan et al., 2019; Ghimire et al., 2022). Substrate effects are species-dependent but often substantial: hemp rooting varied markedly across media, with substrate composition exerting the greatest effect in that study (Campbell et al., 2021), and grape cuttings rooted best in perlite or coarse-particle substrates that improved aeration (Zheng et al., 2025). Cutting diameter, leaf retention, stem wounding, humidity, season, and mother-plant health also modify rooting success by changing transpiration, endogenous hormone supply, and carbon availability.

3 Selection and Pretreatment of Cutting Materials

3.1 Selection of elite mother plants and cultivation of cutting materials

The first prerequisite for standardized cutting propagation is the selection of elite mother plants with stable phenotype, strong vegetative vigor, and high regenerative capacity, because poor stock-plant management directly lowers cutting quality. Vegetative propagation is valuable precisely because it preserves true-to-type traits from the stock plant, so the quality of the donor plant determines the quality uniformity of the seedling population (Quan et al., 2022). Mother-plant physiological status is a major determinant of rooting success, and reviews across fruit and woody crops identify it alongside cutting type, season, substrate, and hormones as a core source of variation (Saini et al., 2025). Age is especially important: hazelnut formed vigorous one-year shoots most intensively from 4-7-year-old mother plants, while younger bushes allocated more growth to plant establishment and older bushes produced weaker shoots (Savina et al., 2025). In *Picea crassifolia*, cuttings from 15-year-old healthy ortets showed better rooting performance than material from younger or older donor trees, indicating that optimal donor age is species-specific but biologically meaningful. Mother-plant origin also matters: tissue-culture-derived eucalyptus stock plants produced cuttings with higher rooting success and superior early growth than conventional mother-bed sources.

Elite mother plants should therefore be maintained under conditions that preserve juvenility, sanitation, and repeated shoot production. Greenhouse guidance emphasizes that healthy stock plants can tolerate frequent harvest, but they must be fully hydrated before cutting collection, and early-morning harvest is preferred because tissues are more turgid. Keeping stock plants in a juvenile state can increase the number of harvestable propagules across successive cutting rounds. Controlled mother-plant systems also improve phytosanitary quality and propagule homogeneity: soilless strawberry mother plants reduced soil-contact contamination risk and increased the quality and uniformity of propagules, while micropropagated mother plants showed substantially higher propagule output than in vivo stocks. For *T. hemsleyanum*, this supports establishing a dedicated mother-stock garden composed of disease-free, vigorous elite clones, managed with rejuvenation pruning, adequate water and nutrition, and protected cultivation to produce uniform juvenile shoots for repeated cutting collection (Morresi et al., 2025).

3.2 Selection of cutting types, positions, and specifications

The second key step is to standardize cutting type, position, and specifications, because rooting capacity varies greatly with tissue maturity, node number, stem diameter, and topophytic origin (Figure 1) (Mohammed et al., 2020). Across many species, softwood or semi-hardwood cuttings often outperform older hardwood material. In *Tecoma stans*, softwood cuttings showed greater sprouting and rooting than hardwood cuttings (Singh et al., 2021). In kiwifruit, semi-hardwood cuttings produced better root traits than hardwood cuttings (Choudhary et al., 2024), and in plum rootstocks, semi-hardwood cuttings reached 100% rooting in one genotype (Seleshi et al., 2021). However, this is not universal: prairie willow rooted better from dormant hardwood than semihardwood cuttings (Schrader et al., 2026). For *T. hemsleyanum*, the most defensible target is physiologically juvenile but partly matured shoots, rather than highly lignified old wood or excessively succulent tissues (Saini et al., 2025). Position within the shoot also matters. Terminal stems often root faster (Singh et al., 2021), but upper-branch softwood cuttings performed best in *Picea crassifolia*, and basal cuttings in *Prunus subhirtella* produced more extensive root systems even when rooting percentage was similar to terminal cuttings. These differences reflect hormone and stress gradients after severance, so the selected cutting position should be defined empirically rather than assumed (Kunc et al., 2026).

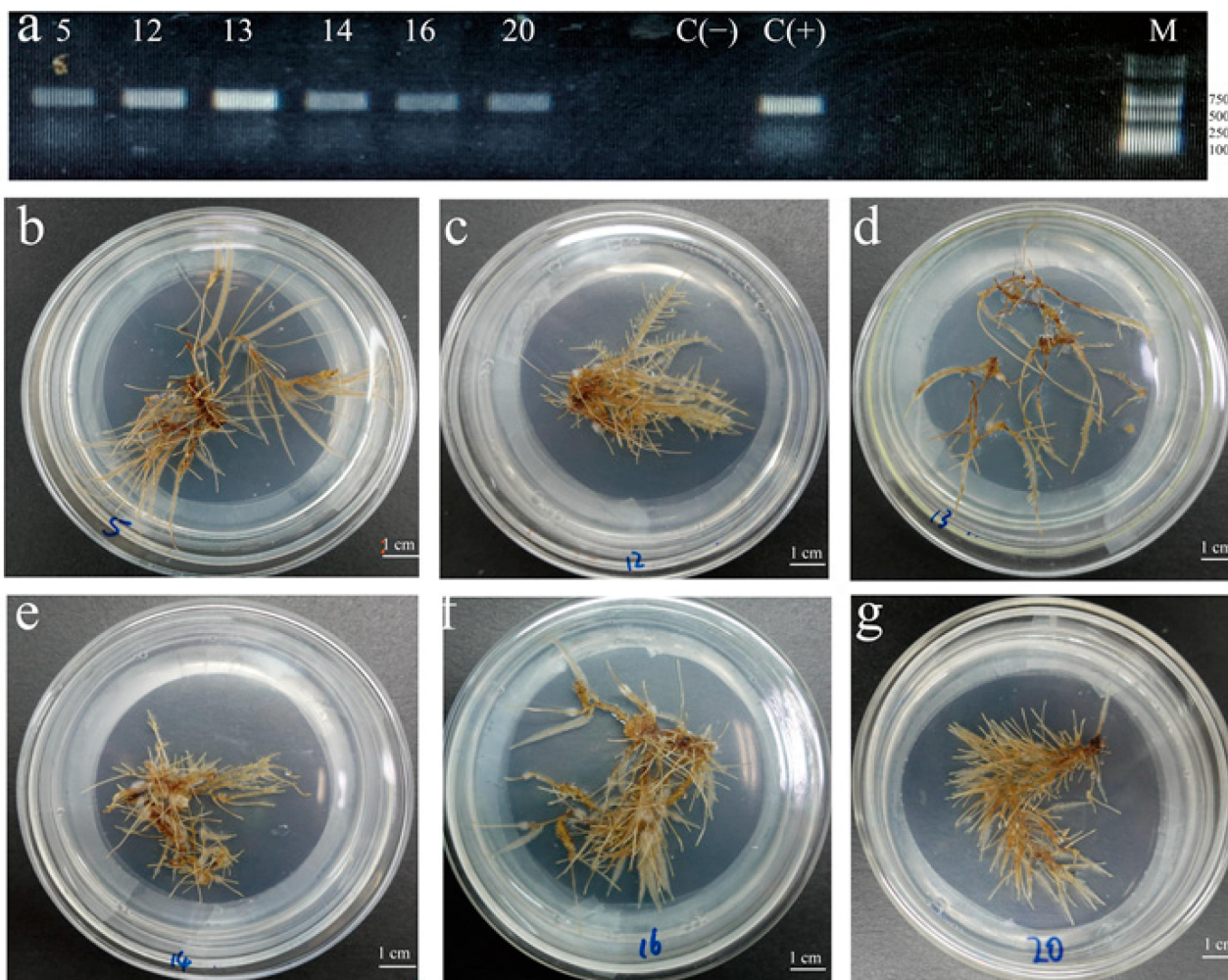


Figure 1 PCR analysis and phenotypes of 6 *T. hemsleyanum* hairy root lines (Adopted from Wang et al., 2023)

Image caption: (a) PCR analysis of the *rolB* gene in the hairy root line of *T. hemsleyanum* [lane M, marker; L1-L6, the hairy roots lines induced by *A. rhizogenes* Ar Qual, named HR4, 5, 12, 13, 14, 16, and 20; C (+), plasmid DNA from *A. rhizogenes* Ar Qual (positive control); C (-), roots from a non-transformed control plant (negative control)]. (b) HR5, (c) HR12, (d) HR13, (e) HR14, (f) HR16, and (g) HR20 (Adopted from Wang et al., 2023)

Standardization also requires defining stem size and nodal specification. Tea softwood cuttings commonly use semi-lignified branches at least 15 cm long, while apple rootstock cuttings were standardized at 20 cm length, 5~10 mm thickness, and 4~6 buds. *Tecoma* cuttings were trimmed to 10 cm and 0.5~1.0 cm diameter (Singh et al., 2021), and *Picea crassifolia* likewise performed well with softwood cuttings 0.5~1.0 cm in diameter. Single-node cuttings can maximize propagation efficiency, but they may root slowly or fail to produce shoots in some species (Schrader et al., 2026), whereas four-node terminal semi-hardwood cuttings are used successfully in camellia. Leaf retention is also critical. Leafy cuttings rooted and sprouted better than leafless cuttings in *Tecoma stans*, likely because retained leaves continued photosynthesis during propagation. For *T. hemsleyanum*, a practical standard is to use vigorous current-season or semi-lignified shoots of moderate thickness, retain a limited functional leaf area, and specify a stable range of node number, length, and diameter to balance carbon supply with water loss (Choudhary et al., 2024).

