https://hortherbpublisher.com/index.php/mpr/

ISSN 1927-6508

Medicinal Plant Research

Vol.16 No.1 2026

2026
01

OPEN ACCESS

Publisher

HortHerb Publisher

Edited by

Editorial Team of Medicinal Plant Research

Email: edit@mpr.hortherbpublisher.com
Website: http://hortherbpublisher.com/index.php/mpr

Address:
11388 Stevenston Hwy,
PO Box 96016,
Richmond, V7A 5J5, British Columbia
Canada

Medicinal Plant Research (ISSN 1927-6508) is an open access, peer reviewed journal published online by HortHerb Publisher.

The journal publishes all the latest and outstanding research articles, letters and reviews in all aspects of medicinal plant research, including plant growth and development, plant biology, plant nutrition, medicinal properties, phytochemical constituents, fitoterapia, pharmacognosy, essential oils, ethno- pharmacology agronomic management, and phytomedicine, as well as chemistry, pharmacology and use of medicinal plants and their derivatives.

HortHerb Publisher is an international Open Access publisher specializing in horticulture, herbal sciences, and tea-related research registered at the publishing platform that is operated by Sophia Publishing Group (SPG), founded in British Columbia of Canada.

HortHerb Publisher uses CrossCheck service to identify academic plagiarism through the world's leading plagiarism prevention tool, iParadigms, and to protect the original authors' copyrights.

Latest Content

Medicinal Plant Research 2026, Vol.16, No.1, 1-10
http://hortherbpublisher.com/index.php/mpr

Research Report Open Access

Bio Active Compounds and Antifungal Efficacy of Aqueous Extracts of *Tridax procumbens* Against Brown Rot of Amber Sweet Orange Fruits During Ambient Storage

Oladele O.O., Oyedokun F.D., Adebomi D.M.
Department of Biology, School of Life Sciences, Federal University of Technology, PMB 704, Akure, Ondo State, Nigeria
Corresponding author: kunle6634@gmail.com

Medicinal Plant Research, 2026, Vol.16, No.1 doi: 10.5376/mpr.2026.16.0001
Received: 04 Feb., 2026
Accepted: 27 Feb., 2026
Published: 10 Mar., 2026

Preferred citation for this article:
Oladele O.O., Oyedokun F.D., and Adebomi D.M., 2026, Bio active compounds and antifungal efficacy of aqueous extracts of *Tridax procumbens* against brown rot of amber sweet orange fruits during ambient storage, Medicinal Plant Research, 16(1): 1-10 (doi: 10.5376/mpr.2026.16.0001)

Abstract This research evaluated the bio active compositions and efficacy of *Tridax procumbens* in controlling brown rot of orange fruits, stored at ambient temperature. Orange fruits infected with spore suspensions (6.50×10^4 cfu/ml) of brown rot pathogen (*Lasiodiplodia* sp) were dipped separately into varying concentrations (5, 10, 15 and 100%) of the aqueous extracts where they were assessed daily for disease severity. Each set up was in replicate of five orange fruits while the untreated fruits served as control. All the varying concentrations of the extracts were effective against *Lasiodiplodia*. However, 15 and 100 % extracts proved most effective against the brown rot pathogen, with none of the fruits showing any sign of infection by day 30 in storage when compared with the control fruits that had started showing rottenness since day 10. The number of bioactive compounds detected in the *Tridax* extract was 21. Consequently, the antifungal efficacy of *Tridax procumbens* could be attributed to these biochemical constituents. Hence, *T. procumbens* could be explored as natural, safe substitute in fruit preservation.

Keywords Bioactive compounds; Disease severity; GC- MS; *Lasiodiplodia*; Preservatives

Background

Citrus fruits especially sweet orange is a good source of vitamin C, folic acid and fibres. In fact, sweet oranges are important exportable cash crops that serve as major source of foreign exchange to Nigeria prior to discovery of crude oil in 1951. In fact, it ranks as the most widely planted tree and earns substantial foreign exchange having produced 4.1 million tonnes in the year 2021 (FAOSTAT, 2023). The fruits are either eaten fresh or used for making canned orange juice. In Nigeria, the recommended varieties of sweet orange fruits include Hamlin, Valencia, Amber sweet, Agege Parson Brown, Umudike, Bende, Etir and Meran (Olaniyan et al., 2000). Nevertheless, the major cause of loss of orange fruits after harvest is pathological deteriorations. Thus, the potential foreign exchange earnings through the export of citrus fruits (sweet oranges) are under serious threats due to post-harvest infections, which could result in up to 40% yield loss. In fact, 40 to 50 percent of horticultural crops including fruits and vegetables are lost before they reach consumers while post-harvest losses in tropical fruits vary widely from 10 to 80 percent in both developed and developing countries.

Damage so produced by diseases and pests is probably the major cause of loss in orange fruits. It was reported that *Pencillium* species, especially *P. digitatum* and *P. italicum* with *Geotrichum citriaurantii* are the major mould species causing post-harvest decay of sweet oranges (Eckert and Ogawa, 1985; Ohr and Eckert, 1985). However, *Lasiodiplodia* sp IMI50324 was reported as a major post-harvest pathogen of orange fruits in Akure, Nigeria, accounting for over 75 % disease incidence of the total rots in their survey study (Oladele and Aborisade, 2015). The fungus was identified by ITS Rdna sequence analysis using the FASTA algorithm with the fungus data base from European Molecular Biology Laboratory (EMBL) and the sequence showed 100% identity to numerous ITS sequences described from different *Lasiodiplodia* species or their *Botryosphaeria* teleomorphs. Even best matches with the fungus included sequences of *Lasiodiplodia* species reported in peer reviewed literature (Orlandelli et al., 2012).

Similarly, *Lasiodiplodia* was also reported as a frequent pathogen among sweet oranges in Brazil (Slippers and Wingfield, 2007), which is consistent with (Dantas et al., 2003) results for 'Pera' variety where the *Lasiodiplodia* rot was 53% of the total fruit rots while Wright and Harmon (2009) reported *Lasiodiplodia* rot as an important post-harvest disease in warm and humid growing regions such as Florida and Caribean. Twenty-four species of *Lasiodiplodia* are known to have been distinguished based on their DNA phylogeny together with their conidial morphology and morphology and size of their paraphyses (Burgess et al., 2006). Generally, all the known species of *Lasiodiplodia* are associated with various symptoms such as dieback, root rot, fruits rot and leaf spots among many others (Punithalingham, 1980). So, *Lasiodiplodia* sp IMI50324 is a common soil pathogen associated with woody hosts in the tropics and which causes brown rot in orange fruit (Oladele and Aborisade, 2015). Initial infection shows as light brown discolouration on any area of the fruit surface. As the decay develops, the lesion becomes more brown, firm and slippery (Ismail and Zhang, 2004).

Currently, these pathogens are primarily controlled by application of fungicides either as dips, sprays, fumigants, treated wraps and box liners or in waxes and coatings. Citrus growers and sellers have routinely applied synthetic fungicides (chemicals) on their fruits for the management of post-harvest diseases. Numerous studies have been conducted to evaluate the effectiveness of various fungicides against common post-harvest pathogens affecting oranges, such as *Penicillium digitatum* and *Penicillium italicum* (Rosenberger et al., 2018), with none on *Lasiodiplodia.* Those studies provide important information for selecting appropriate fungicides and application protocols for combating post-harvest diseases in citrus fruits.

Nonetheless, synthetic fungicides could result in health hazards during application process as well as residual accumulation in the fruits. Synthetic preservatives have raised concerns regarding their potential health risks and environmental impact, underscoring the need for innovative and eco-friendly solutions (Gupta et al., 2014). Besides, export markets are increasingly more sensitive to the use of chemicals for disease control coupled with the fact that most chemicals are expensive and inaccessible to local farmers who are the major bulk producers of this fruit in Nigeria. The escalating demand for safe and sustainable food preservation methods has prompted researchers to explore alternative solutions beyond conventional synthetic preservatives. Hence, the use of non-chemical ecofriendly means of control such as botanicals have emerged as viable alternatives.

Besides, the rising awareness of health and environmental concerns associated with synthetic additives has led to a renewed interest in natural antimicrobial compounds derived from plant sources, thus making the utilization of plant-derived compounds as potential alternatives to synthetic additives to gain prominence, Therefore, the research investigated the antifungal efficacy of aqueous extract of *Tridax procumbens* against brown rot pathogen of orange fruits during ambient storage and its potential as a suitable alternative to synthetic preservatives. Phytochemical and bio active compositions of the aqueous extract was also investigated.

1 Materials and Methods

1.1 Source of fruits

Mature, green healthy orange fruits were harvested from a commercial orchard in September 2023 from a citrus farm in Igbatoro, Akure North, Nigeria. Fruits of uniform size and colour were selected. Before treatment, the fruits were washed with clean water, disinfected for 10 min in 10 % sodium hypochlorite and allowed to air-dry at room temperature.

1.2 Preparation of spore suspension

A ten-day old agar slant culture of *Lasiodiplodia* sp (IMI Number: 503248) on malt extract agar (MEA) was used to prepare spore suspension. Sterile water was poured into the slant and shaken vigorously to dislodge the spores from the vegetative hyphae. The wash water was collected in a sterilized beaker. One milliliter of the suspension was spread on an area of 1 cm^2 and allowed to dry on a clean microscope slide before counting spores using the formula of Breed Direct Counting Technique (Ogundana, 1989) under the high dry ×40 objective microscope (Olympus).

1.3 Pathogenicity test
Spore suspension of *Lasiodiplodia* was used to inoculate fresh fruits 1mm deep at the equator and incubated at 28±2℃ and 75% relative humidity inside sterilized desiccators. The disease symptoms were noted and re-isolation from infected fruit tissue was performed on fresh sterile MEA plate and its cultural characteristics were compared with the original isolate.

1.4 Preparation of extract of *Tridax procumbens*
Detached *Tridax procumbens* leaves were air dried for 14 days. The dried leaves were pulverized with a blender to a smooth powdery form. About 28 g of the pulverized leaves were dissolved in 1 L of water, thoroughly shaken together and later filtered with a muslin cloth to obtain the crude /stock solution. Varying concentrations (5, 10, 15 and 100%) of the aqueous extract were then prepared from the stock / crude extract with appropriate volumes of water.

1.5 Inoculation and Treatment of orange fruits with *Tridax procumbens* extract
The orange fruits were artificially infected with spores (6.50×10^4 cfu/ml) of *Lasiodiplodia* and later dipped separately into each concentration (5%, 10%, 15% and 100%) of the prepared extract for 5 min while benlated (fungicide) and untreated orange fruits served as positive and negative control respectively. Each set up consisted of 3 fruits. After treatment, the fruits were then placed inside a sterilized Petri dish and transferred into desiccators, and stored at 28± 2℃ and 75% relative humidity and assessed daily for disease severity

1.6 Assessment of rot severity
Assessment of disease severity was done using the scale of (Arekemase and Oyeyiola, 2007) but with slight modification where 1=disease free, 2=slight rot /decay up to 10% of the fruit, 3=moderate rot /decay up to 25% of the fruit, and 4=severe rots/decay ≥35% of the fruit surface. Rot/decay was recognized by light brown discolouration on the fruit or by appearance of mycelium on the fruit surface.

1.7 Phytochemical screening of the aqueous extract of *Tridax procumbens*
The phytochemical screening of the aqueous extract was done according to the method described by (Trease and Evans, 2004). The phytochemicals screened for were tannin, saponin, phlobatinnin, flavoniod, alkaloid and cardiac glycosides.

1.8 Gas chromatography-mass spectrophotometry (GC-MS) of *Tridax procumbens* extract
The *Tridax* extract was subjected to chromatographic analysis using a Varian 3800/4000 gas chromatograph mass spectrometer equipped with an Agilent Technologies and a BP5 (30 m×0.25 mm×0.25 microns) capillary column. Nitrogen was used as a gas carrier. 1.0 µL volumes of the extract were injected using a splitless mode at an injector temperature of 270 ℃. The oven temperature was ramped from 80 to 200 ℃ (1 min hold) at a rate of 5 ℃/min. The oven temperature was held at 280 ℃ for 6 min following each analysis. The total run time for each sample was approximately 45 min. The GC-MS interface temperature was set to 280 ℃. The peaks of the organic compounds in the samples were identified in Wiley's NIST 08 Mass Spectral Library and expressed in terms of its balance and retention time.

1.9 Statistical analysis
The data obtained for the disease severity were subjected to analysis of variance and where significant, the means were compared at 5% level of probability using Tukey's Test (SPSS version 20).

2 Results
2.1 Effects of different concentrations of *Tridax procumbens* extracts on disease severity in orange fruits pre- inoculated with *Lasiodiplodia* sp and stored at 28±2 ºC and 75 % relative humidity
All treated and control fruits recorded mean disease severity values of 1.00±0.00 by day 5 of storage (Figure 1), indicating that they were all disease free. As storage duration progressed till day 10, except the control fruits that had shown slight rottenness as evident by their mean disease severity values of 2.00±0.52, all treated fruits were still disease free (healthy), though with mean disease severity values that were not significantly different ($p\geqslant0.05$)

(Figure 2). For instance, fruits treated with both 15 and 100 % extracts of *T. procumbens* still maintained 1.00±0.00 as their disease severity values while fruits treated with 5, 10 % extracts of *T. procumbens* and fungicide had their severity values increase non-significantly ($p \geq 0.05$) to 1.67±0.44, 1.33±0.38 and 1.33±0.38 respectively (Figure 2).

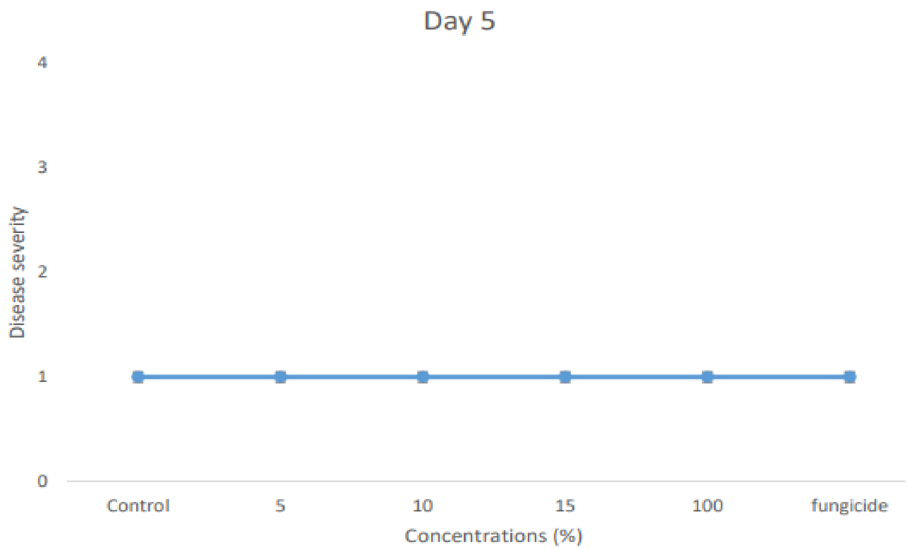


Figure 1 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 5 days

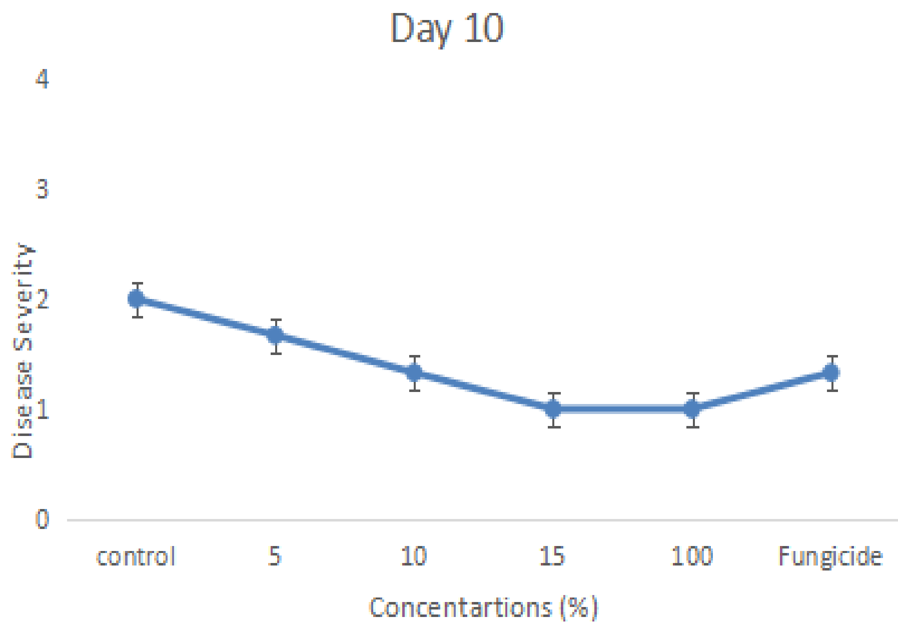


Figure 2 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 10 days

Meanwhile by day 15 in storage, only fruits treated with 15 and 100% *T. procumbens* extracts maintained their diseased free status (1.00±0.00) when compared with control and other treated fruits. In fact, the severity values of control fruits had increased to 3.00±0.33 (moderate rottenness) while all the other treated fruits recorded same severity values (2.00±0.25) and had started showing slight rottenness (Figure 3). By day 20 in storage, only fruits treated with 15 and 100% *T. procumbens* extracts still maintained their diseased free status (1.00±0.00) when compared with control and other treated fruits (Figure 4). Unfortunately, the control fruits had become completely rotten (4.00±0.52) but fruits treated with 5 and 10% extracts of *T. procumbens* and fungicide still showed slight rottenness as evident by their respective severity values of 2.67±0.44, 2.50±0.50 and 3.00±0.33 (Figure 4).