3.3 Collection, trimming, and rooting pretreatment of cuttings

The final step is the collection, trimming, and rooting pretreatment of cuttings before insertion. Clean handling begins at harvest: stock plants should be well hydrated, cuttings should be taken in the early morning, and tools and hands should be disinfected to reduce contamination. Several studies also used fungicidal sanitation before hormone treatment, including 0.2% Bavistin for 10 min in *Tecoma stans* and Rizolex at 3 g/L for 5 min in fig cuttings (Singh et al., 2021). Trimming is usually standardized around the basal node, because nodes are common sites of adventitious root formation, and basal cut pattern can influence rooting depending on species (Mohammed et al., 2020). In tea, excess leaves 3~5 cm above the base were removed before sticking in perlite, while general greenhouse guidance recommends each cutting retain several leaves rather than becoming excessively leggy. Pretreatments that wound the basal region can improve rooting in some species by stimulating root initials or enhancing auxin responsiveness. Basal longitudinal or unilateral wounding was applied successfully in fig, apple rootstock, and camellia, and wounded apple cuttings showed better root and shoot parameters than unwounded ones. The effect is not universal, however, because bottle brush showed no wounding effect by itself (Hameed and Adil, 2019).

Auxin pretreatment is the most consistent rooting intervention, but concentration and application method must be standardized by species and cutting type. Quick-dip basal treatments are widely used, including 15 s in apple rootstock, short basal dips in fig, talc formulations in *Tecoma stans*, and 5 min immersion or 15 s basal dip in camellia. IBA repeatedly outperformed or matched other auxins, with optimal reported concentrations of 1 000 mg/L in catalpa (Quan et al., 2022), 2 000 ppm in apple rootstock, and 0.4% IBA in *Tecoma stans* (Singh et al., 2021). Auxin combinations can further improve rooting in some species, as in magnolia with NAA:IBA (2:1) and fig with wounding plus IBA and NAA. Because *T. hemsleyanum* needs a reproducible nursery protocol, its cuttings should be harvested from hydrated elite mother plants, disinfected, trimmed to a fixed nodal and leaf standard, optionally wounded at the base, and subjected to a calibrated IBA-based quick-dip treatment before insertion into the rooting substrate.

4 Optimization of Key Techniques for Rooting of Cuttings

4.1 Selection and optimization of rooting substrates

The rooting substrate should first satisfy the physical requirements of water retention plus aeration, because adventitious rooting responds strongly to pore structure, oxygen availability, and moisture balance rather than to any single substrate ingredient (Hoover et al., 2025; Saini et al., 2025). Across species, mixed media often outperform single materials when they balance these properties, as peat+perlite outperformed perlite alone in Caucasian whortleberry and cocopeat+perlite (1:1) gave optimum rooting in carnation (Zheng et al., 2020; Yazar et al., 2025). Similar advantages appear in woody and succulent systems, where perlite-cocopeat (1:1) gave the best juniper protocol and sand:perlite or sand:vermiculite supported the highest rooting percentage and root number in *Pedilanthus tithymaloides* (Abass et al., 2024). In chrysanthemum, vermiculite+perlite (1:1) supported the best response under the optimal auxin-temperature combination, again indicating that porous, well-aerated mixtures are broadly favorable for cutting propagation (Ghimire et al., 2022).

At the same time, the best substrate remains species-dependent, so standardization for *T. hemsleyanum* should define a preferred range of structure rather than assume one universal medium (Zheng et al., 2020; Mello et al., 2025). Some species root best in highly aerated coarse media, as grape cuttings rooted best in pure perlite and in other large-particle substrates such as coarse sand mixtures (Zheng et al., 2025). Others favor alternative materials, such as Kanuma soil in *Apocynum lancifolium*, which gave the highest survival and rooting rate among the tested substrates (Seo et al., 2023). Substrate design also has to consider later plug quality, because stratifying peat-based media with coarse amendments did not clearly improve root growth but reduced plug structural stability in herbaceous cuttings (Hoover et al., 2025). For *T. hemsleyanum*, the most defensible standard is therefore a clean, moderately fine but aerated substrate, with perlite-based or peat/cocopeat-perlite mixtures prioritized for rooting trials and plug integrity evaluated together with rooting percentage, root length, and root biomass (Abshahi et al., 2022).

4.2 Types, concentrations, and application methods of plant growth regulators

Among plant growth regulators, IBA is the most consistently effective rooting auxin across cutting systems, although the optimum dose varies by species, cutting type, and physiological state (Quan et al., 2022; Seo et al., 2023; Saini et al., 2025). IBA improved rooting percentage, root number, root length, and root quality in juniper, chrysanthemum, guava, bottle brush, dragon fruit, and *Solanum procumbens*, with species-specific optima ranging from 500 to 3 000 ppm (Abshahi et al., 2022; Marappan et al., 2026). In *T. hemsleyanum*, the direct evidence points to 1 000 mg/L IBA for 10 s as the best tested treatment, which is notably consistent with the 1 000 ppm optima reported in juniper, catalpa, and bottle brush (Quan et al., 2022; Muniandi et al., 2025). Mechanistically, exogenous auxin promotes cell division, assimilate mobilization, root primordium differentiation, and favorable endogenous hormone ratios such as higher IAA/ABA and IAA/ZR, which together accelerate root initiation and improve uniformity (Abass et al., 2024).

However, more auxin is not always better, and several studies show a threshold beyond which rooting declines or root systems become short and coarse (Ghimire et al., 2022). In carnation, rooting percentage did not increase with increasing auxin concentration, and higher concentrations inhibited rooting (Zheng et al., 2020). In *Apocynum lancifolium*, Rootone gave the highest rooting rate, while 500~1 000 mg/L IBA reduced survival relative to lower-dose or control treatments, despite 1 000 mg/L producing more roots (Seo et al., 2023). By contrast, some species require higher IBA doses, including 3 000 ppm in dragon fruit and 3 000 ppm in guava single-node cuttings, while ivy gourd responded best to 1 500 ppm IBA and *Solanum procumbens* to 500 ppm (Jayaganesh et al., 2025; Choudhary et al., 2026). Combined auxin treatments can also be useful in some systems, since IBA+NAA improved rooting in carnation and dragon fruit, but IBA alone still outperformed NAA in catalpa and bottle brush (Quan et al., 2022; Marappan et al., 2026). For *T. hemsleyanum*, the present evidence supports adopting a short basal dip in IBA as the standard core treatment, then refining concentration by cutting age and season rather than broadly increasing dose (Saini et al., 2025).

4.3 Regulation of cutting time, planting depth, and density

The timing of cutting collection should match periods of high physiological activity but moderate stress, because season strongly affects rooting capacity, sprouting, and subsequent seedling growth (Seo et al., 2023). Across species, spring and early autumn repeatedly perform well: juniper rooted best in spring, tea cuttings performed best when collected from early September to late October, bamboo rooted best in spring-summer, and camellia showed higher survival and bud sprouting in spring and autumn than in summer or winter (Abshahi et al., 2022; Kumar et al., 2022). Caucasian whortleberry also showed its highest rooting in September with semi-hardwood cuttings, while cerrado pitaya performed better in spring and was not recommended for autumn preparation (Yazar et al., 2025; Mello et al., 2025). Reviews of fruit-cutting propagation similarly conclude that early planting, especially February-March, often enhances rooting because carbohydrate accumulation is more favorable (Saini et al., 2025). For *T. hemsleyanum*, this supports scheduling propagation in spring or early autumn and avoiding periods of extreme summer heat or deep winter dormancy.

Cutting specification and planting layout should also be standardized, because rooting varies with shoot position, cutting size, node number, and likely with insertion geometry and crowding (Kumar et al., 2022). Mid or basal shoot portions often perform better than top portions, as shown in tea and moringa, although apical sections can perform best in some species such as chrysanthemum, confirming that positional effects are real but genotype-specific (Ghimire et al., 2022). Cutting size also shows a consistent trade-off: medium diameters gave the best overall efficiency in camellia, thicker cuttings improved rooting in one bamboo species, and moringa showed that larger cuttings favor shoot growth whereas smaller ones favor root initiation (Muniandi et al., 2025). Single-node cuttings can maximize propagation efficiency when stock is limited, as shown in tea and guava, provided leaf area and humidity are sufficient to avoid desiccation stress. Direct evidence on planting depth and density is limited in the supplied literature, but the same studies indicate that resource competition, leaf retention, and cutting stability affect rooting outcomes, so *T. hemsleyanum* should use shallow-to-moderate insertion of the basal node region in a loose substrate and a spacing density that prevents leaf overlap, preserves aeration, and facilitates uniform misting and disease control (Seo et al., 2023).

5 Environmental Regulation and Seedling Management during Cutting Propagation

5.1 Regulation of temperature, humidity, and water supply

During the rooting stage of *Tetrastigma hemsleyanum* cuttings, temperature, humidity, and water supply should be managed as an integrated environmental unit, because high survival before root emergence depends on limiting desiccation while maintaining metabolic conditions favorable to callus formation and adventitious root initiation (Table 1) (Rock et al., 2022; Hu et al., 2023). Studies across propagation systems show that high relative humidity consistently supports rooting by reducing transpiration from unrooted shoots; in rose, 98~100% relative humidity is recommended initially and then gradually reduced, while in cannabis high humidity promoted rooting across cultivars and in forest-tree mist chambers successful rooting was maintained near 85% relative humidity (Yang et al., 2022; Kim et al., 2025; Kamara et al., 2025). Fine misting or fogging is preferred because it maintains humid air and supplies moisture without heavy wetting, whereas excessive droplet retention raises the risk of rot and mortality (Shen et al., 2025). Substrate water status also requires moderation rather than saturation: lavender cuttings showed the highest survival at about -2.5 kPa, high rooting at -1.0 to -2.5 kPa, and mortality above 50% under the driest treatment, indicating that the rooting medium should remain evenly moist but aerated until roots are established.