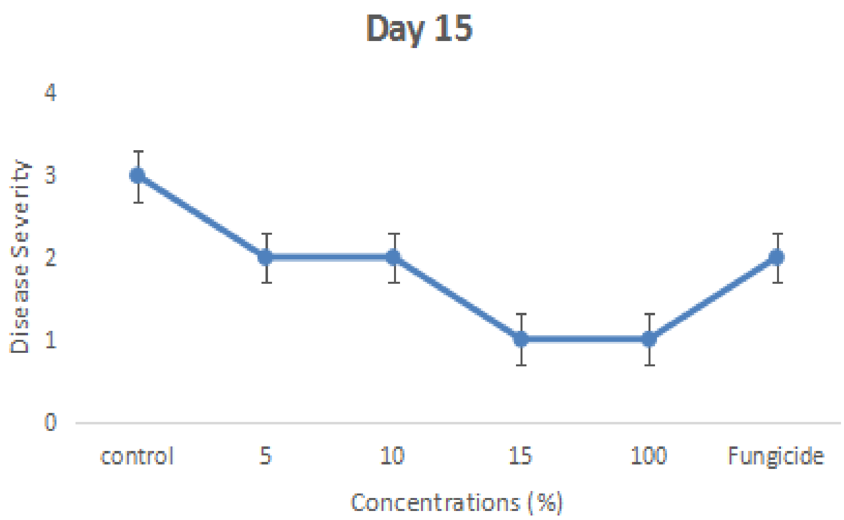


Figure 3 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 15 days

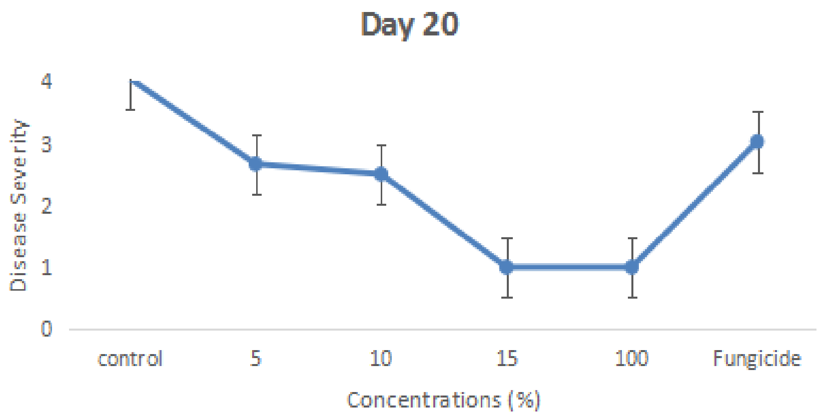


Figure 4 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 20 days

Again by day 25 in storage, except fruits treated with 15 and 100% *T. procumbens* extracts that were still diseased free and control fruits that had become completely rotten, the severity values of all the other treated fruits with fungicide, 5 and 10% *T. procumbens* extracts had increased significantly to 3.67±0.67, 3.33±0.37 and 3.00±0.33 respectively, indicating moderate rottenness (Figure 5). The same trend of results was observed for all the fruits (control and treated) as the storage durations became further extended to day 30 (Figure 6).

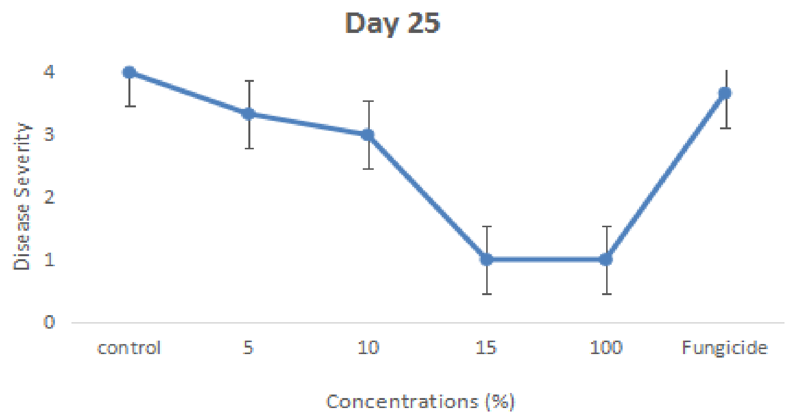


Figure 5 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 25 days

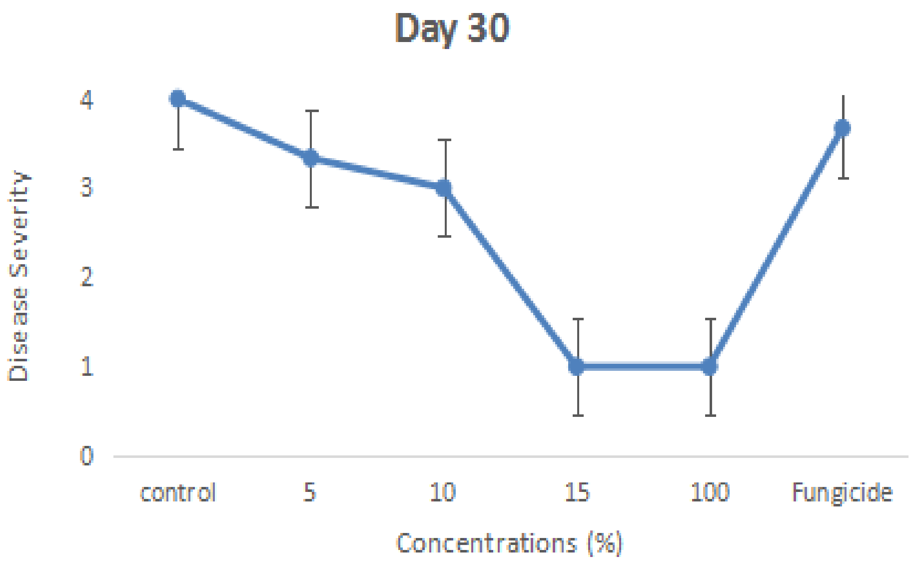


Figure 6 Effect of different concentrations of *Tridax procumbens* on disease severity in orange fruits pre-inoculated with *Lasiodiplodia* sp and stored for 30 days

2.1 Phytochemical compositions of the aqueous extract of *Tridax procumbens*

Tannins, alkaloids, cardiac glycosides, saponins and flavonoids were all detected in the *Tridax* extracts (Table 1).

Table 1 Phytochemical constituents in *Tridax procumbens*

Phytochemicals	Aqueous extract
Tannins	+
Alkaloids	+
Cardiac glycosides	+
Saponins	+
Flavonoids	+

2.2 Bioactive compounds detected in aqueous *Tridax procumbens* extracts

Table 2 shows the bioactive compounds with their peak area (%) detected in *Tridax* extract included 2,3-Butanediol (10.05), Hexanoic acid (11.77), Benzaldehyde,4-ethyl-(12.92), 4H-Pyran-4-one, 2,3 dihdro-3,5-dihydroxyl-6-methy-(6.89), Ethanone,1-(2-hydroxy-5-methylphenyl) (2.58), Methyl 4-(hydroxymethyl) benzoate (8.04), p-Menth-3-en-9-ol (3.73), Eugenol (1.44), Acetamide, N-tetrahydrofurfuryl-2-methoxy-(4.30), n-Hexadecanoic acid (12.64), 9,12-Octadecadienoic acid methy ester (1.03), Oleic acid (10.33), Octadecanoic acid (6.32) while the chromatograph of the aqueous extract of *Tridax procumbens* using GC-MS is shown in Figure 7.

Table 2 Bioactive compounds detected in aqueous *Tridax procumbens*

S/N	Retention Time (min)	Compound detected	Chemical symbol	Peak area (%)
1	8.00	2,3-Butanediol	$C_4H_{10}O_2$	10.05
2	9.46	Hexanoic acid	$C_6H_{12}O_2$	11.77
3	15.00	Benzaldehyde, 4-ethyl-	$C_9H_{10}O$	12.92
4	16.62	4H-Pyran-4-one, 2,3-dihydro-3,5- dihydroxy-6-methyl-	$C_6H_8O_4$	6.89
5	21.00	Ethanone, 1-(2-hydroxy-5-methylphenyl)-	$C_9H_{10}O_2$	2.58
6	22.00	Methyl 4-(hydroxymethyl) Benzoate	$C_9H_{10}O_3$	8.04
7	22.50	p-Menth-3-en-9-ol	$C_{10}H_{18}O$	3.73
8	24.51	Eugenol	$C_{10}H_{12}O_2$	1.44
9	26.00	Acetamide, N-tetrahydro furfuryl-2-methoxy-	$C_8H_{15}NO_3$	4.30
10	27.00	n-Hexadecanoic acid	$C_{16}H_{32}O_2$	12.64
11	29.57	9,12-Octadecadienoic acid methyl ester	$C_{19}H_{34}O_2$	1.03
12	30.84	Oleic acid	$C_{18}H_{34}O_2$	10.33
13	32.50	Octadecanoic acid	$C_{18}H_{36}O_2$	6.32

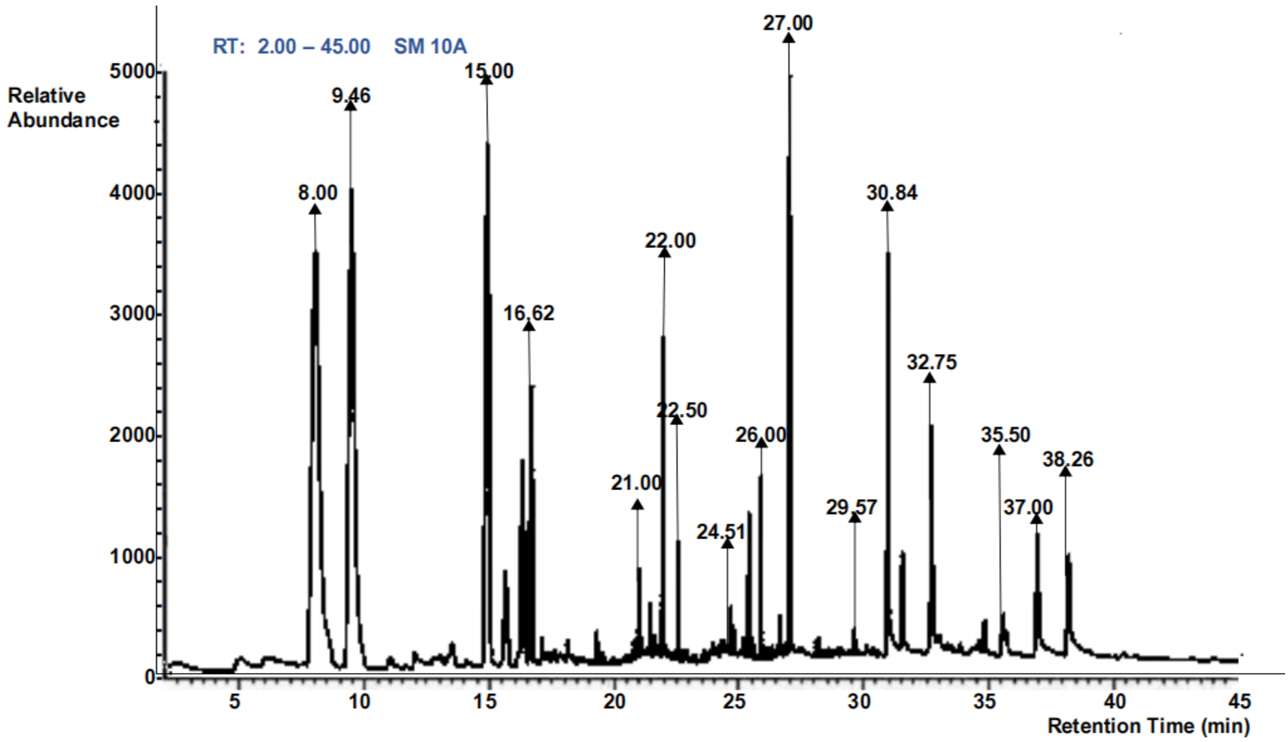


Figure 7 Chromatogram of aqueous extract of *Tridax procumbens*

3 Discussion

This study explored the efficacy of aqueous leaf extracts of *Tridax procumbens* in controlling brown rot of orange fruits during ambient storage. In fact, the study showed that all the orange fruits treated with all the varying concentrations (5, 10, 15 and 100%) of the *Tridax* extracts were disease free (healthy), showing no sign of any infection by day 10 in storage, whereas the control fruits had started showing slight rottenness. Even when the storage durations became extended till day 30 and the control fruits had become completely rotten, fruits treated with 15 and 100% *T. procumbens* extracts were still disease free, without any sign of infection. Even performed better than the fungicide used (mancozeb) because all mancozeb treated fruits were moderately rotten by day 30. Though Rosenberger et al. (2018) demonstrated the effectiveness of various fungicides in controlling post-harvest rots of stone fruits, this work has further confirmed the use of botanicals in extending the shelf life of fruits better than fungicide because the aqueous leaf extracts of *Tridax procumbens* particularly 15 and 100% extracts, best protects the orange fruits for 30 days with no sign of brown rot/infection. This observation is also consistent with the works of Efunwoye et al. (2024) who observed that all the Padma tomato fruits treated with *Tridax procumbens* in their investigation exhibited significantly lower disease incidences ($p \leq 0.05$) than the control fruits throughout the storage period.

This showed the efficacy of botanicals in controlling fruit pathogens as equally buttressed by Zakawa et al. (2018) who investigated the use of neem leaf extracts in the control of post-harvest fungal pathogens on mango fruits in Yola, Adamawa state, Nigeria emphasizing the potential of the extract as a biofungicide and Udomlak et al. (2008) who demonstrated the antifungal efficacy of clove and cinnamon oil in preventing post-harvest decay in grape fruits, showing the synergistic potential of both oils in combating post-harvest fungi of grape fruits *in vitro*. Equally, Oladele (2019) investigated the antifungal activity of garlic extracts against three post-harvest pathogens that affect fruits, demonstrating garlic's potential as a natural preservative. In recent years, researchers have investigated the antimicrobial and antioxidant properties of *Tridax procumbens* extracts in fruit preservation. No wonder, Narendhirakannan and Subramanian (2005) reported that *Tridax procumbens* has been traditionally employed in various medicines for its pharmacological properties and antimicrobial activities in food preservation. Similarly, it has been reported that *T. procumbens* has played a major role in food preservation due to its rich phytochemical compositions with potential antimicrobial properties (Gupta et al., 2019). Notably, tannins, alkaloids, cardiac glycosides, saponins and flavonoids were all detected as phytochemical constituents in the *Tridax* extracts in this work. This is in consonance with the findings of Jisha et al. (2016) and Palou et al. (2001) who reported a number of active chemical constituents such as alkaloids, flavonoids, carotenoids, β-sitosterol, fumeric acid, myristic, palmitic, arachidic, linoleic acid and tannin from botanicals and all these phytochemical composition, makes the plant a natural bio pesticide with potential antimicrobial efficacy against a broad spectrum of microorganisms (Nair et al. 2015; Mishra et al., 2018).

Each of these phytochemical constituents as enunciated by others authors, is connected with significant antimicrobial properties. For instance, alkaloids and flavonoids when present exhibit antimicrobial properties. These compounds inhibit the growth of spoilage-causing microorganisms, extending the shelf life of fruits (Das, 2014). These compounds possess antioxidant properties, which play a crucial role in fruit preservation by inhibiting oxidative processes and prevent the degradation of fruits by scavenging free radicals that contribute to spoilage (Nair et al., 2015). This is further buttressed by the reports of Vasudevan et al. (2017) that alkaloids and flavonoids act as natural antimicrobial agents, inhibiting the growth of bacteria and fungi that contribute to fruit spoilage. Also, tannins act as natural preservatives by forming complexes with proteins and enzymes, thereby inhibiting microbial growth and enzymatic browning (Okigbo et al., 2010).