Temperature control should aim at a warm and stable rooting zone while avoiding excessive heat, because both direct rooting responses and water relations deteriorate under thermal stress (De Almeida et al., 2017). In mulberry aeroponic propagation, maintaining 25~27°C together with 90~100% humidity increased rooting by 41.40%, callusing by 58.89%, and reduced mortality by 55.85% relative to non-regulated conditions (Shen et al., 2025). Juniper cuttings rooted best when the rooting table was maintained at (25±2)°C rather than (20±2)°C (Güney et al., 2021), and microcuttings of *Corymbia* and *Eucalyptus* performed best in controlled environments where mean temperatures remained moderate, with an estimated ideal maximum of 28.4°C and minimum of 20.3°C. Temperature effects also extend to donor-plant conditioning: reduced nighttime temperature lowered rooting in *Eucalyptus dunnii*, decreased soluble carbohydrates at the cutting base by about 25%, and reduced foliar nutrient status, showing that stable thermal management helps preserve the physiological quality of propagation materials before and after excision (Nión et al., 2026). Therefore, *T. hemsleyanum* cuttings should be kept under warm, humid, and finely misted conditions, with moderate substrate moisture and careful avoidance of prolonged leaf wetness or overheating (Rock et al., 2022).

5.2 Management of light, shading, and ventilation

Light regulation during cutting propagation should balance protection from excessive radiation with maintenance of minimum photosynthetic function, because both over-shading and excessive light reduce seedling vigor through different mechanisms (Huang et al., 2025). Moderate shading often improves seedling quality in shade-sensitive or heat-stressed nursery crops. In *Castanopsis hystrix*, 60% shade produced the highest quality index and improved root characteristics relative to no shade, while excessive shading restricted dry matter

accumulation (Xue et al., 2023). In *Hopea hainanensis*, 0~30% shading was most favorable overall, and a dynamic strategy of initial 30% shading followed by gradual reduction was proposed to support early establishment and later biomass partitioning. In plastic-greenhouse cultivation of *Cyclocarya*, shading increased survival, reduced leaf burn, and improved biomass compared with the unshaded control, which suffered inhibited growth under summer heat (Feng et al., 2023). These results indicate that *T. hemsleyanum* cuttings and young rooted seedlings should be protected from intense direct radiation, especially in warm seasons or enclosed facilities, but should not be maintained under chronically deep shade.

Table 1 Four planting modes of *T. hemsleyanum* (Adopted from Hu et al., 2023)

Planting modes	Main steps	Renderings
Greenhouse-ridge	Build artificial greenhouse; Arrange the land into ridges; Planting <i>T. hemsleyanum</i>	
Understory-ridge	Select suitable understory planting land; Arrange the land into ridges; Planting <i>T. hemsleyanum</i>	
Greenhouse-container	Build artificial greenhouses; Put the soil in a suitable container and place it neatly; Planting <i>T. hemsleyanum</i>	
Understory-container	Select suitable understory planting areas; Put the soil in a suitable container and place it neatly; Planting <i>T. hemsleyanum</i>	

Ventilation should be coordinated with shading and humidity management rather than maximized indiscriminately, because air exchange can reduce heat accumulation and disease-favoring stagnation but may also disrupt the high-humidity microclimate required for unrooted cuttings (Ventura et al., 2019). In microcutting systems, a shade

house without fogging and a greenhouse without ventilation but with fogging gave the best rooting, root growth, and survival, whereas greenhouse environments with ventilation had poorer performance and in one case higher temperatures. Heated mini-tunnels likewise improved winter rooting and physiological performance in *Eucalyptus dunnii* by protecting plants from low temperatures and maintaining adequate humidity, while supplemental lighting served mainly to overcome seasonal constraints rather than replace environmental conditioning (Schilisting et al., 2025). Practical regulation should therefore use shade nets or protected structures to buffer radiation and temperature, maintain gentle ventilation sufficient to renew air, and gradually increase light exposure and air movement only after rooted cuttings begin active leaf expansion (Xue et al., 2023; Shen et al., 2025).

5.3 Nutrient supply and pest and disease control during the seedling stage

After initial callus and root formation, nutrient supply becomes necessary to sustain the transition from root induction to seedling growth, but fertilization should remain balanced and stage-specific because excessive or poorly matched nutrition can impair seedlings rather than improve them (Pascual et al., 2018). In mulberry rapid propagation, only clean water was used during the first four days after insertion, after which Hoagland nutrient solution was introduced and replaced every five days in summer, illustrating the principle that nutrient supply should follow rather than precede early rooting stabilization (Shen et al., 2025). Fertilization can substantially improve cutting and seedling growth when correctly managed: NPK at 20~30 g/L increased rooting and sprouting of apical forest-tree cuttings, moderate N and P improved cocoa cutting growth, and balanced mineral nutrition is repeatedly identified as a determinant of adventitious rooting and survival (De Almeida et al., 2017). Substrate-linked nutrient strategies also matter. Cocopeat improved aeration and water-holding capacity over sterilized soil in clonal forestry cuttings, cattle-manure-containing substrates improved seedling growth and nutrient accumulation in African mahogany, and bio-inoculants such as AMF or PGPR enhanced P, K, Ca, and chlorophyll in rooted hazelnut cuttings, although nitrogen remained limiting when N supply was inadequate (Kamara et al., 2025).

Pest and disease control during the seedling stage should emphasize prevention, sanitation, and environmental regulation, because contaminated cuttings, substrates, irrigation water, and poorly ventilated wet nursery conditions allow pathogens to spread early and persist into field planting. Integrated management begins with healthy propagules and clean infrastructure: cuttings can carry surface microorganisms, so disinfection of plant material, tools, hands, containers, and substrates is essential, and contaminated media may require steam or other disinfestation measures (Shen et al., 2025). Disease suppression can also be supported biologically and culturally, since compost-based substrates may provide pathogen suppressiveness, beneficial microorganisms can improve nutrition and resistance, and irrigation, humidity, storage, and nursery hygiene all directly affect seedling health (Pascual et al., 2018). Nursery production should therefore include routine removal of diseased seedlings and residues, maintenance of irrigation-water quality, controlled access and operation records, and balanced nutrition that avoids weakening seedlings or predisposing them to infection (Ventura et al., 2019).

6 Construction of a Standardized Seedling Production System for *Tetrastigma hemsleyanum*

6.1 Hardening, transplanting, and establishment management of rooted cuttings

Hardening of rooted cuttings should proceed by gradual acclimatization, not abrupt transfer, because newly rooted propagules often suffer transplant shock before they become fully coupled to the field environment (Grossnickle and Macdonald, 2018). In carob, rooted cuttings were transplanted into sterilized sand:soil substrate and kept under rooting-phase conditions for four weeks before relative humidity was progressively reduced to normal greenhouse conditions, showing a practical model for staged acclimation (Essahibi et al., 2017). Comparable medicinal-plant studies also show that post-rooting hardening can determine final survival, with rooted *Aphanamixis polystachya* reaching 72% survival after hardening and micropropagated *Alangium salviifolium* achieving 60% transfer to soil after greenhouse acclimatization (Pandey et al., 2022; Gurav et al., 2025). By contrast, *Ruta chalepensis* plantlets survived at 95.2% after effective hardening, indicating that acclimatization quality can sharply change establishment outcomes even when rooting has already occurred (Qahtan et al., 2021).

Transplanting management should therefore prioritize root protection, gradual humidity reduction, suitable substrate transition, and early establishment vigor. Evidence across cutting systems indicates that survival after transplanting improves when rooted propagules are moved into clean, aerated substrates and maintained under moderated conditions before full field exposure (Izadi et al., 2022). Physiologically, cutting quality after rooting still depends on leaf vitality, source-sink balance, and uniform root development, and delayed or uneven rooting can impair synchronous later growth among individuals (Druege, 2020). For *T. hemsleyanum*, hardening should thus retain moderate shade and humidity at first, then gradually increase ventilation and reduce protection, while transplanting should use rooted cuttings with intact leaves, healthy white roots, and no basal decay so that establishment management begins from physiologically functional planting stock (Sarolia et al., 2021; Mataruga et al., 2023).

6.2 Seedling quality evaluation, grading, and nursery release standards

Seedling quality evaluation for *T. hemsleyanum* should combine morphological indicators with selected physiological or functional indicators, because morphology remains the operational basis of quality control, but morphology alone does not capture all differences in transplant performance. Reviews of seedling quality practice show that morphological attributes are widely used and often mandatory, while physiological attributes are used less often despite their value for monitoring crop development, nutrient status, viability, and post-planting performance (Grossnickle and Macdonald, 2018). The broader seedling-quality literature also rejects a single universal test: no “silver bullet” applies across nursery, lifting, and pre-planting stages, so quality control must use stage-appropriate indicators and explicit testing purposes. For rooted cuttings specifically, additional quality requirements apply beyond ordinary seedling stock, reinforcing the need for a dedicated standard for clonal *T. hemsleyanum* nursery material.

A practical grading system should be simple enough for nursery use but sufficiently predictive of later medicinal production. In *Panax notoginseng*, unclear seedling sources and uneven quality reduced emergence and acclimatization, and the establishment of a grading standard improved normative industry management. That study found that root length, root diameter, and bud diameter correlated positively with fresh weight, and finally simplified grading to fresh weight plus rootlet number, with higher grades showing better emergence, photosynthetic performance, and medicinal output after transplanting. Similar patterns appear in other medicinal crops: graded transplantation in *Astragalus membranaceus* changed both yield and active component content after transplanting, and licorice seedling grades based on plant weight produced 1.5-2-fold differences in several bioactive constituents in the harvested roots (Li et al., 2023). Accordingly, nursery release standards for *T. hemsleyanum* should classify rooted cuttings into at least premium, standard, and cull grades using easily measured indices such as seedling height, stem thickness, leaf number, root number, root length, root fresh weight, and root system integrity, while excluding seedlings with deformities, weak growth, pest damage, or poor plug development (Grossnickle and Macdonald, 2018; Sarolia et al., 2021).