Even the GC - MS analysis of the *Tridax* extract revealed a lot of bioactive compounds and these natural compounds exert their effects through various mechanisms, making them effective against different types of microorganisms. For instance, n-Hexadecanoic acid identified in the extract is reported to have pesticide activities (Rajasekaran and Cary, 2014). Also, 9-octadecenoic acid methyl ester possesses anti-microbial properties while stearic acid were also found to exhibit antibacterial and antifungal activities (Gehan et al., 2009). Remarkably, the presence of bioactive compounds in *Tridax procumbens* may contribute to natural pest resistance, presenting opportunities for sustainable pest management in agriculture. The method typically involves the application of plant extracts onto the fruit surface or as part of coatings, creating a protective barrier against fungal colonization. Besides, their anti-microbial properties inhibit the growth and development of post-harvest pathogens, thereby preserving the quality of the orange fruits.

4 Conclusions

The study demonstrates antifungal efficacy of the aqueous extracts of *Tridax procumbens* against *Lasiodiplodia* sp (IMI: 50324), the brown rot pathogen of amber sweet orange fruits. The findings reveal the effectiveness of the aqueous extract at all tested concentrations against the brown rot pathogen by keeping the infected orange fruits healthy (disease free) for the first 10 days of storage under ambient temperature when compared with the untreated fruits. Further investigations even show that 15 and 100% concentrations of the aqueous extract still maintain the healthy status (wholesomeness) of the orange fruits for 30 days without any sign of rottenness as against the untreated and fungicide treated fruits that had already become unwholesome and diseased. Thus, we adjudge 15 and 100% of the *Tridax* aqueous extracts the most effective among the tested concentrations. They show potential for further development as safe, ecofriendly and effective natural substitutes against fruit pathogens.

Author's Contributions

Oladele O.O. carried out the conceptualization, methodology, investigation, supervision, formal analysis and writing of original manuscript while Oyedokun F.D. and Adebomi D.M. were involved in the methodology, investigation, resources and data analysis. All authors read and approved the final manuscript.

Acknowledgements

The authors thank Life Technologies, UK for PCR purification and sequencing reactions of the fungi isolate.

References

Arekemase M.O., and Oyeyiola G.P., 2007, Fungi associated with spoiled citrus fruits obtained from Ilorin, Centre Point Science (Edition), 4: 138-149.

Burgess T.I., Barber P.A., Mohali S., Pegg G., and Wingfield M.J., 2006, Three new *Lasiodiplodia* spp. from the tropics, recognized based on DNA sequence comparisons and morphology, Mycologia, 98(3): 423-435.
https://doi.org/10.1080/15572536.2006.11832677

Dantas K., Suzana K.F., and Mauz D.E., 2003, Diseases in papaya and oranges marketed in the distribution centre of Recife, Brazil, Fitopatologia Brasileira, 28: 528-533.
https://doi.org/10.1590/S0100-41582003000500010

Das K., 2014, Phytochemical evaluation and comparative antibiocide efficacy of aqueous, ethanolic and equal mixture of aqueous (1:1) bark extract of *Lannea coromandelica* L. procured from Eastern region of India, International Letters of Natural Sciences, 21: 21-31.
https://doi.org/10.56431/p-1eu719

Eckert J.W., and Ogawa J.M., 1985, The chemical control of postharvest diseases: subtropical and tropical fruits, Annual Review of Phytopathology, 23: 421-454.
https://doi.org/10.1146/annurev.phyto.23.1.421

Efunwoye O.O., Aborisade A.T., and Oladele O.O., 2024, Treatment of tomato (*Solanum lycopersicum* L.) fruits with powders and ashes from *Tridax procumbens* and *Chromolaena odorata* for shelf-life extension, African Journal of Agriculture and Food Science, 7(4): 273-287.
https://doi.org/10.52589/AJAFS-CXMSBTBE

Efunwoye O.O., Aborisade A.T., and Oladele O.O., 2024, Storability of inoculated tomato fruits at ambient conditions after treatment with powders of *Tridax procumbens* and *Chromolaena odorata*, FUTA Journal of Life Sciences, 5(3): 25-37.

FAOSTAT, 2023, Crops and livestock production, Food and Agriculture Organization of the United Nations, Rome.

Gehan M.A., Hassan A.H.I., and Okbah M.A., 2009, Marine natural products and their potential applications as anti-infective agents, World Science Journal, 7(7): 872-880.

Gupta R., Sharma A.K., Dobhal M.P., Sharma M.C., and Gupta R.S., 2019, Antimicrobial potential of *Tridax procumbens* Linn., Evidence-Based Complementary and Alternative Medicine, 2019: Article ID 7981031.

Ismail M., and Zhang J., 2004, Post-harvest citrus diseases and their control, Outlooks on Pest Management, 15(1): 29.
https://doi.org/10.1564/15feb12

Jisha M., Zeinul Hukuman N.H., and Leena P., 2016, GC-MS analysis of leaves and flowers of *Pogostemon quadrifolius* (Benth.) F.Muell. (Lamiaceae), World Journal of Pharmaceutical Research, 5(12): 667-681.

Mishra N., Patel N., and Bajpai R., 2018, Chemical composition and in vitro antioxidant and antimicrobial activities of essential oil and methanol extract of *Tridax procumbens* Linn., Journal of Food Science and Technology, 55(1): 188-196.

Nair R., Kalariya T., and Sumitra C., 2005, Antibacterial activity of some selected Indian medicinal flora, Turkish Journal of Biology, 29(1): 41-47.

Narendhirakannan R.T., and Subramanian S., 2005, Antioxidant activity of ethanolic extract of *Tridax procumbens* (Linn.) in vitro, Indian Journal of Experimental Biology, 43(5): 440-443.

Ogundana S.K., 1989, Introductory Microbiology, 1st ed., Obafemi Awolowo University Press, Ile-Ife, Nigeria, 215 pp.

Ohr H.D., and Eckert J.W., 1985, Post-harvest diseases of citrus fruits in California, University of California Cooperative Extension Service, Riverside, California, Leaflet No. 21407.

Okigbo R.N., Anuagasi C.L., and Amadi J.E., 2010, Antimicrobial and antioxidant properties of alkaloids from *Curtisia dentata*, Journal of Medicinal Plants Research, 4(24): 2674-2681.
https://doi.org/10.5897/JMPR09.464

Oladele O.O., 2019, Screening for antifungal activity of garlic (*Allium sativum*) powder against mycelial growth of three post-harvest pathogens, European Journal of Biological Research, 9(2): 57-63.
https://doi.org/10.15625/2525-2518/57/3B/14045

Oladele O.O., and Aborisade A.T., 2015, Integrated control of Lasiodiplodia rot on sweet orange fruits using hot water-fungicide treatment, Nigerian Journal of Mycology, 7: 93-99.

Olaniyan A., Olajide-Taiwo L.O., Amin C.A., and Afolayan S.O., 2000, Growth performance of Nigerian sweet orange cultivars (*Citrus sinensis*) in the nursery, Nigerian Journal of Horticultural Science, 6: 24-28.

Orlandelli R.C., Alberto R.N., Rubin Filho C.J., and Pamphile J.A., 2012, Diversity of endophytic fungal community associated with *Piper hispidum* leaves, Genetics and Molecular Research, 11: 1575-1585.
https://doi.org/10.4238/2012.May.22.7

Palou L., Smilanick J.L., Droby S., and Wilson C., 2001, Control of postharvest diseases of fruits and vegetables by promising antifungal microbial and plant extracts, International Journal of Food Microbiology, 67(3): 189-197.

Punithalingam E., 1980, Plant diseases attributed to *Botryodiplodia theobromae* Pat., Letters in Applied Microbiology, 1: 17-20.

Rajasekaran K.M., and Cary J.W., 2014, *Tridax procumbens* essential oil effectively protects stored maize against *Sitophilus zeamais*, Industrial Crops and Products, 61: 1-5.

Rosenberger D.A., Cox K.D., and Cheng G., 2018, Managing fungicide resistance in apple diseases, Plant Health Progress, 19(3): 213-220.

Schmourlo G., Mendonça-Filho R.R., Alviano C.S., and Costa S.S., 2005, Screening of antifungal agents using ethanol precipitation and bioautography of medicinal and food plants, Journal of Ethnopharmacology, 96: 563-568.
https://doi.org/10.1016/j.jep.2004.10.007

Slippers B., and Wingfield M.J., 2007, Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact, Fungal Biology Reviews, 21: 90-106.
https://doi.org/10.1016/j.fbr.2007.06.002

Spooner D.M., Hetterscheid W.L.A., Vandenberg R.G., and Brandenburg W., 2003, Plant nomenclature and taxonomy: a horticultural and agronomic perspective, Journal of Horticultural Science, 28: 1-60.
https://doi.org/10.1002/9780470650851.ch1

Trease E., and Evans W.C., 2004, Pharmacognosy, 15th ed., Saunders Publisher, London, pp. 137-440.

Udomlak S., Vichai H., Walairut C., Uraiwan D., and Panuwat S., 2008, Antifungal effect of clove and cinnamon oil and their synergistic activity against post-harvest decay of grape in vitro, Kasetsart Journal of Natural Science, 42: 160-174.

Vasudevan M., Parle M., Kumar G.P., and Rekha S., 2017, Phytochemical analysis and antioxidant activity of *Tridax procumbens* Linn., Research Journal of Pharmacy, Biology and Chemistry Sciences, 8(6): 1447-1455.

Wright A.F., and Harmon P.F., 2009, First report of *Lasiodiplodia theobromae* associated with stem blight of southern highbush blueberry in Florida, Plant Disease, 93: 962.
https://doi.org/10.1094/PDIS-93-9-0962C

Zakawa N.N., Channaya K.F., Magga B., and Akesa T.M., 2018, Antifungal activity of neem (*Azadirachta indica*) leaf extract on mango fruits post-harvest rot agents in Yola, Adamawa State, Journal of Pharmacognosy and Phytochemistry, 7(1): 23-26.

Feature Review Open Access

Environmental Control and Standardized Production in Facility-Based *Ganoderma lucidum* Cultivation

Xiaotong Wang
Jinhua Shouxiangu Pharmaceutical Co. Ltd., Jinhua, 321200, Zhejiang, China
Corresponding email: 378968737@qq.com

Medicinal Plant Research, 2026, Vol.16, No.1 doi: 10.5376/mpr.2026.16.0002
Received: 15 Jan., 2026
Accepted: 01 Mar., 2026
Published: 16 Mar., 2026

Preferred citation for this article:
Wang X.Y., 2026, Environmental control and standardized production in facility-based *Ganoderma lucidum* cultivation, Medicinal Plant Research, 16(1): 11-30 (doi: 10.5376/mpr.2026.16.0002)

Abstract This study explores the key technical pathways for environmental control and standardized production in facility-based *Ganoderma lucidum* cultivation. As market demand for *G. lucidum* products continues to expand, the limitations of traditional cultivation methods in precise environmental regulation, product quality consistency, and production standardization have become increasingly evident. This paper analyzes the specific requirements of *G. lucidum* growth for temperature, humidity, light, CO_2 concentration, substrate, and a clean cultivation environment. It summarizes facility-based production models, including greenhouse cultivation, intelligent mushroom houses, multi-layer bag cultivation, and liquid fermentation, with emphasis on temperature and humidity control, ventilation and light regulation, clean-environment management, and pest and disease prevention. Meanwhile, the standardized production process of *G. lucidum* is reviewed in terms of strain selection, substrate standardization, cultivation bag preparation, sterilization and inoculation, fruiting management, harvesting and processing, and quality evaluation. The study suggests that the application of IoT monitoring, automated regulation, data analysis, and intelligent management technologies can improve the precision, standardization, and traceability of *G. lucidum* production. In the future, regionalized cultivation technology systems, breeding and promotion of superior varieties, and branding and product traceability systems should be further strengthened to promote the high-quality, green, and intelligent development of the *G. lucidum* industry.

Keywords *Ganoderma lucidum*; Facility-based cultivation; Environmental control; Standardized production; Intelligent management

1 Introduction

Ganoderma lucidum is one of the traditional valuable medicinal fungi in China. It was classified as a “superior-grade” medicinal material in *Shennong’s Classic of Materia Medica* and has long been recognized for its medicinal value in tonifying qi, calming the mind, and strengthening healthy qi. Modern studies have shown that *G. lucidum* is rich in bioactive compounds such as polysaccharides and triterpenoids, which exhibit various pharmacological activities, including immunomodulatory, antioxidant, antitumor, and metabolic regulatory effects. Therefore, its application value in food, nutritional supplements, pharmaceuticals, functional products, and wellness markets has continued to increase (Thakur et al., 2024). In recent years, with the rapid development of the health industry and the increasing health awareness of consumers, market demand for *G. lucidum*-related products has continued to expand. The stable and large-scale supply of safe, high-quality *G. lucidum* raw materials and derivative products has become an important foundation for supporting industrial development (Wu et al., 2024). However, traditional *G. lucidum* cultivation systems still have certain limitations in yield stability, quality consistency, resource-use efficiency, and contamination control. Some production practices still rely on experience-based management, which may lead to imprecise environmental regulation, large variations in product quality, frequent occurrence of pests and diseases, and inconsistent production standards. These problems make it difficult to meet modern market demand for high-quality, safe, and stable *G. lucidum* products (Ghafoor et al., 2024). Therefore, promoting technological upgrading and the construction of standardized production systems has become a practical requirement for the high-quality development of the *G. lucidum* industry.

G. lucidum is a typical wood-decaying fungus, and its mycelial growth and fruiting body formation are highly sensitive to environmental conditions such as temperature, humidity, light, air circulation, CO_2 concentration, and nutrient supply. Under traditional open-field cultivation or simple greenhouse cultivation, *G. lucidum* production is easily affected by seasonal changes, climatic fluctuations, and natural disasters, often resulting in slow mycelial growth, abnormal fruiting body morphology, unstable yield, and fluctuations in active component contents. Meanwhile, the scarcity and instability of wild resources, high dependence on wood-based substrates, and obvious batch-to-batch differences in active components further highlight the need to establish efficient, controllable, and sustainable production systems. With the development of modern agricultural facility technologies and bioprocessing technologies, facility-based cultivation has gradually become an important direction for the transformation and upgrading of the *G. lucidum* industry. Indoor mushroom houses, environmentally controllable "mushroom factories," liquid spawn systems, and submerged fermentation technologies can precisely regulate temperature, humidity, gas composition, light, and nutritional conditions, thereby improving production stability and quality consistency (Feng et al., 2024; Ghafoor et al., 2024; Liu et al., 2024). In addition, facility-based cultivation can reduce the risks associated with heavy metals, toxic residues, and competitive microorganisms by separating substrates from soil, while also supporting standardized operations that comply with pharmacopoeial requirements and good manufacturing practices (Wu et al., 2024).

In facility-based *G. lucidum* cultivation, environmental control technology is a core factor affecting production performance and product quality. Temperature and humidity are directly related to mycelial expansion, primordium formation, and fruiting body development; ventilation affects changes in CO_2 concentration and plays an important role in pileus formation, stipe elongation, and morphogenesis; light conditions are closely associated with primordium differentiation, color formation, and the accumulation of bioactive substances. Studies have shown that controlled environments can optimize fruiting body morphology, yield, and the accumulation of bioactive components such as polysaccharides and triterpenoids by regulating key factors such as light spectrum, temperature profiles, and oxygen supply. Improper environmental regulation can easily lead to contamination, excessive stipe elongation, malformed pilei, and insufficient accumulation of active components. Therefore, establishing a scientific, stable, and reproducible environmental control system is an important basis for improving the level of facility-based *G. lucidum* cultivation. Meanwhile, the application of low-cost IoT-based temperature and humidity sensing, automatic control, and real-time monitoring technologies has further enhanced environmental management during *G. lucidum* production, helping to achieve contaminant control, compliance with quality indicators, and standardized whole-process management (Nguyen et al., 2023; Liu et al., 2024).

This study will explore the key technical pathways for environmental control and standardized production in facility-based *G. lucidum* cultivation. It will focus on the environmental regulation points, key production procedures, and quality control systems of facility-based *G. lucidum* cultivation; examine the application value of intelligent and digital technologies in *G. lucidum* production; and propose development pathways for standardized production in light of the current industrial context. The study aims to integrate the development needs of the *G. lucidum* industry with modern controllable cultivation technologies. By summarizing research progress in facility design, temperature, humidity, CO_2, light quality, ventilation regulation, liquid spawn, and fermentation processes, it seeks to provide technical references for stable and high-quality *G. lucidum* production. This study will also examine how precise environmental regulation can support emerging quality standards, increase the yield of fruiting bodies and bioactive metabolites, reduce contamination and resource consumption, and thereby promote *G. lucidum* production toward precision, standardization, and intelligentization, enhance product quality and industrial competitiveness, and facilitate the sustainable and high-quality development of the *G. lucidum* industry.

2 Basic Characteristics of Facility-Based *Ganoderma lucidum* Cultivation

2.1 Specific environmental requirements for *Ganoderma lucidum* growth

Ganoderma lucidum is a thermophilic wood-decaying fungus. Its mycelial growth, primordium differentiation, and fruiting body formation show distinct stage-specific requirements for temperature, humidity, light, CO_2 concentration, pH, and substrate conditions. Studies have shown that *G. lucidum* mycelia generally grow well at 25℃~32℃, under near-neutral to slightly acidic pH and relatively high humidity, whereas fruiting body formation depends more on stable temperature and humidity, appropriate light, and favorable gas exchange conditions (Al-Kaabi and Hussien, 2025). For example, Magday (2014) found that a wild Philippine strain of *G. lucidum* showed better mycelial growth at pH 6.0, 32℃, and under light conditions; Lengare et al. (2023) reported that vegetative growth performed well at 25℃, 95%-100% relative humidity, and a 12 h light/12 h dark cycle. Therefore, facility-based *G. lucidum* cultivation is not merely the control of a single environmental parameter, but requires integrated regulation according to different growth stages.

During fruiting body formation, *G. lucidum* has stricter requirements for air humidity, light, and ventilation. Appropriate humidity promotes primordium formation and pileus expansion, whereas insufficient ventilation may lead to elevated CO_2 concentration in the facility, resulting in elongated stipes, poor pileus development, or abnormal morphology. A Korean bed-cultivation study showed that 28℃~30℃, light intensity of 1 000~1 500 lux, and approximately 1% CO_2 were suitable for fruiting body formation. Recent studies on light quality regulation further indicate that green light can promote stipe elongation, pileus expansion, fresh weight increase, and the contents of crude protein, polysaccharides, triterpenoids, and extracellular enzyme activity, whereas red light may inhibit fruiting body differentiation. Therefore, spectral selection and lighting regime design should be emphasized in factory cultivation (Liu et al., 2024). This suggests that light not only affects the appearance quality of *G. lucidum*, but is also closely related to the accumulation of active components.

In addition to physical environmental factors, substrate chemical properties and facility cleanliness are also important factors affecting stable *G. lucidum* production. Continuous cultivation can alter organic matter, pH, salinity, and enzyme activities in soil or substrates, leading to changes in the metabolite composition of fruiting bodies (Wang et al., 2022). Meanwhile, competitive fungi such as *Trichoderma* can proliferate readily in *G. lucidum* cultivation environments and inhibit *G. lucidum* growth through volatile and non-volatile metabolites, causing contamination and yield loss (Lim et al., 2024). Therefore, facility-based *G. lucidum* production should integrate temperature and humidity regulation, light management, CO_2 control, pH and salinity adjustment, substrate disinfection, and spatial sanitation management to establish a stable and reproducible environmental control system.

2.2 Main models of facility-based *Ganoderma lucidum* cultivation

With the development of modern agricultural facility technologies, *G. lucidum* production has gradually shifted from traditional open-field cultivation and simple greenhouse cultivation toward facility-based, controllable, and standardized models. At present, greenhouses and indoor mushroom houses are common solid-state cultivation models for fruiting body production. They usually use sawdust, agricultural residues, or logs as substrates, and are equipped with functional areas such as inoculation rooms, incubation rooms, sterilization rooms, fruiting rooms, packaging rooms, and waste disposal areas (Thakur et al., 2024; Akçay et al., 2025). Standardized bed cultivation generally uses formulated sawdust-based substrates and promotes fruiting body formation under controlled temperature, light, and CO_2 conditions. Compared with traditional open-field cultivation, greenhouse and mushroom-house cultivation can reduce the influence of external climate fluctuations and improve production stability and year-round supply capacity.

In solid-state facility cultivation, bag cultivation and multi-layer rack cultivation are important forms of current large-scale production. Bag cultivation uses lignocellulosic wastes such as sawdust, rice straw, wheat straw, and hazelnut shells as main raw materials. By optimizing substrate formulations, it can shorten mycelial colonization time and improve yield and the number of fruiting flushes (Akçay et al., 2025). Multi-layer rack cultivation improves space utilization by vertically arranging cultivation bags, facilitating unified sterilization, inoculation, incubation, and fruiting management. Some regions have also developed permanent greenhouse sand-bed cultivation models, in which cultivation substrates are separated from soil using plastic membranes and combined with sprinkler and shading systems. This can reduce the risks of heavy metals, pesticide residues, and competitive microbial contamination, and increase yield by approximately 30% compared with traditional open-field methods. This type of model combines environmental controllability with quality and safety advantages, making it suitable for standardized medicinal *G. lucidum* production.

In addition to solid-state fruiting body production, liquid cultivation and bioreactor systems have gradually become important components of facility-based *G. lucidum* production. Liquid facility-based models mainly target mycelial biomass, extracellular polysaccharides (EPS), triterpenoids, and other metabolites, and generally use shake flasks, stirred-tank reactors, or specially designed bioreactors for closed cultivation (Alsaheb et al., 2020). For example, new reactors such as the Air-L-Shaped Bioreactor (ALSB) can reduce mycelial adhesion to the reactor wall and clumping, thereby improving mass transfer efficiency and process economics (Supramani et al., 2023). In addition, two-stage liquid static cultivation and bag-type static bioreactors can be used for efficient accumulation of triterpenoids, indicating that facility-based *G. lucidum* cultivation has expanded from simple fruiting body production to targeted production of mycelia and functional metabolites. Overall, facility-based *G. lucidum* cultivation is forming a diversified system ranging from greenhouse cultivation, intelligent mushroom houses, and multi-layer bag cultivation to liquid fermentation and bioreactor production.

2.3 Development characteristics of large-scale *Ganoderma lucidum* production

In recent years, the *G. lucidum* industry has increasingly shown trends toward scaling-up, intensification, engineering, and standardization. Traditional solid-state cultivation based on logs or beds has a relatively long production cycle and high labor intensity, and is vulnerable to contamination, continuous cropping obstacles, and environmental fluctuations. These limitations make it difficult to meet global market demand for stable supply and quality consistency (Araque et al., 2020; Wu et al., 2024). As *G. lucidum* is increasingly used in dietary supplements, pharmaceuticals, functional foods, and health products, large-scale production requires not only higher yield, but also unified standards for active components, safety, and batch consistency. Through unified strain supply, standardized substrate preparation, centralized cultivation management, and batch-based production processes, production costs per unit can be effectively reduced, production efficiency can be improved, and product quality stability can be enhanced.

During large-scale development, facility-based cultivation and process engineering have become important technical supports. Engineering simulation studies have shown that tools such as SuperPro Designer can be used to simulate industrial-scale submerged cultivation of *G. lucidum*, predict equipment requirements, energy consumption, and operating costs, and evaluate the economic effects of bioreactor scale-up. For example, increasing bioreactor volume from 2 m^3 to 20 m^3 can significantly reduce the unit production cost of extracellular polysaccharides and other products, demonstrating the importance of economies of scale and process optimization (Araque et al., 2020). Semi-industrial and pilot-scale studies have also shown that controlled pH, optimized carbon and nitrogen sources, and appropriate reactor configurations can significantly improve the yields of extracellular polysaccharides and other metabolites (Alsaheb et al., 2020; Supramani et al., 2023). This indicates that large-scale *G. lucidum* production is no longer limited to traditional cultivation experience, but is gradually moving toward process design, parameter optimization, and engineering scale-up.

Standardized management is an important approach to enhancing the competitiveness of the large-scale *G. lucidum* industry. At present, *G. lucidum* production has shifted from merely pursuing yield to placing greater emphasis on quality, safety, traceability, and market standardization. Relevant reviews have indicated that industrial standardization of *G. lucidum* is promoting the standardization of raw material sources, processing procedures, quality control, and product circulation, while emphasizing the importance of active component content, hygiene and safety, and production consistency in industrial development. Meanwhile, facility-based cultivation, non-soil-contact systems, and clean-environment management can help reduce heavy metal contamination and the hazards of competitive fungi, thereby improving production reproducibility and quality stability (Lim et al., 2024; Wu et al., 2024). In the future, with the further application of environmental monitoring, intelligent ventilation, automatic spraying, data analysis platforms, and bioreactor technologies, large-scale *G. lucidum* production will place greater emphasis on precise regulation, green production, brand-oriented operation, and alignment with international quality standards, thereby promoting the industry toward high-quality development.

3 Key Points of Environmental Control in Facility-Based *Ganoderma lucidum* Cultivation

3.1 Temperature and humidity control during *Ganoderma lucidum* growth

Temperature and humidity are the core environmental factors affecting mycelial growth, primordium formation, fruiting body development, and active component accumulation in *Ganoderma lucidum*. During the mycelial incubation stage, *G. lucidum* generally shows the growth characteristics of a relatively thermophilic fungus, with the suitable temperature mostly concentrated around 25℃~30℃. Laboratory and facility-based studies have shown that *G. lucidum* mycelia can exhibit strong radial growth at 25℃~30 ℃ or 30℃~35℃, although the specific suitable range may vary depending on the medium, strain, and cultivation system (Lengare et al., 2023; Al-Kaabi and Hussien, 2025). In bag and substrate cultivation, early mycelial colonization is usually suitable at 25℃~30 ℃, 60%~70% relative humidity, and under clean, low-light or dark conditions (Huynh and To, 2023). If the temperature is below the suitable range, mycelial growth slows significantly and the cultivation cycle is prolonged; if the temperature is too high, it may lead to mycelial aging, abnormal substrate fermentation, and an increased risk of contamination. Therefore, facility-based cultivation should dynamically adjust temperature according to different growth stages of *G. lucidum* and maintain environmental stability through heat preservation, cooling, shading, and ventilation measures.

Humidity management should be matched with the growth stage of *G. lucidum* to balance water supply, gas exchange, and contamination risk. During the mycelial incubation stage, air humidity can generally be maintained at 60%~70% to prevent substrate water loss and mycelial shrinkage. After entering the stages of primordium formation and fruiting body development, air humidity should be appropriately increased to promote primordium differentiation, pileus expansion, and tissue fullness of fruiting bodies. Studies have shown that in controllable mushroom houses, when the temperature is maintained at approximately 28℃, a relative humidity close to 90% during the fruiting stage is conducive to pileus expansion and fruiting body weight gain (Liu et al., 2024). Stage-specific humidity management, such as maintaining 60%-70% humidity during early colonization, increasing it to 80%~90% during active fruiting body development, and then reducing it back to 60%~70% before harvest, has also been associated with relatively high polysaccharide content around day 75 of cultivation on lignocellulosic substrates (Huynh and To, 2023). This indicates that humidity regulation affects not only the morphogenesis of *G. lucidum*, but also the accumulation of functional components such as polysaccharides.

Climatic conditions vary greatly across seasons and regions, placing higher requirements on facility-based *G. lucidum* management. Field and semi-controlled system studies have shown that, compared with cooler environments, warmer cultivation sites can shorten the cultivation cycle and accelerate primordium and fruiting body development, indicating that temperature differences significantly affect the developmental process of *G. lucidum* (Figure 1) (Bijalwan et al., 2021). During high-temperature summers, shading, wet-pad cooling, air circulation, and automatic spraying should be used to reduce the internal temperature of the facility. In winter, heat preservation and heating management should be strengthened to prevent low temperatures from inhibiting mycelial activity. In recent years, low-cost IoT systems have been applied to continuous temperature and humidity monitoring in indoor *G. lucidum* cultivation, enabling real-time tracking of environmental fluctuations and helping maintain facility conditions within suitable ranges, thereby supporting both yield improvement and quality compliance (Nguyen et al., 2023). Therefore, temperature and humidity control should shift from traditional experience-based management to precise regulation based on real-time data.

3.2 Ventilation and light regulation during fruiting body formation of *Ganoderma lucidum*

During fruiting body formation, ventilation management mainly regulates CO_2 concentration and oxygen supply within the facility, and is an important factor ensuring normal fruiting body morphogenesis. *G. lucidum* continuously respires during growth. If air exchange in the facility is insufficient, CO_2 concentration increases, which may easily lead to elongated stipes, smaller pilei, incomplete pileus expansion, and even atypical fruiting body structures. In log and bag cultivation systems, sufficient ventilation during the fruiting stage is usually as important as moisture management and helps maintain suitable air and substrate conditions (Bijalwan et al., 2021). Studies on CO_2 regulation have shown that elevated CO_2 levels, such as approximately 0.3% or below 5%, can induce antler-like or other atypical fruiting structures and are accompanied by changes in metabolite profiles and increased accumulation of phenolics, polysaccharides, triterpenoids, and steroids; however, they may also inhibit normal pileus formation and cell-division-related processes (Fang et al., 2025). Therefore, in facility-based production, the ventilation strategy should be determined according to product goals. If standard pileus-type *G. lucidum* is produced, air exchange should be strengthened; if special morphotypes such as antler-type *G. lucidum* are produced, CO_2 accumulation may be regulated within a controllable range.

Figure 1 Different growth stages of *Ganoderma lucidum* (Adopted from Bijalwan et al., 2021)

Ventilation regulation can also improve the humid and hot environment inside the facility, reduce localized water accumulation and stuffiness, and lower the risk of pathogen proliferation. In actual production, the ventilation demand is relatively low during the mycelial incubation stage, whereas air exchange should be strengthened during primordium differentiation and pileus development to ensure oxygen supply and reduce CO_2 concentration. However, excessive ventilation may reduce air humidity, causing fruiting body margins to crack or growth to stagnate. Therefore, ventilation management should be synchronized with humidity regulation. Natural air exchange, mechanical ventilation, circulation fans, and CO_2 monitoring systems can be used to achieve a dynamic balance between ventilation and moisture retention. Fang et al. (2025) pointed out that facility-based cultivation requires adjustable ventilation and CO_2 monitoring equipment so that management strategies can be switched according to the production goals of normal fruiting bodies or special morphotypes.

Light is another key factor affecting primordium induction, fruiting body differentiation, and quality formation in *G. lucidum*. *G. lucidum* exhibits obvious photosensitivity during the fruiting stage. Appropriate light can promote primordium formation and pileus differentiation, whereas darkness is more favorable for vegetative mycelial growth. Although *G. lucidum* is not a strong light-demanding fungus, a certain intensity of scattered light is beneficial for pigment formation, pileus expansion, and appearance quality improvement. Studies in environmentally controllable "mushroom factories" have shown that, under conditions of approximately 28°C, about 90% humidity, and a 12 h light/12 h dark cycle, continuous or intermittent green light promotes stipe length, pileus diameter, fruiting body weight, crude protein, triterpenoid and polysaccharide contents, and extracellular enzyme activity more effectively than white light. In contrast, continuous or intermittent red light delays or even completely inhibits fruiting body differentiation and is unfavorable for production (Liu et al., 2024). Earlier studies also found that light alone can induce primordium formation on agar medium, while the combined effects of light and ventilation can induce atypical fruiting structures with basidia and basidiospores, indicating a significant interaction between light and aeration. Therefore, facility-based *G. lucidum* production should rationally design light spectrum, light intensity, photoperiod, and ventilation regimes according to different growth stages and product goals.

3.3 Clean cultivation environment and pest and disease control in *Ganoderma lucidum* cultivation

Facility-based *G. lucidum* cultivation has a relatively long production cycle, and the substrates are rich in organic nutrients. In addition, high-temperature and high-humidity conditions can easily promote the proliferation of antagonistic fungi and pests. Therefore, clean-environment management is an important foundation for ensuring high-yield and high-quality production. Before production begins, cultivation rooms, inoculation rooms, cultivation racks, spraying systems, and production tools should be thoroughly cleaned and disinfected to reduce pathogen residues. Workers entering the production area should also undergo sanitation procedures to prevent external contamination sources from entering the cultivation environment. Studies have shown that in intensive *G. lucidum* facilities, colonies of *Trichoderma* and *Mucor* on the soil surface can increase significantly during cultivation, by up to 9~15 times; these fungi show strong antagonistic effects against *G. lucidum* in vitro and are closely associated with cultivation obstacles and failure of fruiting body development (Tong et al., 2020; Wang et al., 2022).

Contamination by competing microorganisms is one of the most common and serious problems in *G. lucidum* production. Contaminants such as *Trichoderma*, *Penicillium*, *Mucor*, and *Neurospora* compete with *G. lucidum* mycelia for nutrients and space and may inhibit *G. lucidum* growth through metabolic products, causing bag failure or even contamination of entire batches in severe cases. Continuous cultivation in the same soil can also lead to increases in organic matter and nitrogen levels, promoting the proliferation of competitive fungi and pathogens such as *Xylogone ganodermophthora*. This pathogen can reduce *G. lucidum* growth by more than 50%, leading to weak growth, aggravated disease, and yield decline (Tong et al., 2020; Huang et al., 2024). Therefore, thorough sterilization, clean substrate preparation, timely removal of contaminated bags, soil or substrate rotation, and avoidance of excessive nutrient accumulation are basic measures for disease control in facility-based *G. lucidum* production.