6.3 Standardized whole-process production and quality traceability for cutting seedlings

Whole-process standardization for *T. hemsleyanum* should begin with the origin control of mother plants and propagules and continue through nursery management, handling, and shipping. Across European systems, control of the origin of seed and vegetative material and pest and disease status are common elements of seedling quality control (Mataruga et al., 2023). Evidence from medicinal-plant production likewise shows that mixed varieties and materials with unclear sources lead to poor field performance, unstable quality, and difficulty in supervision. Standardization also needs explicit nursery protocols for watering, shading, fertilization, growing media, root pruning, weed control, storage, transport, and handling, because these operational steps are already recognized as determinants of seedling quality (Sarolia et al., 2021). This matters especially for cuttings, since quality can decline during storage, shipping, or transition between production environments, and unsuitable transport and handling are a known cause of reduced seedling quality (Druege, 2020).

Traceability should convert that standardized process into a recorded and auditable production chain. Barcode-based in vitro seedling management systems already show that recording medium composition, culture

stage, multiplication generation, and production operations can solve fragmented recordkeeping and provide a practical tool for quality control and supervision. IoT-based greenhouse traceability systems extend this principle by continuously tracking luminosity, humidity, temperature, and water consumption, while also enabling automated environmental control and internal traceability from early growth to final output. More general production frameworks likewise emphasize four linked layers: genetic integrity, field or nursery production standards, post-harvest or post-production handling and testing, and certification with traceability. Therefore, the standardized seedling production system for *T. hemsleyanum* should assign each cutting lot a unique identity linked to mother plant source, collection date, cutting specification, pretreatment formula, substrate batch, environmental records, rooting and hardening results, grading outcome, release destination, and any later field feedback, thereby establishing a closed-loop quality traceability system from elite mother plant to commercial seedling.

7 Current Problems and Future Directions

Insufficient selection of elite mother plants and high-rooting propagules remains a major problem, because clonal propagation only delivers stable medicinal quality when the source genotype is first screened for desirable agronomic and phytochemical traits. Studies in medicinal species show that wild collections are often heterogeneous and produce variable end products, whereas clonal lines derived from selected accessions improve uniformity of essential oil or metabolite profiles. Mother stock management is equally important, since homogeneous juvenile explants produced under controlled ex situ conditions are more suitable for protocol development than irregular materials taken directly from the wild. Evidence across medicinal and woody species also shows that rooting capacity depends on propagule type and source, including apical versus basal position, cutting girth, tissue maturity, and leaf retention, but the optimal combination is genotype-specific rather than universal. For *T. hemsleyanum*, this means future work should shift from general collection of mother vines toward the establishment of elite source gardens, with selection based on genotype identity, growth vigor, medicinal constituent stability, and repeatable rooting performance of defined cutting types.

The lack of unified technical parameters for cutting propagation and seedling quality evaluation remains a recognized barrier even in other medicinal crops already under commercialization. Reviews of medicinal and aromatic plants show strong consensus that standardization of vegetative propagation is essential for cultivation, conservation, and commercial uniformity, yet rooting success still varies widely with cutting maturity, season, length, hormone concentration, substrate, and greenhouse environment. Species-specific studies illustrate how large these parameter effects can be: apical shoots outperformed basal stem cuttings in one medicinal cannabis system, apical cuttings with 2 000 ppm IBA rooted best in *Chrysanthemum indicum* at 25°C in vermiculite:perlite 1:1, and selected *Valeriana jatamansi* clones required 50 ppm NAA for 30 min with media such as sand or cocopeat for reliable large-scale multiplication. At the seedling stage, the absence of grading standards also weakens quality control, because high-quality planting material is the precondition for standardized herb production and formal grading criteria can be built around measurable vigor indices. For *T. hemsleyanum*, the next step is to convert current empirical experience into unified SOPs that specify mother plant age, cutting position and size, leaf retention, pretreatment formula, substrate composition, environmental set points, rooting benchmarks, and nursery release grades for qualified seedlings.

Seedling production systems remain insufficiently facility-based, large-scale, and digital, even though commercial propagation increasingly depends on controlled environments and process automation. Large-scale medicinal plant propagation has already shown that root trainers, shade structures, and multi-tier nursery layouts can sharply expand output while reducing land demand; in *Valeriana jatamansi*, three multiplication cycles from ten starter plants could produce about 80 000 plants, and vertical nursery arrangements could further reduce space requirements. Recent engineering studies also show that automation can improve seedling handling efficiency and reproducibility: machine-vision systems can guide robotic implantation and tray logistics, automated plug-seedling equipment can integrate sowing, covering, fertilizing, watering, and cloud-based monitoring of depth, temperature, and humidity, and smart transplanting frameworks using sensors and PLC control can reduce missed seedlings and improve operational reliability. Digital twin systems go further by linking real-time sensing,

predictive modeling, simulation, and robotic execution in a closed loop, with more than 90% localization accuracy reported in greenhouse operations. For *T. hemsleyanum*, future development should therefore combine protected facility propagation with digital traceability, environmental monitoring, automated irrigation and mist control, and eventually intelligent transplanting and grading, so that cutting seedling production becomes not only standardized but also scalable, auditable, and less dependent on manual experience.

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

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Analysis of Wild Resource Decline and Artificial Germplasm Restoration Pathways of *Paris* spp.

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Abstract *Paris* spp. are important medicinal plant resources in China, and their rhizomes are rich in bioactive compounds, particularly steroidal saponins, which possess high medicinal value and considerable potential for industrial utilization. However, long-term dependence on wild harvesting, habitat degradation, and limited natural regeneration capacity have resulted in continuous declines of wild *Paris* resources, increasing the risk of losing valuable germplasm and making it difficult to meet the sustainable development needs of the traditional Chinese medicine industry. This study investigates the causes of wild resource decline and the pathways for artificial germplasm restoration of *Paris* spp. This article analyzes population dynamics, and impacts of excessive harvesting and ecological changes on resource stability. Furthermore, the major constraints in artificial germplasm development are summarized, including high dependence on wild germplasm sources, long propagation cycles, insufficient rapid propagation systems, and incomplete genetic background and quality evaluation frameworks. To address these challenges, this study proposes a restoration strategy based on wild germplasm conservation and elite germplasm selection, supported by efficient propagation technologies, understory ecological cultivation, and standardized production systems. The potential applications of molecular markers, genomics-assisted breeding, and long-term resource management strategies in *Paris* germplasm innovation are also discussed. Future efforts should focus on wild resource conservation, core germplasm construction, precise evaluation of elite materials, and ecological adaptation-based cultivation to promote the transition of *Paris* resource utilization from wild collection-dependent exploitation toward artificial germplasm-driven and ecologically sustainable production systems. This review proposes theoretical references for genetic resource conservation, stable medicinal material supply, and sustainable industrial development of *Paris* spp.

Keywords *Paris* spp.; Wild resource decline; Artificial germplasm; Germplasm conservation; Propagation

1 Introduction

Paris spp. are a group of medicinally important perennial herbs with long-standing use in Asian traditional medicine and substantial contemporary value for the pharmaceutical industry. The genus has been used in China for more than 2 000 years, and several *Paris* taxa, especially *P. polyphylla*, *P. polyphylla* var. *yunnanensis*, and *P. polyphylla* var. *chinensis*, are widely employed in ethnomedicine and formal medicinal systems for treating trauma, bleeding, inflammation, swelling, skin disorders, and related conditions (Jiang et al., 2022; Ye et al., 2025). Modern phytochemical and pharmacological studies show that *Paris* species are rich in bioactive secondary metabolites, especially steroidal saponins, which account for more than 80% of identified active compounds and are regarded as the principal medicinal constituents and chemotaxonomic markers of the genus (Ding et al., 2021; Rawat et al., 2023; Zhang et al., 2025). Since 1960, more than 320-330 compounds have been isolated from *Paris* plants, including steroidal saponins, flavonoids, phytosterols, triterpenes, polysaccharides, and related constituents, reflecting both chemical richness and broad development potential (Thapa et al., 2022). Representative steroidal saponins such as polyphyllins and *Paris* saponins exhibit anticancer, hemostatic, anti-inflammatory, antimicrobial, antiviral, immunomodulatory, and other activities, and recent compound-level studies continue to identify new molecules with notable cytotoxic or anti-inflammatory effects (Thakur et al., 2023). This medicinal importance has driven intense utilization of rhizomes as the source material for traditional remedies and for more than 100 proprietary Chinese medicines, making *Paris* spp. both biologically valuable and economically strategic (Kunwar et al., 2020).

However, the same high medicinal and commercial value that has promoted the use of *Paris* spp. has also accelerated the depletion of wild resources. Before the 2000s, *Paris* species were not cultivated in plantations, and the pharmaceutical industry relied primarily on Rhizoma Paridis collected from wild populations; with annual raw-material consumption estimated at about 3 000 000 kg, overharvesting has caused dramatic declines in natural populations. Multiple studies identify overexploitation, illegal collection, habitat degradation, habitat fragmentation, logging, farming, trampling, and weak management as key drivers of decline, and several reviews now describe *P. polyphylla* as vulnerable, endangered, or rare and threatened in different regional and conservation contexts (Thapa et al., 2022; Thakur et al., 2023). Field evidence from the Indian Himalayan Region recorded very low population densities of only 0.42~1.48 individuals/m² and emphasized that unsustainable extraction, poor natural regeneration, and rhizome-focused harvesting place wild populations at risk of local extinction. Similar patterns are reported from Nepal, where accelerating demand has promoted unsustainable legal and illegal harvest, premature collection, and habitat degradation, while trade pressure continues across broad distribution areas (Kunwar et al., 2020). Recent cultivation-oriented work further underscores the severity of the supply crisis, noting that approximately 80% of wild resources are exploited annually and that, in Yunnan alone, demand exceeds 1 000 tons while annual wild production is less than 100 tons (Zhang et al., 2025). Because *Paris* species also grow slowly, regenerate inefficiently, and often depend on harvested rhizomes for both medicinal use and vegetative persistence, wild-resource decline has become a coupled ecological and industrial problem (Wang et al., 2021).