Pest and disease control should follow the principle of “prevention first and integrated control,” combining physical control, biological control, environmental regulation, and necessary chemical intervention. Studies have shown that waterlogging treatment of cultivation soil can significantly reduce the numbers of *Trichoderma* and *Mucor* colonies, restore normal fruiting, and recover spore yield in soils where unsanitized conditions completely failed to produce spores, indicating the feasibility of physical sanitation treatment in large-scale application (Tong et al., 2020). For continuous cropping obstacles caused by *X. ganodermophthora*, low-concentration imazalil can effectively suppress the pathogen and promote *G. lucidum* growth when physical measures such as temperature and light are ineffective (Huang et al., 2024). At the same time, *Trichoderma*, as a typical biocontrol fungus, can exert antagonistic effects through competition, mycoparasitism, and antibiotic production. This indicates both its risk as a contaminant in *G. lucidum* cultivation and its potential value in ecological control of other plant diseases. Therefore, facility-based *G. lucidum* production should establish an integrated control system combining contaminant flora monitoring, preventive sanitation management, timely disinfection, and scientifically selected control agents to improve cultivation stability and product safety.

4 Key Technical Procedures for Standardized *Ganoderma lucidum* Production

4.1 *Ganoderma lucidum* strain selection and substrate standardization

Standardized production of *Ganoderma lucidum* first depends on the selection of superior strains and the optimization of substrate formulations. Strain quality directly determines mycelial growth rate, fruiting stability, fruiting body yield, and the accumulation of active components such as polysaccharides and triterpenoids.

Therefore, in facility-based production, priority should be given to strains with stable genetic traits, strong stress resistance, good adaptability to facility environments, high yield, and superior quality. Comparative studies have shown that different *G. lucidum* strains cultivated on the same woody substrates differ significantly in fruiting probability, yield, and β-glucan content, indicating a clear compatibility relationship between strains and substrates (Cortina-Escribano et al., 2020). Meanwhile, strain origin and genetic background also affect the nutritional quality and metabolic characteristics of fruiting bodies. For example, strains from different sources may vary in protein, carbohydrates, fatty acids, mineral elements, and antioxidant components (Sadiq et al., 2021). Therefore, *G. lucidum* strain selection should focus not only on mycelial vigor and yield, but also on active component profiles, contamination resistance, and regional adaptability.

Substrate is an important nutritional basis for *G. lucidum* growth. Its standardization focuses on establishing stable and reproducible raw material formulations, and controlling particle size, moisture content, carbon-to-nitrogen ratio, and mineral element levels. *G. lucidum* prefers substrates rich in cellulose and lignin, with low nitrogen content, a high C/N ratio, and a relatively high cellulose/lignin ratio. Yield is generally positively correlated with cellulose and lignin contents, but negatively correlated with excessive nitrogen content. At present, sawdust, cottonseed hulls, wheat bran, corn flour, and gypsum are commonly used as basic raw materials in production. Sawdust provides the main carbon source, while wheat bran and oilseed meal supplements provide nitrogen and mineral elements. Meanwhile, wheat straw, bean straw, corn cobs, peanut stems, cottonseed hulls, and other agricultural residues can also partially replace wood resources, reducing production costs while maintaining or improving biological efficiency, protein content, and mineral content (Roy et al., 2015; Mahmoud et al., 2026). For example, adding 40% corn cobs to sawdust can increase fruiting body protein and key mineral contents without reducing yield or biological efficiency; a 1:1 mixture of wheat straw and sawdust supplemented with 20% wheat bran can achieve favorable biological efficiency in seasonal cultivation.

Moisture content and pH are also key indicators that need to be controlled in standardized substrate production. In general, maintaining substrate moisture content at 60%~65% is suitable. Excessive moisture reduces aeration and increases the risk of contamination, whereas insufficient moisture affects mycelial expansion and substrate conversion efficiency. Substrate pH is usually maintained in the slightly acidic to near-neutral range, which is conducive to normal mycelial growth of *G. lucidum*. In actual production, standardized procedures should be established for raw material inspection, crushing and screening, formula weighing, water addition and mixing, and pH adjustment, so as to avoid batch-to-batch differences caused by moldy or contaminated raw materials, unstable proportions, or moisture fluctuations. Overall, substrate standardization should comprehensively consider raw material availability, cost control, nutritional balance, strain compatibility, and product quality targets, and should be validated through production practice to form stable formulation systems (Roy et al., 2015; Mahmoud et al., 2026).

4.2 *Ganoderma lucidum* cultivation bag preparation, sterilization, and inoculation management

Cultivation bag preparation is a core operational step in standardized *G. lucidum* production and serves as the basic unit linking substrate standardization with facility-based environmental control. A typical cultivation bag preparation process includes raw material drying, crushing, screening, proportional mixing, moisture adjustment, pre-fermentation when necessary, bag filling, and compaction. In production, raw materials such as sawdust, cottonseed hulls, peanut stems, bean stalks, wheat bran, gypsum, lime, and $MgSO_4$ are commonly used to prepare substrates, which are then filled into polypropylene or plastic cultivation bags to form bags with uniform specifications and density (Roy et al., 2015; Atila, 2020). During bag filling, the tightness should be reasonably controlled according to substrate characteristics. The substrate should have good aeration while maintaining an appropriate degree of compactness to facilitate uniform mycelial expansion. If the bag is too loose, the substrate may collapse and moisture distribution may become uneven; if it is too compact, gas exchange will be restricted and mycelial growth rate will decrease.

Sterilization is an important technical measure for preventing contamination and improving the qualified rate of cultivation bags. Bagged substrates are usually sterilized by high-pressure moist heat or atmospheric-pressure sterilization, in which high temperature is used to kill contaminating spores and harmful microorganisms in the substrate. Some processes also involve disinfection after pre-fermentation to improve substrate stability and reduce contamination risk (Roy et al., 2015). During sterilization, temperature, pressure, and time should be strictly controlled to ensure complete sterilization both inside and outside the substrate. If sterilization is insufficient, contaminants such as *Trichoderma* and *Penicillium* may rapidly proliferate during spawn run; if sterilization is excessive, the nutritional structure of the substrate may be damaged, affecting *G. lucidum* mycelial activity. Therefore, establishing standardized sterilization parameters and batch recording systems is an important guarantee for stable production.

Inoculation management should be carried out under aseptic or clean conditions to reduce contamination by external microorganisms. The inoculation room should be disinfected with ultraviolet light in advance, air purification should be performed, and the workbench should be cleaned. Operators should wear clean work clothes and strictly follow sanitation protocols. During inoculation, mycelial blocks or grain spawn can be inserted into the central hole or multiple inoculation points of the cultivation bag, followed by sealing and incubation. The spawn medium itself also needs to be optimized. For example, wheat grain or corn grain spawn can support faster colonization and stronger mycelial growth, providing vigorous inoculum for production bags. After inoculation, cultivation bags should be transferred to the incubation room and cultivated under dark or low-light conditions, at approximately 25℃~30℃, relatively high humidity, and suitable CO_2 levels until the mycelia fully colonize the substrate (Roy et al., 2015). During spawn run, contamination, water accumulation, mycelial degeneration, and uneven growth should be checked regularly, and abnormal bags should be removed or treated in time to ensure batch production stability.

4.3 Fruiting management, harvesting, and processing standards of *Ganoderma lucidum*

The fruiting stage of *G. lucidum* is a critical period determining fruiting body quality, yield, and commercial consistency. After the mycelia fully colonize the cultivation bags, primordium formation should be induced through bag opening, humidity enhancement, ventilation, appropriate light, and necessary physiological stimulation. Studies have shown that, in some boreal strains, cold stimulation at 5℃ can improve primordium formation and fruiting probability in indoor systems, especially for *G. lucidum* cultivation on *Populus tremula* and *Betula* substrates (Table 1) (Cortina-Escribano et al., 2020).

Table 1 Effect of the factors strain, wood and treatment on the yield of *G. lucidum* (Adopted from Cortina-Escribano et al., 2020)

Source	Numerator df	Denominator df	F	*p*-Value
Intercept	1	69	308.99	<0.001
Strain	5	69	3.40	0.008
Wood	4	69	9.71	<0.001
Treatment	1	69	0.48	0.492
Strain * Wood	14	69	1.12	0.361
Wood* Treatment	1	69	0.15	0.697

Table caption: The interaction between variables is shown with an asterisk between variables names (Adopted from Cortina-Escribano et al., 2020)

In general bag cultivation, the fruiting stage requires 25℃~32℃, 85%~95% relative humidity, moderate light, and good aeration to support fruiting body formation and pileus expansion (Roy et al., 2015). In seasonal mushroom-house cultivation, approximately (30±1)℃, high CO_2, and 90% relative humidity can be maintained during spawn run and primordium formation; during fruiting, CO_2 should be reduced and temperature and humidity adjusted to promote normal fruiting body development. This indicates that fruiting management should be regulated stage by stage according to strain, substrate, facility type, and product goals.

During fruiting body development, temperature, humidity, ventilation, and light should be managed synergistically. Low air humidity can easily cause cracking at the margin of *G. lucidum* fruiting bodies, thin pilei, and growth stagnation, whereas excessive humidity increases the risk of disease and contamination. Insufficient ventilation can cause CO_2 accumulation, leading to excessive stipe elongation and poor pileus development. Appropriate scattered light is conducive to pileus color formation and morphological integrity. Facility-based cultivation usually maintains a stable fruiting environment through scheduled spraying, mechanical ventilation, shading and light regulation, and environmental monitoring systems. In wild-simulated cultivation models, a relatively natural but still controllable fruiting environment can be created by removing the bags, covering beds with soil, managing dim light under the forest canopy, and biologically disinfecting ridges and surrounding areas (Dong et al., 2019). Potted and ornamental *G. lucidum* production places greater emphasis on fine control of temperature, humidity, and light to form fruiting bodies with ornamental value (Atila, 2020).

Mature *G. lucidum* should be harvested in a timely manner to avoid over-maturation, decline in appearance quality, and loss of active components. Harvesting is usually carried out when the pileus has fully expanded, the white growth ring at the margin disappears, spores begin to release, or the fruiting body reaches the target maturity stage. After harvesting, impurities should be removed promptly, and slicing, drying, grading, and packaging should be conducted according to product use. Drying methods significantly affect *G. lucidum* quality, as different drying methods can alter moisture content, rehydration capacity, phenolics, flavonoids, triterpenoids, polysaccharides, and antioxidant capacity (Atila, 2020; Naseri et al., 2023). Studies have shown that microwave drying, vacuum drying, freeze drying, hot-air drying, and infrared drying each have their own advantages. Among them, vacuum drying performs well in retaining active substances, bioavailability, and sensory quality, while infrared drying can shorten drying time and reduce energy consumption (Naseri et al., 2023). At the same time, HPLC fingerprints of multiple ganoderic acids and related markers can be used for quality control of dried fruiting body and spore products (Yeung et al., 2021). Therefore, standardized processing should clearly define harvest maturity, slice specifications, drying method, drying temperature, final moisture content, and chemical marker ranges to improve product quality stability and market competitiveness.

5 Quality Control System in Facility-Based *Ganoderma lucidum* Production

5.1 Whole-process record management of *Ganoderma lucidum* production

In facility-based production of *Ganoderma lucidum*, establishing a whole-process record management system covering pre-production, mid-production, and post-production stages is an important foundation for standardized production, quality control, and product traceability. Because the production cycle of *G. lucidum* is relatively long and involves multiple links, including germplasm resource management, strain cultivation, substrate preparation, sterilization and inoculation, mycelial incubation, fruiting management, harvesting and processing, packaging and storage, and product circulation, any deviation in any link may affect the final product quality. Wu et al. (2024) proposed that the *G. lucidum* industrial chain can be divided into pre-production links, including germplasm resource management and production area planning; mid-production links, including cultivation, harvesting, processing, and in-process quality control; and post-production links, including packaging, storage, circulation, quality evaluation, and traceability (Figure 2). Therefore, in facility-based production, information such as strain identity, raw material batches, substrate formulation, sterilization parameters, inoculation time, environmental control data, harvest stage, and processing conditions should be systematically recorded to ensure that each batch of products is traceable in source, controllable in process, and accountable in responsibility.

Environmental data recording is one of the core components of whole-process management. Environmental parameters such as temperature, humidity, light intensity, CO_2 concentration, ventilation status, and cleanliness directly affect mycelial growth, fruiting body formation, and active component accumulation in *G. lucidum*. Under facility-based cultivation conditions, intelligent sensors and automatic monitoring systems can be used to collect key environmental parameters in real time and establish dynamic production records. When abnormal growth, pest and disease occurrence, or quality fluctuations occur during production, environmental records and production operation records can be used for cause tracing, enabling timely adjustment of management measures.

Previous studies have indicated that ganoderic acids and other constituents show growth-stage-specific differences; therefore, accurate recording of growth stage and harvest time is an important prerequisite for ensuring stable product chemical profiles (Zhang et al., 2023).

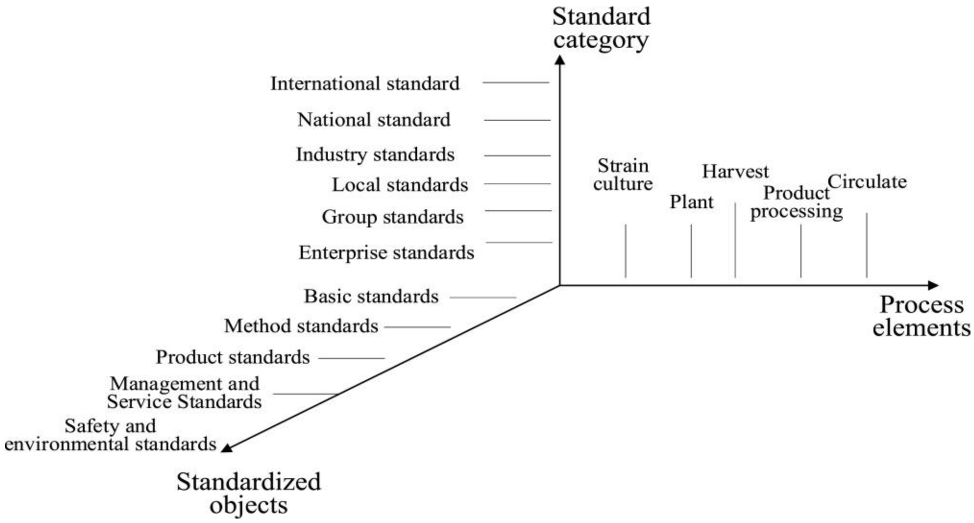


Figure 2 A three-dimensional framework model of the standard system for the entire industry chain of GL (Adopted from Wu et al., 2024)

Whole-process records should also be integrated with modern analytical authentication technologies to improve the scientific reliability and credibility of the traceability system. Elemental and stable isotope fingerprints, such as $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, C%, and N%, combined with chemometric methods, can be used to distinguish the geographical origin, cultivar, and growth stage of *G. lucidum*, providing technical support for verifying origin information and production records (Zhang et al., 2023; Wadood et al., 2023). HPLC fingerprints and multivariate analysis can also be used to identify sample origin, cultivation method, and consistency with declared information. Therefore, facility-based *G. lucidum* production should integrate batch records, environmental monitoring, quality testing, and analytical authentication technologies on the basis of unified record templates, thereby forming a closed-loop quality assurance system.

5.2 Quality evaluation and grading standards for *Ganoderma lucidum* products

Quality evaluation of *G. lucidum* products is an important basis for assessing the level of facility-based production and the market value of products. Current market requirements for *G. lucidum* products have gradually shifted from simply pursuing yield to focusing on quality, safety, active component content, and batch consistency. Therefore, quality evaluation should include not only sensory indicators such as appearance, pileus size, color, integrity, degree of drying, impurity content, and mildew status, but also active component indicators such as polysaccharides, triterpenoids, and ganoderic acids. Polysaccharides and triterpenoids are widely recognized as the main active components of *G. lucidum* and have been adopted as important quality control indicators in pharmacopoeias and related standards (Wu et al., 2023; Yang et al., 2025). Therefore, facility-based production should establish a comprehensive evaluation system composed of appearance grade, physicochemical indicators, active components, and safety indicators.

Modern detection technologies provide an objective basis for grading *G. lucidum* products. HPLC-DAD can quantitatively detect multiple major ganoderic acids and related triterpenoids in fruiting body and spore extracts, accurately reflecting the level of active components in products and serving as an important tool for grading based on content levels and fingerprint similarity (Yeung et al., 2021). In addition, HPLC and HPLC-MS fingerprints combined with chemometric methods such as PCA, HCA, and PLS-DA can be used to distinguish *G. lucidum* samples from different origins, cultivation methods, and quality grades, and to identify key discriminant markers (Chen et al., 2008). This indicates that quality evaluation of *G. lucidum* products should shift from single-index testing toward a combined model integrating multiple markers, whole fingerprints, and comprehensive grading.