Under these conditions, artificial germplasm restoration has become essential for both conservation and sustainable utilization of *Paris* spp. Conventional propagation remains constrained by slow seed germination, secondary dormancy, long juvenile growth, low multiplication rates, and disease or rot associated with rhizome cutting, while interspecific hybridization can also compromise the uniformity of medicinal raw materials and complicate seed-based breeding. These constraints explain why traditional breeding and propagation have not kept pace with rising herbal-drug demand and why researchers increasingly emphasize ex situ conservation, clonal multiplication, and tissue-culture-based restoration pathways (Thapa et al., 2022). Encouragingly, several studies have demonstrated feasible artificial propagation routes. Direct somatic embryogenesis has achieved successful regeneration with high germination and ploidy stability in regenerated plants. In vitro propagation using optimized plant growth regulators has produced strong shoot induction and 94.4% greenhouse establishment (Puwein and Thomas, 2022). GA₃ treatment can rapidly break dormancy and induce polyapical shoots at 100%, offering a more efficient rhizome propagation strategy. Somatic embryogenesis-based clonal propagation can also generate homogeneous elite materials, support cryopreservation-compatible conservation, and shorten plantlet production by 12~15 months while maintaining favorable biomass and saponin traits (Wang et al., 2023). In parallel, emerging work on seed dormancy regulation indicates that improving reproductive efficiency remains a central scientific challenge for large-scale restoration.

Accordingly, research on the decline of wild *Paris* resources and the pathways for artificial germplasm restoration has both theoretical and practical significance. At the scientific level, the taxonomic complexity of the genus, disputed species boundaries based on morphology, and demand for robust phylogenetic markers indicate that conservation must be linked with accurate germplasm identification and genetic-resource management. At the applied level, restoration research should clarify patterns of wild-resource depletion, identify the biological bottlenecks limiting natural and artificial regeneration, screen elite germplasm with stable medicinal quality, and integrate in situ protection, ex situ conservation, standardized cultivation, and traceable supply systems. It should also connect germplasm restoration with quality formation, since saponin accumulation varies with developmental stage and growth duration, making the relationship between propagation strategy, growth years, and medicinal quality especially important for sustainable production. More broadly, effective restoration can reduce harvesting pressure on wild populations, preserve genetic diversity, stabilize raw-material supply, support rural cultivation economies, and improve the long-term sustainability of biodiversity use under intensifying market demand. For these reasons, analyzing wild resource decline and constructing practical artificial germplasm restoration pathways for *Paris* spp. is a necessary foundation for reconciling medicinal use, industrial development, and species conservation.

2 Current Status and Main Factors Driving the Decline of Wild *Paris* spp. Resources

2.1 Distribution characteristics and population changes of wild resources

Paris spp. are distributed mainly in temperate and subtropical mountain systems of Eurasia, with clear diversity centers in Southwest China and the Himalayan region. The genus has been described as a small but taxonomically complex understory herb group concentrated in East Asia, with the Yunnan-Guizhou Plateau recognized as a major center of diversity, while *P. polyphylla* is reported across Bhutan, China, India, Laos, Myanmar, Nepal, Thailand, and Vietnam (Ding et al., 2021). Within this broad range, wild populations show strong geographic structuring and uneven local occurrence. In Nepal, field surveys recorded the species in 51 districts, while use and trade records were concentrated in fewer districts, indicating spatial heterogeneity in occurrence and exploitation intensity (Kunwar et al., 2020). Genetic and phylogeographic studies further show obvious geographic structure in wild populations of *P. polyphylla* var. *yunnanensis*, with Guizhou and western Yunnan identified as important conservation areas because they retain distinctive wild lineages and higher diversity (Huang et al., 2019; Zhao et al., 2021).

Despite this relatively wide distribution, most studies describe wild resources as sparse, fragmented, and declining. Field surveys in Arunachal Pradesh reported densities ranging from 0.42 to 1.48 individuals/m² in one study and 2.48 to 8.2 individuals/m² in another, showing that local populations can persist but are often thin and highly site-dependent (Kalita et al., 2026). In Sikkim, density ranged from 0.45 to 3.89 plants/m², and in Manipur from 1.3 to 2.4 individuals/m², again indicating low to moderate abundance with substantial variation among habitats (Lepcha et al., 2019; Singh et al., 2026). Nepalese ecological work reported an average density of only 1.78 individuals/m², while recent reviews note that many contemporary wild populations now occur as small isolated groups, with larger populations mostly restricted to remote areas or protected sites (Ye et al., 2025). Across regions, the consensus is that wild *Paris* resources are undergoing continuous decline under combined pressure from overexploitation, illegal collection, and habitat degradation, and several papers explicitly describe the taxa as vulnerable, endangered, or at risk of extinction (Thakur et al., 2023).

2.2 Effects of excessive harvesting on wild population regeneration

Excessive harvesting is the most consistently identified direct driver of wild *Paris* decline because medicinal use depends primarily on rhizomes, the same organs that support perennial survival and vegetative regeneration. Reviews and field studies agree that demand has risen rapidly in recent decades, stimulating both legal and illegal trade and intensifying extraction across China, Nepal, India, and neighboring range states (Cunningham et al., 2018; Kunwar et al., 2020). Price escalation has reinforced this pressure: one review documented a roughly 400-fold rise in rhizome prices in China since the 1980s, while more recent work notes that soaring prices since 2013 have encouraged large-scale farmer collection from wild stands. Because human activity is repeatedly identified as the primary factor affecting population size, commercially valuable populations near settlements or trade routes appear especially vulnerable to depletion (Singh et al., 2026).

The biological consequences of overharvesting are severe because *Paris* regenerates slowly and reproduces inefficiently under disturbance. Several studies state that the rhizome is the principal mode of regeneration in the field, while seed-based recruitment is constrained by low viability, poor germination, and long dormancy. Harvesting before seed maturation is singled out as especially damaging because it reduces seed formation and germination and removes plants before recruitment can occur (Thapa et al., 2022). Competitive and unscientific collection practices often remove the whole underground portion without leaving propagative fragments, directly interrupting vegetative recovery and accelerating population collapse. This harvesting pressure interacts with intrinsic life-history limits, including slow growth, delayed reproductive maturity, many non-flowering individuals, and lengthy breeding cycles, so wild populations recover far more slowly than they are being depleted (Ye et al., 2025).

2.3 Habitat alteration and ecological adaptation stress

Wild *Paris* populations are also highly sensitive to habitat alteration because the plants occupy relatively narrow understory niches. Ecological studies consistently place *P. polyphylla* in shady, moist, relatively undisturbed

forest habitats, commonly under canopy cover greater than 80%, in humus-rich, well-drained soils, and often on slopes or streamside microsites (Singh et al., 2026). Distribution modeling reinforces that this niche is environmentally constrained: precipitation, elevation, slope, vegetation type, and temperature range were all identified as important predictors of suitable habitat in regional models from Sikkim, Uttarakhand, and China (Tariq et al., 2021; Wang et al., 2026). Disturbed habitats repeatedly show poorer agreement with predicted suitable occurrence, implying that even climatically suitable areas may fail to support stable populations once human disturbance alters forest structure (Lepcha et al., 2019).

Habitat degradation therefore acts not only by reducing area, but by imposing ecological stress that suppresses growth and reproduction. Forest loss, fragmentation, logging, agricultural expansion, slash-and-burn cultivation, fire, landslides, grazing, trampling, and urbanization are all reported as pressures that thin populations and degrade understory conditions (Singh et al., 2026). Experimental and field evidence indicates that the species has poor adaptability to altered environments and reduced reproductive vigor under changed climatic or habitat conditions, while less than 50% shade significantly lowers seed productivity and waterlogging can be lethal. Metapopulation modeling from Sikkim further shows that disturbance and forest fragmentation substantially worsen long-term persistence, increasing extinction risk under disturbed scenarios and supporting the priority of protecting reproductive individuals in undisturbed forest matrices (Lyngdoh et al., 2018). Overall, the decline of wild *Paris* spp. reflects the interaction of commercial overexploitation with narrow habitat requirements and weak natural regeneration, making integrated in situ protection, cultivation, and habitat restoration necessary for long-term conservation (Thakur et al., 2023).

3 Current Status and Key Constraints of Artificial Germplasm Development in *Paris* spp.

3.1 Dependence on wild germplasm sources and insufficient foundations for artificial propagation

Artificial germplasm development in *Paris* spp. remains strongly dependent on wild resources, because domestication has started late and cultivated materials are still closely tied to wild-collected source populations. Several studies note that wild *P. polyphylla* has been excessively harvested and pushed toward endangerment, while cultivation has been promoted mainly as a compensatory response to the collapse of natural supplies rather than as a long-established breeding system (Puwein and Thomas, 2019; Tang et al., 2022). This weak domestication history is reflected genetically: cultivated and wild populations show little differentiation in some marker studies, with only 1.35% variation reported between 15 wild and 17 cultivated populations, indicating that cultivated stocks still largely derive from recently introduced and mixed wild origins rather than from stabilized breeding lines (Huang et al., 2019). At the same time, artificial cultivation has become essential because wild resources are now rare, and some cultivation-population studies were conducted precisely because representative planting areas already depended on scarce wild germplasm collected earlier from multiple origins (Gao et al., 2022).

The second constraint is that the biological basis for large-scale artificial propagation remains weak. *Paris* spp. show long growth cycles of about 7–10 years, extremely long dormancy release, and low reproductive efficiency, which together create a persistent bottleneck for seedling production and industrial planting (Wang et al., 2023). Seeds require more than 18 months to break dormancy in some studies, only about 40% germinate under natural conditions, and dormancy is described as morphophysiological or “double dormancy,” which makes routine nursery establishment slow and unreliable (Tang et al., 2022). Even where artificial treatment improves germination, the gains remain limited: one seed-dormancy study achieved a 40% germination rate after combined cold storage, temperature fluctuation, infrared treatment, and chemical soaking, underscoring that the propagation foundation is still technically demanding rather than straightforward. Reviews therefore conclude that conventional breeding and propagation cannot keep pace with medicinal demand, and that advanced biotechnological approaches in *Paris* remain comparatively rare or insufficiently developed (Figure 1) (Rawat et al., 2023).



Figure 1 *Paris polyphylla* plants in their natural habitat and exposed aboveground and belowground (Adopted from Rawat et al., 2023)

3.2 Limitations of *Paris* spp. propagation technologies

Current propagation technologies for *Paris* spp. have made clear progress, but each major route still carries practical limitations. Traditional rhizome cutting is widely used because the species grows slowly and clonal propagation can bypass seed dormancy, yet the method has low multiplication efficiency because axillary meristems are limited, and cutting can sharply reduce net rhizome yield (Wang et al., 2021). Rhizome injury also creates phytosanitary problems: cut segments are susceptible to insects, disease, and rotting, causing substantial yield losses during multiplication (Wang et al., 2023). Even when rhizome splitting works, propagation rates are variable rather than uniformly high. In one three-year study, sprouted shoot buds averaged 49.33% from cut rhizomes and 75% from group rhizome fragmentation, which is useful for conservation but still indicates incomplete and method-dependent conversion efficiency. Other patented or nursery-based methods improve latent-bud induction or avoid direct rhizome damage, but these are still technique-specific optimizations rather than evidence of a universally standardized propagation system.

In vitro propagation and hormone-based regulation offer promising alternatives, but they also show that successful multiplication depends on highly specific developmental stages, explant types, and culture conditions. Tissue culture protocols have reported strong outcomes, including 80% shoot response and 94.4% greenhouse establishment under optimized BAP and NAA conditions, while other systems achieved bud germination within 6-8 days, multiplication factors above 5, rooting rates above 90%, and transplant survival above 90% (Puwein and Thomas, 2022). Somatic embryogenesis can further increase scale, producing an average of 63 somatic embryos per gram of callus in six weeks and shortening plantlet production by 12~15 months (Wang et al., 2023). However, these gains depend on precise regulation of medium composition, photoperiod, sucrose concentration, temperature, plant growth regulators, and rhizome developmental stage, indicating that the technology remains sensitive and not yet simple for broad field deployment (Kumar et al., 2025). Hormone-based rhizome induction shows similar conditionality: GA₃ can break dormancy within two weeks and induce polyapical shoots at 100%, with 7.2 apical shoots per treated rhizome, but this is still a controlled treatment protocol rather than a low-input routine practice for all germplasm types and planting settings (Wang et al., 2021).

3.3 Genetic background and quality evaluation deficiencies of artificial germplasm

A major constraint in artificial germplasm development is the incomplete understanding and control of genetic background. The genus has strong interspecific hybridization capacity, and unintended hybridization between *P.*

polyphylla and related taxa can generate forms that are difficult to distinguish morphologically, which disrupts seed-based breeding and weakens the uniformity of medicinal raw materials. Marker studies also show that cultivated materials often carry high admixture and mixed ancestry. EST-SSR analysis found low differentiation among cultivated populations but high diversity among individuals, with populations likely derived from two ancestral groups and with evidence of cross-pollination among cultivars (Gao et al., 2022). AFLP results likewise showed that cultivated populations can have high variation, probably because they originated from mixed provenances, which means provenance screening is still urgently needed before artificial germplasm can be treated as genetically standardized breeding material (Huang et al., 2019).

Quality evaluation is similarly underdeveloped because medicinal value is not determined by survival alone, but by stable biomass and saponin accumulation across propagules, growth stages, and lineages. One recent study had to select elite wild accessions and then clone them as candidate cultivars on the basis of biomass production and polyphyllin content, showing that quality-assured artificial germplasm is still being built from screened wild founders rather than from mature breeding pools (Wang et al., 2023). Developmental-stage effects further complicate evaluation, because extraction yield, antioxidant activity, phenolics, flavonoids, and diosgenin content all change with plant age, and reproductive-stage rhizomes can differ substantially from juvenile or vegetative materials (Kumar et al., 2025). At the molecular level, researchers still emphasize that marker resources are limited, complete genomes are unavailable, EST resources are scarce, and the lack of marker information has constrained collection, conservation, and utilization of *Paris* germplasm (Gao et al., 2022). Although SSR, AFLP, SCoT, and SRAP studies now provide an emerging basis for diversity analysis and genetic improvement, these tools are still being established as foundational resources rather than functioning as a fully integrated quality-control system for artificial germplasm development (Zhao et al., 2020).

4 Key Technical Pathways for Artificial Germplasm Restoration of *Paris* spp.

4.1 Conservation of wild germplasm resources and selection of elite germplasm

Artificial germplasm restoration of *Paris* spp. should begin with the protection and systematic evaluation of wild germplasm, because wild populations remain the original reservoir of genetic diversity, adaptive traits, and medicinal-quality variation (Gao et al., 2022). Current evidence indicates that in situ conservation should remain the fundamental strategy even when ex situ cultivation and artificial propagation are expanding (Huang et al., 2019). Population genetic and phylogeographic studies show clear geographic structure in wild *P. polyphylla* var. *yunnanensis*, with Guizhou, western Yunnan, and parts of southern Sichuan retaining high conservation value and therefore deserving priority protection and restricted harvesting (Zhao et al., 2021). Wild populations in Guizhou appear especially important because they showed richer genetic diversity than those in Yunnan and were explicitly proposed as priority areas both for protection and for provenance selection. Broader regional work in Nepal and the Dabie Mountains similarly found substantial within-population variation and geographic clustering of germplasm, supporting region-based conservation sampling rather than random collection (Zhao et al., 2020; Oliya et al., 2023).

Elite germplasm selection should therefore combine ecological provenance, genetic diversity, and medicinal-quality screening instead of relying only on morphology or yield (Gao et al., 2022). This is especially necessary because cultivated populations often originate from mixed provenances and show admixture, gene flow, and weak domestication differentiation from wild sources, which can obscure genetic background and reduce breeding precision. Several studies now support using molecular markers such as AFLP, cpDNA haplotypes, SSR, EST-SSR, SCoT, and SRAP to define core germplasm, identify superior provenances, and guide conservation-oriented breeding (Zhao et al., 2020; Zhao et al., 2021). At the applied level, elite wild accessions have already been selected and clonally reproduced as candidate cultivars on the basis of biomass and saponin content, showing that restoration can move from passive conservation to targeted domestication when representative wild founders are first secured (Wang et al., 2023). Reasonable interventions in protected habitats, such as improving seed germination before sowing back into wild sites, may also strengthen renewal of effective wild populations and link conservation directly with germplasm recovery (Huang et al., 2019).

4.2 Establishment of efficient propagation technology systems

The second technical pathway is the establishment of efficient, scalable propagation systems that overcome the slow growth, long seed dormancy, and low multiplication efficiency of *Paris* spp. (Kumar et al., 2025). Conventional rhizome cutting remains useful, but its multiplication rate is limited by axillary meristem number and it can reduce net rhizome yield while increasing susceptibility to insects, disease, and rot (Wang et al., 2023). Improved rhizome-based techniques therefore focus on increasing bud activation without damaging the parent rhizome. Stratification-induced latent-bud propagation and related rapid seedling systems can raise propagation coefficient, preserve genetic stability, and produce robust field-surviving seedlings, while avoiding some of the losses associated with direct segment cutting. Hormone regulation offers another effective route: GA₃ can break rhizome dormancy within two weeks and induce polyapical shoots at 100%, with about 7.2 apical shoots per treated rhizome, markedly improving clonal multiplication efficiency (Wang et al., 2021).

Tissue culture and somatic embryogenesis now appear to be the most promising high-efficiency restoration platform for large-scale artificial germplasm production (Thapa et al., 2022; Wang et al., 2023). Direct regeneration systems based on thin cell layer culture, mini-rhizome induction, and optimized hormone combinations have achieved 86.6% mini-rhizome formation, more than 95% acclimatization in greenhouse conditions, and strong shoot regeneration under defined medium compositions. Somatic embryogenesis is especially valuable because it can generate about 63 embryos per gram of callus within six weeks, shorten plantlet production by 12~15 months, and maintain high transplant establishment, thereby enabling rapid multiplication of elite lines (Figure 2) (Wang et al., 2023). However, the evidence also shows that propagation success depends strongly on explant position, developmental stage, photoperiod, temperature, sucrose concentration, and plant growth regulator regime, so the next step is not merely inventing more methods but integrating them into standardized, stage-specific propagation systems for different germplasm types (Kumar et al., 2025).