Industrial and regulatory standards are further promoting the standardization of the *G. lucidum* product quality evaluation system. Wu et al. (2024) noted that national and industry standards have incorporated indicators such as ganoderic acids, total triterpenoids, and spore powder wall-breaking rate into quality evaluation systems, and relevant standards are gradually covering product processing, circulation, and traceability. Meanwhile, related reviews emphasize that *G. lucidum* polysaccharides and triterpenoids have complex structures and obvious batch-to-batch variation, requiring multi-index and whole-fingerprint evaluation methods to control quality stability (Wu et al., 2023). Notably, a U.S. market survey showed that only about 26% of commercial *G. lucidum* dietary supplements matched the triterpenoid and polysaccharide contents declared on their labels, suggesting that quality consistency remains a major issue for *G. lucidum* products. Therefore, in facility-based production, quantitative testing, fingerprint analysis, appearance grading, and whole-process records should be combined to establish grading standards such as high-quality, qualified, and unqualified categories, in order to meet the different needs of medicinal use, health food production, and functional product development.

5.3 Safety risk control in *Ganoderma lucidum* production

Safety risk control is an important component of the quality management system in facility-based *G. lucidum* production, directly affecting product safety, consumer health, and sustainable industrial development. As *G. lucidum* is a medicinal and edible product, its production process requires high standards for raw material safety, cultivation environment cleanliness, and processing hygiene. During substrate selection, the sources of sawdust, cottonseed hulls, wheat bran, agricultural residues, and production water should be strictly controlled to avoid raw materials contaminated with heavy metals or pesticide residues. Studies have shown that some *G. lucidum* products have risks of excessive heavy metal contents. For example, among commercial Lingzhi products from China and Southeast Asia, approximately one-third of samples exceeded the allowable limit for arsenic, and more than half exceeded the allowable limit for cadmium (Wong et al., 2020). Another Beijing market survey found that some *G. lucidum* samples, mainly from wild sources, had excessive mercury levels, indicating that wild and cultivated sources may present different safety risks.

Although facility-based production can reduce some safety risks by controlling substrates, water sources, and production environments, regular testing and process supervision mechanisms are still necessary. Regional risk assessments based on ICP-MS have shown that the overall population risk from potentially toxic elements such as arsenic, cadmium, chromium, copper, mercury, nickel, and lead in *G. lucidum* is relatively low, but arsenic, chromium, and high-frequency consumers still require special attention. Pesticide residues are another important factor affecting the safety of *G. lucidum* products. A large-scale screening of Chinese herbal medicines showed that 29 pesticides were detected in 100 *G. lucidum* samples, with more than 90% of samples containing pesticide residues and 27.7% exceeding the maximum residue limits for foods, indicating that pesticide residue standards and supervision for Chinese herbal medicines still need to be strengthened (Chen et al., 2024). Broader studies on agricultural products have also shown that heavy metals and pesticides have bioaccumulative properties and potential health risks; therefore, preventive control measures should be adopted in medicinal fungal production chains (Alengebawy et al., 2021).

In addition to chemical contamination, microbial contamination and pests and diseases also affect the safety of *G. lucidum* production. Under high-temperature and high-humidity conditions, contaminants such as *Trichoderma* and *Penicillium* can proliferate rapidly. They not only inhibit normal *G. lucidum* growth, but may also produce harmful metabolites, thereby affecting product quality and safety. Therefore, facility-based production should strictly implement systems for raw material inspection, substrate sterilization, inoculation disinfection, clean cultivation environment management, and removal of contaminated bags, while minimizing the use of chemical agents to avoid residue risks. Overall, safety risk control in *G. lucidum* should comprehensively include the selection and regular testing of substrates and inputs, implementation of GAP/GMP requirements, batch testing for heavy metals and key pesticide residues, incorporation of safety testing results into traceability and quality grading records, and the establishment of a unified and standardized safety assurance system combining physical control, biological control, and environmental regulation (Wong et al., 2020; Chen et al., 2024; Wu et al., 2024).

6 Application of Intelligent and Digital Technologies in *Ganoderma lucidum* Cultivation

6.1 Real-time monitoring of environmental data in *Ganoderma lucidum* cultivation

In facility-based cultivation of *Ganoderma lucidum*, the stability of environmental conditions such as temperature, humidity, CO_2, light, substrate moisture, pH, and air circulation directly affects mycelial growth rate, fruiting body formation, and final product quality. Traditional manual management mainly relies on empirical judgment and is prone to delayed monitoring, discontinuous data collection, and imprecise regulation, making it difficult to meet the needs of modern large-scale and standardized *G. lucidum* production. With the development of Internet of Things (IoT) technology, sensor-network-based environmental monitoring systems have gradually been applied to edible mushroom and *G. lucidum* cultivation. These systems can continuously collect environmental data inside mushroom houses or cultivation rooms through temperature and humidity sensors, CO_2 sensors, light sensors, substrate or soil moisture sensors, and pH sensors, and upload the data to digital platforms via microcontrollers and wireless communication modules (Chong et al., 2023; Nguyen et al., 2023; Adebayo et al., 2025).

In indoor *G. lucidum* cultivation, low-cost IoT monitoring systems have been used for real-time monitoring of temperature and humidity changes. The study by Nguyen et al. (2023) showed that although temperature and humidity fluctuated with external weather conditions, real-time monitoring could still help maintain the cultivation environment within the required production range and ensure that *G. lucidum* product quality met relevant standards. Other edible mushroom production systems commonly use DHT or AM2301 temperature and humidity sensors, SCD30 CO_2 sensors, MQ-135 gas sensors, soil moisture probes, and light sensors, and upload data to cloud platforms through ESP8266, ESP32, and similar modules to enable remote access and environmental alerts (Chong et al., 2023). Calibration results between sensors and reference instruments generally show only small deviations, indicating that low-cost sensors have good practical applicability in facility-based environmental monitoring.

In addition to real-time recording, emerging technologies such as edge computing and TinyML are also improving the intelligence level of environmental monitoring systems. TinyML-based monitoring devices can integrate CO_2, temperature and humidity, light, soil moisture, soil pH, and soil temperature sensors at the microcontroller end, and directly control actuators such as humidifiers, heaters, coolers, and fans through local models, thereby reducing dependence on cloud communication and improving response speed (Adebayo et al., 2025). Edge-cloud collaborative architectures can also combine IoT sensor data with RGB images, completing data compression, anomaly detection, and real-time recognition at the edge end. This saves network resources while retaining key environmental information (Nguyen et al., 2024). Therefore, embedding real-time monitoring, edge computing, and cloud platform management into dedicated *G. lucidum* cultivation rooms or “mushroom factories” can provide a stable data foundation for precise environmental control and standardized production.

6.2 Construction of automated regulation systems for *Ganoderma lucidum* production

Automated regulation systems are an important technical foundation for achieving precise management in facility-based *G. lucidum* cultivation. Based on continuous environmental sensing, automated systems can connect data such as temperature, humidity, CO_2, light, and substrate moisture with control algorithms and actuators, enabling automatic control of spraying, ventilation, heating, cooling, shading, and supplementary lighting equipment. This reduces manual regulation errors and improves production management efficiency. IoT-based climate control systems for mushroom houses can automatically turn spraying, irrigation, and ventilation equipment on or off according to feedback from temperature, humidity, and CO_2 sensors, keeping temperature within a suitable biological range, such as 25℃~33℃, and maintaining humidity within an appropriate range, while also supporting remote monitoring and management (Chong et al., 2023).

In terms of temperature and humidity regulation, automated systems can dynamically adjust the internal environment of facilities through heating equipment, cooling fans, wet-pad systems, automatic spraying devices, and circulation fans. When humidity is lower than the set value, the system can automatically activate spraying or humidification equipment; when humidity is too high or CO_2 concentration is elevated, ventilation equipment can be automatically activated for air exchange. Small-scale cultivation systems based on NodeMCU microcontrollers and cloud platforms such as Blynk can already monitor temperature, humidity, light, and substrate moisture simultaneously, and automatically control fans, humidifiers, heaters, and lighting equipment according to user-defined thresholds (Chong et al., 2023). Such systems show that automated control is not only applicable to large *G. lucidum* factories, but can also be extended to medium- and small-scale facility-based production scenarios.

More advanced automated systems further introduce fuzzy logic, predictive control, machine learning, and industrial automation technologies to improve regulation precision and resource-use efficiency. Intelligent substrate management frameworks can use multi-source sensor data, including soil moisture, temperature and humidity, light, and pest movement, and apply fuzzy rules to determine watering, ventilation, light regulation, and pest alert needs, thereby improving environmental stability (Irwanto et al., 2024). Sustainable mushroom house systems using IoT sensors, Raspberry Pi-based actuator control, fuzzy logic, and predictive analytics can control temperature within±0.5°C and humidity within ±2%, while reducing water use by approximately 30% and energy consumption by 20% compared with manual systems (Kavaliauskas et al., 2022). In factory-based edible mushroom production, electrical automation combined with fuzzy PID control can reduce contamination rates and significantly increase fresh mushroom yield. These studies provide a technical pathway for the transition of *G. lucidum* production from experience-based manual regulation to integrated, algorithm-driven, and precise environmental control.

6.3 Production data analysis and intelligent management of *Ganoderma lucidum*

The development of digital technologies is gradually transforming *G. lucidum* production from experience-based management to data-driven and model-based management. In modern facility-based cultivation, sensor networks and automated systems continuously generate large amounts of time-series data, including temperature, humidity, CO_2, light, water flow, equipment status, cultivation bag batches, growth cycles, contamination rates, yield, and quality testing results. Through cloud platforms or IoT platforms such as NETPIE 2020, ThingSpeak, and Blynk, these data can be centrally stored, visualized as trends, used for remote regulation, and analyzed for resource consumption, helping producers understand environmental changes and management effects at different production stages (Kavaliauskas et al., 2022). Cloud-connected systems can also export data in CSV format for further calibration, performance evaluation, and optimization of control rules (Chong et al., 2023).

Data analysis technologies can help producers promptly identify abnormal problems in *G. lucidum* production and provide decision-making support for process optimization. For example, by comparing spawn-running time, fruiting cycle, contamination rate, yield, and active component contents among different batches of *G. lucidum*, producers can analyze deficiencies in environmental control, substrate formulation, ventilation regime, or spraying frequency, and thereby optimize production processes. Edge-cloud architectures further support real-time anomaly detection and quality control. AI models can be used to identify abnormal environmental patterns or abnormal growth conditions while reducing bandwidth and storage costs (Nguyen et al., 2024). With the long-term accumulation of production data, *G. lucidum* production can gradually establish correlation models linking “environmental parameters-growth performance-yield and quality,” providing a scientific basis for facility design, parameter setting, and standardized production.

From a broader perspective, artificial intelligence and big data technologies are reshaping edible mushroom cultivation and can be further extended to factory-based *G. lucidum* production. Reviews have noted that combining IoT-based environmental monitoring with machine learning models such as LSTM can predict diurnal temperature and humidity changes and guide proactive regulation of ventilation, humidification, and heating, thereby achieving a more stable microclimate and reducing energy consumption (Jacob et al., 2025). Adaptive control models based on fuzzy logic, reinforcement learning, and sensor data can also be used to optimize resource allocation and maintain stable growth conditions in commercial farms (Chen et al., 2022). Computer vision and machine learning technologies can further be applied to species identification, quality grading, digital phenotyping, automatic yield estimation, and harvest timing judgment. Therefore, intelligent management systems for *G. lucidum* should build integrated data pipelines from cultivation rooms to central databases, and use AI for yield prediction, anomaly detection, process modeling, quality grading, and decision support, so as to continuously improve production efficiency, quality stability, and industrial sustainability.

7 Development Pathways for Facility-Based and Standardized *Ganoderma lucidum* Production

7.1 Construction of regionalized *Ganoderma lucidum* cultivation technology systems

China has a vast territory, and different regions vary significantly in climatic conditions, ecological environments, raw material resources, and industrial foundations. Therefore, facility-based production of *Ganoderma lucidum* cannot completely adopt a single unified model; instead, appropriate cultivation technology systems should be established according to regional characteristics. Relevant studies have pointed out that the standardization of the *G. lucidum* industry should cover the whole industrial chain, including pre-production planning, germplasm management, cultivation production, postharvest processing, circulation and sales, and quality traceability. At the same time, differences in resource conditions and ecological environments among regions should be fully considered to form regionally adaptive technical routes (Wu et al., 2024; Thakur et al., 2024). For example, in southern regions with high temperature and humidity, emphasis should be placed on cooling, ventilation, and disease control to reduce contamination by competing microorganisms and heat stress under humid conditions. In northern regions, winter heat preservation, air humidity regulation, and improvement of facility insulation should be strengthened to ensure the stability of mycelial growth and fruiting body formation.

The construction of regionalized cultivation technology systems should also be optimized according to local resource conditions and market positioning. Regions rich in wood resources may focus on sawdust-based bag cultivation, while regions with favorable under-forest resources may explore facility-based wild-simulated cultivation models to balance *G. lucidum* quality, ecological benefits, and market differentiation. International studies have also shown that the adaptation between local strains and local substrate resources is an important pathway for improving regional production efficiency. A Finnish study on laccate *Ganoderma* found that local wild strains could be successfully domesticated on regional wood by-products, among which *Populus tremula* and *Betula* substrates significantly improved fruiting probability, yield, and β-glucan content, whereas *Pinus sylvestris* was unsuitable for fruiting body production. Research from Pakistan showed that indigenous *G. lucidum* strains could be efficiently cultivated indoors using locally available lignocellulosic wastes, with a sawdust and wheat straw combination producing higher yields and more fruiting flushes while maintaining a mineral composition close to that of wild basidiomata (Ghafoor et al., 2024). These studies indicate that regionalized cultivation can promote the high-value utilization of local biomass resources while providing a localized basis for standardized facility-based production.

In addition, the construction of regionalized technology systems requires strengthened collaboration among research institutions, production enterprises, cultivation bases, and market participants. By conducting regional trials on strain screening, substrate formulation optimization, environmental parameter regulation, and pest and disease control, production parameters and technical protocols suitable for different regions can gradually be established. In some parts of China, permanent sand-bed greenhouse models have been promoted, in which plastic membranes are used to separate substrates from soil in order to reduce the risks of heavy metal and pesticide residues and support stable production that meets medicinal material quality requirements. At the international level, standards such as ISO 21315, *Traditional Chinese Medicine-Ganoderma lucidum Fruiting Body*, as well as relevant standards for cold storage, transportation, and quality evaluation, also provide a basis for embedding international standards into regionalized production systems (Wu et al., 2024). Therefore, regionalized *G. lucidum* cultivation technology systems should form synergy among local resource utilization, domestication of local strains, facility structure optimization, and alignment with standardized protocols, thereby promoting coordinated development of the *G. lucidum* industry.

7.2 Breeding and promotion of superior *Ganoderma lucidum* varieties

Superior varieties are the foundation for improving the yield, quality, and stress resistance of *G. lucidum*, and they are also the core component of facility-based standardized production. The genotype of *G. lucidum* strains directly affects mycelial growth rate, fruiting stability, contamination resistance, spore yield, and the accumulation of active components such as polysaccharides and triterpenoids. With the continuous increase in market demand, *G. lucidum* production has gradually shifted from simply pursuing high yield to multi-objective breeding that considers high yield, superior quality, disease resistance, stable active component accumulation, and adaptability to facility-based management. Studies have shown that the mutant strain UV119 obtained through ultraviolet mutagenesis had a basidiospore yield 19.27% higher than that of the parent strain and 20.56% higher than that of the major commercial cultivar "Longzhi No. 1," while its fruiting body yield and contamination resistance were also improved (Tang et al., 2023). Another radiation-induced mutant strain, XZ-2, showed 9.7%~30.1% higher fruiting body yields and 20.2%~45.7% higher basidiospore yields than control varieties across multiple locations, while also exhibiting stable annual yields and relatively high polysaccharide and triterpenoid contents. These results indicate that superior variety breeding can directly improve the stability and industrial value of facility-based *G. lucidum* production.