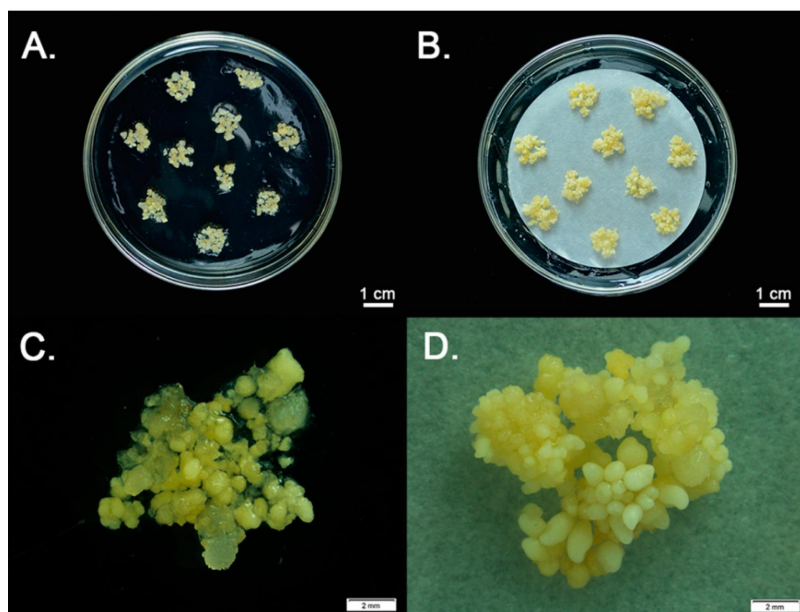


Figure 2 Somatic embryo innovation platform for *Paris polyphylla* (Adopted from Wang et al., 2023)

Image caption: Somatic embryos grown on medium (A,C) compared with stronger growth on filter paper+medium (B,D) (Adopted from Wang et al., 2023)

4.3 Quality control and standardized production of artificial germplasm

Artificial germplasm restoration cannot be judged by survival and multiplication alone; it must also ensure stable medicinal quality, especially for steroidal saponins, which are the main active constituents of *Paris* spp. (Thapa et al., 2022; Kumar et al., 2025). A central quality-control challenge is that interspecific hybridization and morphological similarity can reduce uniformity of medicinal raw materials and complicate seed-based breeding, making genotype authentication essential (Wang et al., 2023). Molecular-marker systems linked to diversity

structure and polyphyllin biosynthesis therefore provide an important foundation for quality-oriented breeding, accession identification, and traceable production (Oliya et al., 2023). At the same time, clonal systems help preserve the natural morphology and active-ingredient profiles of elite wild founders, offering a practical route to homogeneous medicinal germplasm (Wang et al., 2023). Standardized production should therefore integrate authenticated founder selection, clonal multiplication, and batch-level chemical evaluation rather than relying on unverified mixed-origin planting stocks (Gao et al., 2022).

Chemical evidence shows that quality in cultivated *Paris* is strongly shaped by plant age, culture conditions, and soil management, so standardized production must define these variables explicitly (Wang and Li, 2018; Zhang et al., 2025). Multiple studies found that major steroidal saponins vary with cultivation year and generally peak around the seventh or eighth year, with one UHPLC-MS/MS study reporting a maximum of 22.65 ± 1.65 mg/g in the eighth year and recommending harvest at year 7 or 8. In vitro systems also affect chemical quality: mini-rhizome cultures showed 1.41-fold higher total steroidal saponins than field rhizomes under one BAP treatment, and salicylic-acid elicitation increased total saponins to 3.6 times the in vivo level, although growth slowed under elicitation. Field management also matters, because biochar and organic fertilizer significantly increased total saponin, polyphyllin I, II, VI, and VII contents through linked changes in soil nutrients, enzyme activity, and microbial communities (Liu et al., 2024). Taken together, standardized artificial germplasm production in *Paris* spp. should be built around authenticated elite lines, stage-specific propagation protocols, defined cultivation years, and chemical quality benchmarks supported by chromatographic and metabolomic evaluation.

5 Ecological Adaptation-Based Models for *Paris* spp. Germplasm Restoration

5.1 Integrated model of wild resource conservation and artificial propagation

An ecological adaptation-based restoration model for *Paris* spp. should begin by coupling in situ protection of wild populations with targeted artificial propagation, because wild populations remain genetically valuable but are increasingly threatened by overcollection, habitat fragmentation, and slow natural renewal (Su et al., 2022; Thakur et al., 2023). This integrated approach is supported by studies showing that cultivation is already a major route for conserving and sustainably using wild *P. polyphylla* var. *yunnanensis*, while in situ and ex situ measures are both necessary for long-term persistence. Population genetic work further indicates that wild germplasm should not be collected indiscriminately, because wild populations retain clear geographic structure and some regions, especially Guizhou and parts of Sichuan and western Yunnan, contain higher-diversity lineages that are better treated as priority conservation and provenance-selection zones (Huang et al., 2019; Yan et al., 2024). SSR analyses in Nepal likewise show that most variation occurs within populations, but germplasm from similar geographic origins clusters together, supporting region-specific conservation sampling and core germplasm construction rather than mixed, undocumented transfer (Oliya et al., 2023).

Within that framework, artificial propagation should serve as a buffer against harvest pressure and as a renewal tool for selected wild founders rather than a replacement for wild conservation. Reviews and field studies agree that in vitro propagation, ex situ cultivation, and ecologically informed niche-based planning can reduce unorganized collection from natural habitats and help design more effective conservation programs (Kunwar et al., 2020; Rawat et al., 2023). Somatic embryogenesis and related clonal systems are especially suited to this model because they can rapidly multiply elite wild accessions, preserve morphology and active-ingredient profiles, and produce plantlets with about 94% survival after transplanting to soil (Wang et al., 2023). Other regeneration platforms, including mini-rhizome production, also provide conservation-ready planting stock, with more than 95% acclimatization success and increased steroidal saponin content relative to field-grown rhizomes. The most defensible integrated model is therefore a closed loop: identify and protect high-value wild populations, select elite accessions from them, propagate those accessions under controlled conditions, and use the propagated material to supply cultivation systems and, where appropriate, reinforce depleted populations.

5.2 Combined model of understory ecological cultivation and germplasm expansion

A second restoration pathway is a combined model of understory ecological cultivation plus germplasm expansion, which fits the basic ecology of *Paris* spp. better than open-field domestication. Multiple ecological studies show that *P. polyphylla* grows and reproduces best in moist, humus-rich, well-drained forest soils under more than 80% canopy cover, with disturbed habitats supporting thinner populations and poorer regeneration. Light conditions are especially important, because less than 50% shade markedly reduces seed productivity, and the species shows poor adaptability to altered environments and climatic stress during reproduction. This explains why Nepal-based distribution and conservation work recommends conserving the species in forests and cultivating it in forest fringe areas across its potential range, rather than separating production completely from its ecological niche (Kunwar et al., 2020). Distribution modeling also indicates that ecological niches differ among medicinally used taxa, with *P. polyphylla* var. *chinensis* and var. *yunnanensis* responding differently to precipitation, temperature range, and human disturbance, so understory expansion should be matched to taxon-specific suitable zones rather than generalized across all planting areas (Wang et al., 2026).

Understory cultivation is not only a habitat-matching strategy; it also appears to support better medicinal chemistry under appropriate conditions. Metabolomic comparison of plants maintained for eight years under natural forest and greenhouse conditions found that naturally forest-grown roots were enriched in steroidal saponins, flavonoids, flavonols, lipids, vitamins, and veratramine alkaloids, supporting a strong association between growth environment and secondary metabolite accumulation (Yan et al., 2024). Even within understory systems, forest type matters: imitation-wild cultivation under Chinese fir and mixed forests generated higher soil organic carbon, microbial biomass carbon, water-soluble organic carbon, and enzyme activity than Moso bamboo forest, creating a more favorable soil microenvironment for *P. polyphylla* growth (Zhang et al., 2026). Community-level work in Arunachal Pradesh further shows that the species persists within diverse associated herb layers and that identifying such supportive ecosystems can guide conservation-oriented cultivation placement (Kalita et al., 2026). The practical implication is that germplasm expansion should use forest-compatible, site-screened understory systems that mimic native shade, litter, and soil conditions, because these systems better align with both species ecology and the formation of medicinally valuable metabolites (Rawat et al., 2023).

5.3 Germplasm renewal and industrial utilization model

The third pathway is a germplasm renewal and industrial utilization model in which elite lines are continuously renewed, authenticated, and routed into standardized production systems. This is necessary because the pharmaceutical value of *Paris* depends mainly on rhizome-derived steroidal saponins and polyphyllins, while current market demand continues to rise faster than wild or conventionally propagated supply (Qiang et al., 2020; Su et al., 2022). Germplasm renewal cannot rely on morphology alone, because interspecific hybridization and weak differentiation between some wild and cultivated materials can compromise raw-material uniformity and obscure breeding identity (Wang et al., 2023). Molecular infrastructure is therefore part of the renewal model itself. EST-SSR markers linked to polyphyllin biosynthesis, SSR population analysis, comparative barcoding, and dedicated biomolecular databases such as PPDP all provide tools to authenticate germplasm, trace origin, and connect genotype with medicinal-quality traits (Gao et al., 2022; Oliya et al., 2023; Wang et al., 2026). This matters for industry because traceable cultivated supply chains have already been recommended as a way to distinguish cultivated from wild-harvested stocks and support ex situ conservation without masking continued wild extraction (Rawat et al., 2023).

Industrial utilization also requires that germplasm renewal be tied to production-stage quality control, not just multiplication speed. Clonal propagation of selected elite wild accessions has already shown that candidate cultivars can be reproduced at scale while preserving morphology and active-ingredient contents, and field-grown clonal lines reached their greatest biomass increase and exceeded pharmaceutical-use polyphyllin requirements by the fifth year (Wang et al., 2023). Growth environment and management further shape industrial value. Elevated CO₂ responses differed between cultivars from different natural habitats, with the western Yunnan cultivar showing stronger growth and maintained total saponin content, which suggests that renewal programs should

match cultivar origin to future cultivation environments (Qiang et al., 2020). Rhizosphere engineering also appears promising: *Pseudomonas palleroniana* P6 increased root biomass, polyphyllin I, II, and VII content, and soil available potassium, indicating that industrial germplasm systems can be strengthened by microbe-assisted cultivation (Wu et al., 2025). Taken together, the renewal-utilization model should connect elite germplasm screening, marker-based authentication, clonal renewal, ecological site matching, and traceable downstream cultivation so that *Paris* spp. production shifts from wild-resource mining to adaptive, quality-controlled industrial regeneration (Oliya et al., 2023; Wang et al., 2026).

6 Challenges and Future Directions in *Paris* spp. Germplasm Restoration

6.1 Further improvement of germplasm evaluation systems

A central challenge in *Paris* spp. germplasm restoration is that evaluation systems remain incomplete, especially for linking population identity, geographic origin, genetic diversity, and medicinal quality into a single usable framework. Current studies show that molecular evaluation has advanced, but remains fragmented across marker types and regions. EST-SSR work in cultivated *P. polyphylla* var. *yunnanensis* found high polymorphism, high within-population diversity, low differentiation among cultivated populations, and clear admixture from two ancestral groups, indicating that existing cultivated materials are genetically mixed rather than standardized breeding stocks (Gao et al., 2022). SSR analysis in Nepal similarly showed that 74% of variation occurred within individuals in populations and only 26% among populations, while germplasms from similar geographic origins clustered together, supporting evaluation systems that combine individual-level diversity with provenance structure rather than relying on morphology alone (Oliya et al., 2023). AFLP studies in China reached a similar conclusion, with most genetic variation occurring within populations and with wild populations showing clear geographic structure, especially in Guizhou, Yunnan, and Sichuan, which supports region-prioritized germplasm assessment and provenance selection (Huang et al., 2019). Additional AFLP analysis from Yunnan also found that inter-population differentiation was relatively small and that gene flow among groups was limited, reinforcing the need to sample broadly while still preserving local lineages in evaluation programs.

The future direction is therefore not simply to add more markers, but to build a multi-dimensional germplasm evaluation system that integrates genetics, phylogeography, traceability, and source-level quality control. Phylogeographic work based on chloroplast trnL-trnF sequences detected 15 haplotypes, including wild-unique and cultivated-unique haplotypes, and identified Guizhou and western Yunnan as likely historical refugia that should be included in protection zones and core germplasm construction (Zhao et al., 2021). SCoT and SRAP markers also produced very high polymorphism in Dabie Mountain materials and were explicitly proposed as suitable tools for diversity analysis, genetic improvement, and conservation (Zhao et al., 2020). Beyond DNA markers, source-traceability systems are becoming feasible: a multi-block MIR/NIR platform distinguished seed germplasm from six Yunnan origins with 96.03% test accuracy, offering a practical route for rapid screening of excellent germplasm and source-based quality control (Li et al., 2022). At the time of the cited marker studies, complete genome and EST resources remained limited, and the field still required expanded molecular databases (Su et al., 2022).

6.2 Potential application of molecular breeding technologies

The second major future direction is the application of molecular breeding technologies to overcome the slow growth cycle, long seed dormancy, mixed genetic background, and unstable quality that limit conventional *Paris* improvement. Current evidence suggests that the species is well positioned for marker-assisted and genomics-assisted breeding, but the enabling resources are still emerging. The most direct *Paris*-specific evidence comes from EST-SSR markers related to polyphyllin backbone biosynthesis, which were developed specifically to characterize cultivated populations and were proposed as tools to facilitate marker-assisted breeding (Gao et al., 2022). That need is strengthened by the fact that cultivated populations show admixture, cross-pollination among cultivars, and little deep domestication differentiation from wild sources, which complicates parent selection and makes phenotype-only breeding inefficient (Huang et al., 2019). Recent assessment work also shows that accurate distinction between *P. polyphylla* var. *chinensis* and var. *yunnanensis* remains a practical issue for cultivation and

quality control, but comparative genomic mini-barcodes can now separate them, providing a needed basis for taxon-specific breeding and deployment (Wang et al., 2026).

The broader breeding literature indicates that marker-assisted selection, genomic resources, and genome editing can sharply improve breeding precision, especially when traits are difficult to assess phenotypically or are strongly affected by environment. DNA markers improve the productivity and accuracy of classical breeding and can shorten the time required to release improved varieties (Hasan et al., 2021). Genomics-assisted breeding further expands this framework by integrating genotyping, phenotyping, and envirotyping, while genomic markers, reference genomes, transcriptomes, and expression profiles support genotype-phenotype analysis, trait mapping, and faster selection (Tyagi et al., 2024). However, the breeding literature also cautions that marker-assisted selection is most straightforward for simpler traits, whereas polygenic traits require new strategies, stronger genomic infrastructure, and more innovative selection schemes. For *Paris* spp., this means that future breeding should first prioritize development of reference genomes, denser diagnostic markers, and phenotype-linked quality traits such as polyphyllin content, stress adaptation, and dormancy behavior before genome editing or genomic selection can be applied effectively (Su et al., 2022; Kumar et al., 2024).

6.3 Establishment of long-term resource restoration mechanisms

The third challenge is that germplasm restoration will not be durable unless it is embedded in long-term ecological and management mechanisms rather than isolated propagation projects. Across the Himalayan and Chinese literature, the same pressures recur: wild populations are vulnerable, slow-growing, destructively harvested, and affected by habitat degradation, illegal trade, and weak management guidelines (Kunwar et al., 2020). Reviews therefore converge on the need for combined in situ and ex situ conservation, while field studies add that local participation, awareness, and large-scale cultivation can reduce pressure on wild populations and support rural livelihoods (Thakur et al., 2023). Long-term mechanisms should also be spatially explicit. Nepal modeling predicted 51 suitable mid-hill and mountainous districts for future growth, and recent ensemble modeling in China showed that the suitable zones of var. *chinensis* and var. *yunnanensis* differ, are shaped by climate and human disturbance, and will change under future emissions scenarios. These results support restoration mechanisms that combine protected wild refugia, taxon-specific ecological cultivation zones, and long-horizon climate adaptation planning (Zhao et al., 2021; Wang et al., 2026).

A durable restoration model should therefore link policy, community, propagation, and monitoring into a continuous renewal system. Socio-ecological work in Nepal explicitly argues that sustainable production depends on understanding distribution, use, trade, and conservation together, while trade control requires stronger harvesting guidelines and more active community involvement (Kunwar et al., 2020). Studies from India likewise recommend placing *P. polyphylla* on priority cultivation lists, promoting rhizome and seed propagation, ecological niche modeling, and awareness programs, and maintaining long-term conservation through both field protection and cultivation support (Singh et al., 2026). Practical restoration infrastructure can include field gene banks, clonal trials, and seed production systems, as exploratory resource work in Northeast India reported conservation of distinct forms, vegetative clonal trials, and establishment of seed production systems for medicinal plant restoration programs. At the information level, PPDP already provides the first dedicated biomolecular database for *Paris*, integrating transcriptome, chloroplast, SSR, and functional analysis resources, and it is intended to expand further, making it a useful base for long-term germplasm documentation, trait mining, and restoration monitoring (Su et al., 2022).

7 Conclusions and Perspectives

Wild resource conservation remains the foundation of *Paris* spp. restoration because wild populations still contain the primary reservoirs of geographic, ecological, and genetic diversity needed for future breeding and provenance selection. This importance is reinforced by population studies showing clear geographic structuring in wild germplasm, with Guizhou, western Yunnan, and related regional groups retaining especially valuable diversity for protection and source selection. Wild *Paris* populations also form part of understory forest biodiversity, because it is an understory species associated with forest biodiversity and ecosystem stability. Yet these populations are

under sustained pressure from overexploitation, habitat degradation, illegal trade, and anthropogenic disturbance, and multiple studies describe continuing decline or vulnerability across the Himalayan region and Southwest China.

Artificial restoration is equally important because dependence on wild rhizomes is not compatible with current medicinal demand or with the species' biology. Demand for *Paris* rhizomes has risen sharply, annual trade volume is large, and cultivation remains the only realistic way to reduce extraction pressure while maintaining pharmaceutical supply. Artificial propagation is especially necessary because *Paris* has a long growth cycle, long seed dormancy, low seed germination, and frequent reliance on vegetative regeneration, all of which slow natural recovery. Recent propagation research shows that somatic embryogenesis, clonal regeneration, mini-rhizome systems, and improved vegetative techniques can produce restoration-ready material at higher speed and survival than conventional methods. The strongest conclusion from the current literature is therefore that in situ conservation and artificial restoration are complementary rather than alternative strategies, and sustainable utilization depends on linking the two.

Future germplasm innovation in *Paris* spp. will depend first on better evaluation and identification systems that connect provenance, genetic background, and medicinal quality. Existing evidence shows that cultivated populations often derive from mixed provenances and contain substantial admixture and gene flow, which complicates variety identification and quality consistency. This problem is intensified by interspecific hybridization and morphological similarity among taxa, which can reduce the uniformity of medicinal raw materials and weaken seed-based breeding. Future work should therefore integrate AFLP, SSR, EST-SSR, SCoT, SRAP, chloroplast haplotypes, and species-specific barcodes into a more complete germplasm evaluation framework. Molecular infrastructure is beginning to support that transition, as PPDP already provides the first dedicated biomolecular database for *Paris* and is designed to expand with additional genomic resources.

Sustainable utilization will also require breeding and cultivation systems that are ecologically adaptive and quality-oriented rather than focused on multiplication alone. Environmental conditions strongly shape both performance and metabolite accumulation in *Paris*, with naturally forest-grown plants showing enrichment of steroidal saponins and related metabolites relative to greenhouse-grown plants. Suitable cultivation zones also differ between var. *chinensis* and var. *yunnanensis*, and future climate and human disturbance are expected to shift those zones, making taxon-specific ecological planning increasingly important. At the production level, microbial inoculants, in vitro mini-rhizome culture, and elite clonal propagation all show potential to increase biomass and polyphyllin accumulation while supplying standardized planting stocks. Long-term restoration mechanisms should therefore combine protected wild source populations, traceable cultivated supply chains, community participation, stricter harvest governance, and continued innovation in propagation and molecular breeding.

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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