In the breeding process, traditional breeding techniques should be combined with modern biotechnologies to systematically screen and evaluate *G. lucidum* genetic resources. Through strain isolation, basidiospore-derived monokaryon crossing, mutation breeding, molecular-assisted screening, and metabolomic evaluation, new *G. lucidum* varieties adapted to different regions and cultivation models can be developed. For example, the hybrid strain H-23, generated by mating basidiospore-derived monokaryons from two commercial cultivars, had relatively high polysaccharide and triterpenoid contents as well as desirable biological efficiency, indicating that sexual crossing can integrate multiple favorable traits into new strains (Liu et al., 2017). In recent years, molecular breeding and high-throughput screening have further expanded breeding pathways. A new variety, GL_V2, obtained through ultraviolet mutagenesis, showed a 1.4-fold increase in total triterpenoid content compared with widely cultivated varieties and exhibited stronger antioxidant activity (Pan et al., 2025). Atmospheric room-temperature plasma mutagenesis combined with microdroplet cultivation technology can rapidly screen mutants with 17%~26% higher biomass and up to 32% higher triterpenoid production in liquid cultivation, with stability maintained over multiple generations (Feng et al., 2024). In addition, new strains obtained by combining genetic engineering with mono-mono crossing can significantly increase the contents of specific ganoderic acids, squalene, and lanosterol, providing new ideas for targeted improvement of active components in *G. lucidum* (Zhou et al., 2024).

The promotion and application of superior varieties are equally critical. At present, some regions still face problems such as non-standardized strain sources, strain degeneration, variety mixing, and insufficient coverage of superior strains, which affect production stability and product consistency. Therefore, standardized strain propagation systems and superior variety promotion mechanisms should be established, and variety registration, regional adaptability trials, strain quality testing, and market supervision should be strengthened. Research on developing *G. lucidum* as a "next-generation cell factory" also suggests that synthetic biology and pathway engineering may be used in the future to optimize the production of target products such as proteins, polysaccharides, and triterpenoids, although the complexity of regulatory mechanisms and the efficiency of genetic manipulation remain bottlenecks to be overcome. Therefore, the promotion of superior varieties should be integrated with facility-based production standards, regional environmental parameters, product uses, and quality evaluation systems, so that breeding outputs can truly serve the needs of large-scale, standardized, and high-value production (Liu et al., 2017; Tang et al., 2023; Feng et al., 2024; Wu et al., 2024).

7.3 Construction of *Ganoderma lucidum* branding and product traceability systems

As consumers increasingly focus on the quality, safety, and authenticity of health products, the *G. lucidum* industry is gradually shifting from traditional raw material sales toward branding, standardization, and high-value-added operations. Brand building can not only increase the added value of *G. lucidum* products, but also enhance consumer recognition and market competitiveness. A recent review on the standardization of the *G. lucidum* industry proposed that a whole-chain standard system should be established, covering germplasm and strain-type standards, cultivation and harvesting standards, processing standards, circulation standards, quality evaluation and traceability standards, and management service standards. Within this framework, *G. lucidum* branding should rely on verifiable quality attributes, such as the contents of marker components including polysaccharides, triterpenoids, and ganoderic acid A, compliance with national standards for spore powder harvesting and processing, and alignment with the testing, packaging, storage, and transportation requirements of ISO 21315 for *G. lucidum* fruiting bodies (Wu et al., 2024). Only by building brand value on stable quality and verifiable quality indicators can conceptual promotion and the impact of low-quality products on the market be avoided.

The construction of product traceability systems is an important component of modern agricultural quality management and brand trust formation. In *G. lucidum* production, QR codes, batch codes, digital management platforms, and even blockchain technology can be used to record whole-process information, including strain source, regional cultivation conditions, substrate formulation, facility environmental parameters, harvesting and processing, quality testing, warehousing and logistics, and sales circulation. This enables product source inquiry, production process tracking, and quality responsibility traceability. Stable isotope and chemometric methods can further strengthen the scientific basis of traceability systems. Studies have shown that by analyzing C, H, O, and N stable isotope ratios as well as elemental C and N contents, and combining PCA, OPLS-DA, PLS, and FLDA methods, the geographical origin and growth stage of *G. lucidum* can be effectively distinguished, with some external validation accuracies reaching 100% (Zhang et al., 2023). These techniques can be used to independently verify origin and growth-stage information on product labels and can be integrated with digital traceability platforms to improve brand credibility.

In addition, the construction of branding and traceability systems helps standardize market order and reduce the circulation of low-quality or counterfeit products. Studies on commercial products have shown that only about 26% of *G. lucidum* dietary supplements in the U.S. market matched the triterpenoid and polysaccharide contents declared on their labels, suggesting that quality inconsistency can significantly damage brand reputation and consumer trust. HPLC fingerprints targeting 11 major ganoderic acids and related triterpenoids have been validated for quality control and batch comparison of fruiting body and spore products, supporting brand quality claims based on multi-marker chemical profiles (Yeung et al., 2021). Therefore, *G. lucidum* brand building should not remain limited to regional culture and packaging promotion, but should be deeply integrated with standardized production, quality testing, fingerprint profiling, origin authentication, and digital traceability. In the future, with the development of e-commerce, smart agriculture, and international trade, *G. lucidum* brand building and digital traceability systems will become further integrated, providing support for high-quality industrial development and international market expansion.

8 Conclusion

With the continuous expansion of market demand for *Ganoderma lucidum* and consumers' increasing requirements for product quality, safety, and stability, traditional cultivation methods that rely on natural environments and experience-based management can no longer meet the needs of modern industrial development. Facility-based cultivation effectively improves production stability and resource-use efficiency through precise regulation of environmental factors such as temperature, humidity, light, and ventilation. It promotes the transformation of the *G. lucidum* industry from dispersed and extensive production toward large-scale, intensive, and modernized development. Therefore, facility-based cultivation has become an important development pathway for the transformation and upgrading of the *G. lucidum* industry and is of great significance for enhancing overall industrial competitiveness and promoting sustainable development.

Mycelial growth and fruiting body formation in *G. lucidum* are highly sensitive to environmental conditions. Factors such as temperature and humidity, air circulation, light intensity, and environmental cleanliness directly affect yield, appearance quality, and the accumulation of active components. In facility-based production, establishing a scientific environmental control system combined with real-time monitoring and dynamic regulation technologies can effectively reduce the adverse effects of environmental fluctuations, lower the incidence of pests, diseases, and microbial contamination, and improve product uniformity and quality stability.

Therefore, precise environmental control is not only an important foundation for efficient *G. lucidum* production, but also a key factor in enhancing its medicinal value and market competitiveness.

Standardized production and intelligent management are important trends in the future development of the *G. lucidum* industry. By establishing unified technical procedures for strain management, substrate preparation, sterilization and inoculation, fruiting management, harvesting, and processing, the standardization level of the production process can be improved, enabling stable product quality and whole-process traceability. Meanwhile, the application of intelligent technologies such as IoT, automated control, and big data analysis is gradually transforming *G. lucidum* production from traditional experience-based management toward precision, digitalization, and smart management. In the future, with the continuous improvement of standardization systems and the sustained development of smart agricultural technologies, the *G. lucidum* industry will further achieve high-quality, green, and modernized development.

Conflict of Interest Disclosure

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

References

Alsaheb R.A., Zjeh K.A., Malek R.A., Abdullah J.O., Baz A.A., Deeb E.A., Dailin D.J., Hanapi S.Z., Sukmawati D., and El Enshasy H.A., 2020, Bioprocess optimization for exopolysaccharides production by *Ganoderma lucidum* in semi-industrial scale, Recent Patents on Food, Nutrition and Agriculture, 11(3): 211-218.
https://doi.org/10.2174/2212798411666200316153148

Adebayo S., Aworinde H., Olufemi O., Osueke C., Adeniyi A., and Aroba O., 2025, Understanding mushroom farm environment using TinyML-based monitoring devices, Environmental Research Communications, 7(4): 045014.
https://doi.org/10.1088/2515-7620/adc5cd

Akçay Ç., Arslan R., and Ceylan F., 2025, Valorization of various lignocellulosic wastes to *Ganoderma lucidum* (Curtis) P. Karst (Reishi Mushroom) cultivation and their FT-IR assessments, PLOS ONE, 20(7): e0328732.
https://doi.org/10.1371/journal.pone.0328732

Alengebawy A., Abdelkhalek S.T., Qureshi S.R., and Wang M.Q., 2021, Heavy metals and pesticides toxicity in agricultural soil and plants: Ecological risks and human health implications, Toxics, 9(3): 42.
https://doi.org/10.3390/toxics9030042

Al-Kaabi A., and Hussien A., 2025, The environmental requirements of three species of Reishi mushroom, *Ganoderma* spp., IOP Conference Series: Earth and Environmental Science, 1487(1): 012020.
https://doi.org/10.1088/1755-1315/1487/1/012020

Araque J., Niño L., and Gelves G., 2020, Industrial scale bioprocess simulation for *Ganoderma lucidum* production using SuperPro Designer, Journal of Physics: Conference Series, 1655(1): 012077.
https://doi.org/10.1088/1742-6596/1655/1/012077

Atila F., 2020, Comparative study on the mycelial growth and yield of *Ganoderma lucidum* (Curt.: Fr.) Karst. on different lignocellulosic wastes, Acta Ecologica Sinica, 40(2): 153-157.
https://doi.org/10.1016/j.chnaes.2018.11.007

Bijalwan A., Bahuguna K., Vasishth A., Singh A., Chaudhary S., Dongariyal A., Thakur T.K., Kaushik S., Ansari M.J., Alfarraj S., Alharbi S.A., Skalický M., and Brestič M., 2021, Growth performance of *Ganoderma lucidum* using billet method in Garhwal Himalaya, India, Saudi Journal of Biological Sciences, 28(5): 2709-2717.
https://doi.org/10.1016/j.sjbs.2021.03.030

Chen F., Zhang T., Xiao P., Shao L., Zhang X., Wang L., Ren X., Qin C., and Jiao Y., 2024, Occurrence and health risk of pesticide residues in Chinese herbal medicines from Shandong Province, China, Environmental Science and Pollution Research, 31: 25940-25951.
https://doi.org/10.1007/s11356-024-32693-4

Chen L., Qian L., Zhang X., Li J.Z., Zhang Z.J., and Chen X.M., 2022, Research progress on indoor environment of mushroom factory, International Journal of Agricultural and Biological Engineering, 15(1): 25-32.
https://doi.org/10.25165/j.ijabe.20221501.6872

Chen Y., Zhu S.B., Xie M.Y., Nie S.P., Liu W., Li C., Gong X.F., and Wang Y.X., 2008, Quality control and original discrimination of *Ganoderma lucidum* based on high-performance liquid chromatographic fingerprints and combined chemometrics methods, Analytica Chimica Acta, 623(2): 146-156.
https://doi.org/10.1016/j.aca.2008.06.018

Chong J.W.R., Chew K.W., Peter A.P., Ting H.Y., and Show P.L., 2023, Internet of Things (IoT)-based environmental monitoring and control system for home-based mushroom cultivation, Biosensors, 13(1): 98.
https://doi.org/10.3390/bios13010098

Cortina-Escribano M., Pihlava J.M., Miina J., Veteli P., Linnakoski R., and Vanhanen H., 2020, Effect of strain, wood substrate and cold treatment on the yield and β-glucan content of *Ganoderma lucidum* fruiting bodies, Molecules, 25(20): 4732.
https://doi.org/10.3390/molecules25204732

Dong Q., He D., Ni X., Zhou H., and Yang H., 2019, Comparative study on phenolic compounds, triterpenoids, and antioxidant activity of *Ganoderma lucidum* affected by different drying methods, Journal of Food Measurement and Characterization, 13: 3198-3205.
https://doi.org/10.1007/s11694-019-00242-0

Fang T., Chen L., Yao H., Li Y., Liu G., Wu S., Lan J., and Chen X., 2026, Combined transcriptomic and metabolomic analyses of the response of *Ganoderma lucidum* to elevated CO_2, Journal of Fungi, 12(1): 5.
https://doi.org/10.3390/jof12010005

Feng J., Tang C., Liu Y., Tang C., and Zhang J., 2024, Enhancing high-efficiency breeding and microbial microdroplet cultivation techniques for *Ganoderma lucidum,* World Journal of Microbiology and Biotechnology, 40(7): 225.
https://doi.org/10.1007/s11274-024-04011-0

Ghafoor A., Rana A.A., and Niazi A.R., 2024, Systematic characterisation, mineral analysis, and valorisation of lignocellulosic waste into sustainable indigenous *Ganoderma lucidum* production from Pakistan, New Zealand Journal of Botany, 63: 2589-2605.
https://doi.org/10.1080/0028825x.2024.2353191

Huang Q., Lu Q., Cao F., Li X., Wu X., Sun H., Zhang J., and Fu J., 2024, Study on the use of Imazalil to continuous cropping obstacle of *Ganoderma lucidum* caused by *Xylogone ganodermophthora*, Chemical and Biological Technologies in Agriculture, 11(1): 57.
https://doi.org/10.1186/s40538-024-00584-y

Huynh T.T., and To N.T., 2023, Factors affect on the total polysaccharide content in *Ganoderma lucidum* (Leyss ex Fr.) Karst, Ganodermataceae, Tạp chí Y Dược học Cần Thơ, 30(5): 140-148.
https://doi.org/10.58490/ctump.2023i5.653

Irwanto F., Hasan U., Lays E., De La Croix N., Mukanyiligira D., Sibomana L., and Ahmad T., 2024, IoT and fuzzy logic integration for improved substrate environment management in mushroom cultivation, Smart Agricultural Technology, 9: 100427.
https://doi.org/10.1016/j.atech.2024.100427

Jacob M., Xu A., Qian K., Qi Z., Li X., and Zhang B., 2025, Artificial intelligence in edible mushroom cultivation, breeding, and classification: A comprehensive review, Journal of Fungi, 11(11): 758.
https://doi.org/10.3390/jof11110758

Kavaliauskas Ž., Šajev I., Gecevičius G., and Čapas V., 2022, Intelligent control of mushroom growing conditions using an electronic system for monitoring and maintaining environmental parameters, Applied Sciences, 12(24): 13040.
https://doi.org/10.3390/app122413040

Lengare K., Ingle Y., Sable Y., and Pol V., 2023, Nutritional and physiological requirements for the improvement of growth of *Ganoderma lucidum*, Journal of Plant Disease Sciences, 18(2): 80-85.
https://doi.org/10.48165/jpds.2023.1802.02

Lim T.F., Ilham Z., and Wan-Mohtar W.A.A.Q.I., 2024, Production of ganodiesel from the biomass of *Ganoderma lucidum* in air-L-shaped bioreactor (ALSB), Heliyon, 10(15): e35170.
https://doi.org/10.1016/j.heliyon.2024.e35170

Liu S.R., Ke B.R., Zhang W.R., Liu X.R., and Wu X.P., 2017, Breeding of new *Ganoderma lucidum* strains simultaneously rich in polysaccharides and triterpenes by mating basidiospore-derived monokaryons of two commercial cultivars, Scientia Horticulturae, 216: 58-65.
https://doi.org/10.1016/j.scienta.2016.12.016

Liu Y., Luo Y., Guo W., Zhang X., Zheng W., and Chen X., 2024, Study on the effects of different light supply modes on the development and extracellular enzyme activity of *Ganoderma lucidum*, Agriculture, 14(6): 835.
https://doi.org/10.3390/agriculture14060835

Magday J.C., 2014, Optimization of mycelial growth and cultivation of fruiting body of Philippine wild strain of *Ganoderma lucidum*, Current Research in Environmental and Applied Mycology, 4(2): 162-172.
https://doi.org/10.5943/cream/4/2/4

Mahmoud A.T., Abed I.A., Almohammedi O.H., and Thakir A.F., 2026, The effect of Ganoderma strain type, growth substrate, and nitrogen supplementation on the concentration of certain biochemical parameters in fruiting bodies, Anbar Journal of Agricultural Sciences, 24(1): 25-34.
https://doi.org/10.32649/ajas.2025.189068

Naseri M., Movagharnejad K., and Nanvakenari S., 2023, Comparison of the dried properties of *Ganoderma lucidum* produced by the convective dryer and infrared dryer, Scientific Reports, 13(1): 12636.
https://doi.org/10.1038/s41598-023-39883-z

Nguyen H., Shin D., Jung W., Kim T., and Lee D., 2024, An integrated IoT sensor-camera system toward leveraging edge computing for smart greenhouse mushroom cultivation, Agriculture, 14(3): 489.
https://doi.org/10.3390/agriculture14030489

Nguyen Q., Huynh H., Dao T., and Kwon H., 2023, Application of Internet of Things based monitoring system for indoor *Ganoderma lucidum* cultivation, The International Journal of Advanced Smart Convergence, 12(2): 153-158.

Pan Z., Lin J., Luo G., Cheng W., Li Y., and Wu C., 2025, Unveiling triterpenoid superiority in a newly developed *Ganoderma lucidum* variety through untargeted metabolomics approach, Frontiers in Nutrition, 12: 1541162.
https://doi.org/10.3389/fnut.2025.1541162

Roy S., Jahan M.A.A., Das K.K., Munshi S.K., and Noor R., 2015, Artificial cultivation of *Ganoderma lucidum* (Reishi medicinal mushroom) using different sawdusts as substrates, American Journal of BioScience, 3(5): 178-182.
https://doi.org/10.11648/j.ajbio.20150305.13

Sadiq N.B., Ryu D.H., Cho J., Lee A., Song D., Dorjsembe B., Kim J., Jung J.H., Nho C.W., Hamayun M., Yang S.H., and Kim H.Y., 2021, Postharvest drying techniques regulate secondary metabolites and anti-neuroinflammatory activities of *Ganoderma lucidum*, Molecules, 26(15): 4484.
https://doi.org/10.3390/molecules26154484

Supramani S., Rejab N.A., Ilham Z., Ahmad R., Show P.L., Ibrahim M.F., and Wan-Mohtar W.A.A.Q.I., 2023, Performance of biomass and exopolysaccharide production from the medicinal mushroom *Ganoderma lucidum* in a new fabricated Air-L-Shaped Bioreactor (ALSB), Processes, 11(3): 670.
https://doi.org/10.3390/pr11030670

Tang C., Tan Y., Zhang J., Zhou S., Honda Y., and Zhang H., 2023, A novel strain breeding of *Ganoderma lucidum* UV119 (Agaricomycetes) with high spores yield and strong resistant ability to other microbes' invasions, Foods, 12(3): 465.
https://doi.org/10.3390/foods12030465

Thakur P., Khanal S., Tapwal A., Kumar D., Verma R.K., Chauhan P., and Sharma N., 2024, Exploring *Ganoderma lucidum*: Morphology, cultivation and market potential, World Journal of Microbiology and Biotechnology, 40(11): 369.
https://doi.org/10.1007/s11274-024-04180-y

Tong X., Jiang H., Liang Y., Rao Y., Mei L., and Wang Y., 2020, Waterlogging reduces soil colonization by antagonistic fungi and restores production in *Ganoderma lucidum* continuous cultivation, Crop Protection, 137: 105314.
https://doi.org/10.1016/j.cropro.2020.105314

Wadood S.A., Nie J., Li Z., Li C., Zhang N., Rogers K.M., Zhang Y., and Yuan Y., 2023, A preliminary elemental and isotopic investigation to develop authentication tools for Chinese *Ganoderma lucidum*, Food Control, 150: 109888.
https://doi.org/10.1016/j.foodcont.2023.109888

Wang Y.J., Zeng L.Z., Wu J.Y., Jiang H., and Mei L., 2022, Diversity and effects of competitive *Trichoderma* species in *Ganoderma lucidum*-cultivated soils, Frontiers in Microbiology, 13: 1067822.
https://doi.org/10.3389/fmicb.2022.1067822

Wong T.H., Lee F.S.C., Hu G.H., Chang L.P., Wang X.H., and Fu P.P., 2007, A survey of heavy metal and organochlorine pesticide contaminations in commercial Lingzhi products, Journal of Food and Drug Analysis, 15(4): 16.
https://doi.org/10.38212/2224-6614.2401

Wu P., Zhang C., Yin Y., Zhang X., Li Q., Yuan L., Sun Y., Zhou S., Ying S., and Wu J., 2024, Bioactivities and industrial standardization status of *Ganoderma lucidum*: a comprehensive review, Heliyon, 10(16): e36987.
https://doi.org/10.1016/j.heliyon.2024.e36987

Wu S.J., Zhang S.Y., Peng B., Tan D.C., Wu M.Y., Wei J.C., Wang Y.T., and Luo H., 2023, *Ganoderma lucidum*: a comprehensive review of phytochemistry, efficacy, safety and clinical study, Food Science and Human Wellness, 13(2): 568-596.
https://doi.org/10.26599/fshw.2022.9250051

Yang M.H., Qin X.M., and Liu X.J., 2025, A review of polysaccharides from *Ganoderma lucidum*: preparation methods, structural characteristics, bioactivities, structure-activity relationships and potential applications, International Journal of Biological Macromolecules, 303: 140645.
https://doi.org/10.1016/j.ijbiomac.2025.140645

Yeung S.Y., Chen Q.L., Yu Y.B., Zhou B.S., Wu W., Li X., Huang Y., and Wang Z.J., 2021, Quality evaluation of commercial products of *Ganoderma lucidum* made from its fruiting body and spore, Acta Chromatographica, 34(1):100-113.
https://doi.org/10.1556/1326.2020.00825

Zhang Y., Jiang K., Chen S., Wang L., Zhang X., Xu W., Yam M.F., Wu C., Xu W., and Lin Y., 2023, Quality control of *Ganoderma lucidum* by using C, H, O, and N stable isotopes and C and N contents for geographical traceability, Frontiers in Plant Science, 14: 1234729.
https://doi.org/10.3389/fpls.2023.1234729

Zhou D.X., Kong X.M., Huang X.M., Li N., Feng N., and Xu J.W., 2024, Breeding a new *Ganoderma lucidum* strain with increased contents of individual ganoderic acids by mono-mono crossing of genetically modified monokaryons, Frontiers in Microbiology, 15: 1410368.
https://doi.org/10.3389/fmicb.2024.1410368

Medicinal Plant Research 2026, Vol.16, No.1, 31-51
http://hortherbpublisher.com/index.php/mpr

Research Insight Open Access

Research on the Understory Ecological Cultivation Model of *Tetrastigma hemsleyanum*

Weiduo Liu [1,2]
1 Zhejiang zhongxin Medical Plant Seed Co. Ltd., Hangzhou, 311402, Zhejiang, China
2 Zhejiang Agronomist College, Hangzhou, 310021, Zhejiang, China
Corresponding email: 454006383@qq.com

Medicinal Plant Research, 2026, Vol.16, No.1 doi: 10.5376/mpr.2026.16.0003
Received: 19 Jan., 2026
Accepted: 05 Mar., 2026
Published: 20 Mar., 2026

Preferred citation for this article:
Liu W.D., 2026, Research on the understory ecological cultivation model of *Tetrastigma hemsleyanum*, Medicinal Plant Research, 16(1): 31-51 (doi: 10.5376/mpr.2026.16.0003)

Abstract This study focuses on the understory ecological cultivation model of *Tetrastigma hemsleyanum* and systematically analyzes its resource value, biological characteristics, understory habitat adaptability, compound cultivation models, key cultivation techniques, and comprehensive benefits. *T. hemsleyanum* is a traditional medicinal plant with high medicinal value and development potential. Its tuberous roots are rich in active compounds such as flavonoids, polysaccharides, and phenolic acids, showing important research value in anti-inflammatory, antioxidant, anti-tumor, and immunomodulatory activities. With increasing market demand and declining wild resources, artificial ecological cultivation has become an important approach for resource conservation and industrial development of *T. hemsleyanum*. *T. hemsleyanum* prefers shaded and humid conditions and is sensitive to strong light. It is suitable for growth in semi-shaded, humid, humus-rich, and well-drained understory environments. Bamboo forests, fruit forests, and broad-leaved forests can all provide suitable ecological cultivation conditions to some extent, but appropriate models should be selected according to stand structure, canopy density, soil conditions, and management objectives. Understory cultivation of *T. hemsleyanum* should focus on high-quality seedling propagation, vine guidance and trellising, water and fertilizer management, green pest and disease control, and timely harvesting, so as to promote tuberous root formation and stable accumulation of medicinal components. Understory ecological cultivation of *T. hemsleyanum* can improve forestland resource utilization efficiency, reduce dependence on wild resources, and promote medicinal plant resource conservation, ecological benefit enhancement, and the development of characteristic Chinese medicinal herb industries. In the future, provenance standardization, cultivation technical protocols, quality control, and industrial promotion systems should be further improved to advance the standardized, large-scale, and sustainable development of understory ecological cultivation of *T. hemsleyanum.*

Keywords *Tetrastigma hemsleyanum*; Understory ecological cultivation; Compound cultivation model; Tuberous root quality; Forest-medicine compound management

1 Introduction

Tetrastigma hemsleyanum Diels et Gilg is a perennial climbing vine of the genus *Tetrastigma* in the family Vitaceae and is one of the important traditional medicinal plant resources in China. Commonly known as "Sanyeqing", it is regarded as a "plant antibiotic" because of its broad medicinal activities (Ji et al., 2020; Hu et al., 2021). Its main medicinal part is the tuberous root, while the whole plant is also used medicinally in some regions. In folk and clinical applications, it is commonly used as an adjuvant treatment for diseases such as high fever in children, pneumonia, hepatitis, gastritis, rheumatism, sore throat, lymphatic tuberculosis, and viral meningitis. Modern pharmacological and phytochemical studies have shown that the tuberous roots and aerial parts of *T. hemsleyanum* contain various active compounds, including flavonoids, polysaccharides, phenolic acids, terpenoids, steroids, and organic acids, and exhibit anti-inflammatory, antioxidant, anti-tumor, antiviral, immunomodulatory, anti-hepatic injury, and antibacterial effects (Ji et al., 2020; Zhu et al., 2020; Hu et al., 2021). Among these compounds, polysaccharides and flavonoids are considered representative active constituents of *T. hemsleyanum* and have shown potential application prospects in the development of food, medicine, and cosmetics (Shi et al., 2022; Wang et al., 2025).

With the increasing recognition of its medicinal value and the continuous growth of market demand, the utilization of *T. hemsleyanum* has gradually expanded in Chinese medicinal material processing, health product development, and the construction of local specialty medicinal herb industries. Its artificial cultivation area has also increased accordingly. However, the development of the *T. hemsleyanum* industry is still in a transitional stage from wild harvesting to standardized artificial cultivation, and shortcomings remain in seedling propagation, cultivation cycles, yield stability, quality control, processing and storage, and industrial chain construction (Hu et al., 2023; Pang et al., 2024). For a long time, *T. hemsleyanum* resources have mainly depended on wild harvesting. Due to its long natural growth cycle, slow tuberous root formation, overharvesting, and habitat destruction, wild resources have declined significantly, and in some major producing areas it has been regarded as a rare, endangered, or even nearly extinct medicinal plant resource (Ji et al., 2020; Zhu et al., 2020; Shi et al., 2022). Therefore, artificial cultivation has become an inevitable choice for alleviating the contradiction between resource supply and demand, protecting wild populations, and promoting sustainable industrial development.

T. hemsleyanum is naturally distributed in shaded and humid habitats such as gullies, valley slopes, and forest margins. It prefers shaded and humid conditions, is sensitive to strong light, and grows well in humus-rich, loose, and well-drained soils. Its growth and secondary metabolite accumulation are highly sensitive to environmental factors such as light, temperature, and moisture (Shi et al., 2022; Wang et al., 2025). Understory cultivation of medicinal plants is a new ecological cultivation model based on the principle of forest-medicine symbiosis, which makes use of forest canopy, light, temperature, moisture, and soil conditions for medicinal plant production (Li et al., 2025). Existing studies have shown that factors in the understory environment, such as light intensity, air temperature and humidity, soil fertility, pH, and microbial communities, can affect the yield and quality of medicinal plants by influencing photosynthesis, respiration, and secondary metabolism. Meanwhile, understory cultivation also contributes to forest resource conservation, biodiversity maintenance, ecological environment improvement, and sustainable forestry development, and has become an important direction for the forest medicinal herb industry (Guo et al., 2026).

This study explores the construction pathway of an understory ecological cultivation model for *T. hemsleyanum*. Existing studies have mainly focused on its pharmacological activity, chemical composition, quality control, and greenhouse or field cultivation, whereas systematic research on its understory ecological cultivation model remains relatively insufficient. Considering that relatively mature technical frameworks have gradually been established for the understory cultivation of other medicinal plants, including the optimization of shading intensity, canopy structure regulation, soil management, economic benefit evaluation, and ecological function analysis, it is necessary to systematically examine the understory ecological cultivation of *T. hemsleyanum* in relation to its biological characteristics and ecological adaptability. Therefore, this study analyzes the resource value, understory habitat adaptability, ecological cultivation model construction, key cultivation techniques, and industrial development needs of *T. hemsleyanum*, with the aim of providing theoretical references and practical support for suitable stand selection, cultivation technology optimization, and standardized production of this species.

2 Biological Characteristics and Growth Requirements of *Tetrastigma hemsleyanum*

2.1 Morphological characteristics and growth habits of *Tetrastigma hemsleyanum*

Tetrastigma hemsleyanum is a perennial herbaceous climbing vine of the genus *Tetrastigma* in the family Vitaceae, with distinct climbing characteristics. Its stems are slender and flexible, with longitudinal ridges, and adventitious roots may develop from the lower nodes. Young stems are mostly green and cylindrical, while older stems gradually become flattened and purplish brown, usually glabrous or sparsely pubescent (Zhu et al., 2020). The leaves of *T. hemsleyanum* are mostly palmately compound, usually composed of three leaflets and arranged alternately along the stem. The leaflets are generally lanceolate to ovate-lanceolate, with serrated margins, acuminate tips, and cuneate or nearly rounded bases. The leaves are dark green and can adapt well to the diffuse light environment under forest canopies (Guo et al., 2019). Its flowers are small and yellow-green, often borne in axillary umbels. The flowering period generally lasts from April to June, and the fruiting period from August to November. The berries turn bright red when mature and may remain on the plant for a relatively long time (Ji et al., 2020).

The underground part of *T. hemsleyanum* forms typical tuberous roots, which may be calabash-shaped, spindle-shaped, or ovoid. These tuberous roots usually occur singly or as several bead-like connected segments. The epidermis is mostly yellowish brown and relatively smooth, although wrinkles, lenticel-like protrusions, or depressions with residual roots may also be observed (Guo et al., 2019; Ji et al., 2020). The tuberous root is the main medicinal part of *T. hemsleyanum* and is also an important indicator for evaluating yield, commercial value, and medicinal quality in artificial cultivation. Anatomical studies have shown obvious differences among fibrous roots, bar-shaped roots, and calabash-shaped roots in vascular bundle integrity and intracellular inclusion accumulation, reflecting the gradual transformation of the underground part from a nutrient-absorbing organ into a medicinal storage organ (Xiang et al., 2021).

In terms of growth habits, *T. hemsleyanum* is naturally distributed mostly in shaded and humid environments, such as forest understories on mountain slopes, valley margins, shrublands, and rock crevices. It exhibits ecological characteristics of preferring shade and moisture, tolerating low light, and being sensitive to strong sunlight exposure (Guo et al., 2019). As a climbing plant, *T. hemsleyanum* mainly relies on tendrils opposite the leaves to twine around surrounding vegetation, supports, or rock walls and grow upward. This characteristic determines its spatial ecological niche in warm-temperate evergreen forests and subtropical understory shrublands (Guo et al., 2019). There is a certain coordination between aboveground vine growth and underground tuberous root enlargement: the early stage is dominated by stem and leaf expansion and vegetative growth, while the later stage gradually shifts toward underground tuberous root accumulation. Therefore, in understory ecological cultivation, the perennial habit, vine-like growth, climbing ability, and medicinal use of the tuberous roots of *T. hemsleyanum* should be comprehensively considered, and suitable support structures, moderate light, and a stable rhizosphere environment should be provided.

2.2 Requirements of *Tetrastigma hemsleyanum* for light, temperature, and humidity

T. hemsleyanum shows strong selectivity for ecological environments, especially in terms of light, temperature, and humidity. In its natural distribution, it is commonly found at elevations of approximately 300~1 300 m in humid grassland patches, mountain slopes, valleys, stream banks, and rock crevices with diffuse light, and it is suitable for growth in cool, humid, humus-rich soils (Guo et al., 2019). Its suitable soils are mostly yellow or yellow-brown acidic soils, with a pH of approximately 4.3~7.7. Meanwhile, *T. hemsleyanum* is highly sensitive to strong light and drought; excessive radiation and water deficit may lead to leaf water loss, reduced photosynthetic efficiency, and inhibited plant growth (Ji et al., 2020). Ecological niche modeling further indicates that the potential suitable habitats of *T. hemsleyanum* are constrained by climatic factors such as mean diurnal temperature range and precipitation during the warmest quarter. Under future climate warming scenarios, its highly suitable distribution areas may shrink significantly, suggesting that this species has a relatively narrow climatic niche.

T. hemsleyanum has strong low-light adaptability and is suitable for growth in semi-shaded or diffuse-light environments. Physiological and cultivation studies have shown that approximately 67% shading is more favorable for the growth of *T. hemsleyanum*, whereas excessive light suppresses its physiological activity and plant development (Zhu et al., 2020). Excessive direct sunlight can easily cause leaf scorching, enhanced transpiration, and decreased photosynthetic efficiency, while excessive shading may also lead to vine overgrowth, thin leaves, and insufficient accumulation of photosynthetic products, which is unfavorable for tuberous root enlargement. Therefore, the key to understory ecological cultivation is not simply to increase shading, but to create an understory microclimate with moderate shading, sufficient diffuse light, and good ventilation. Light quality and other environmental factors can also regulate biomass and active compound accumulation in *T. hemsleyanum*. Continuous low-intensity blue light treatment can increase tuberous root yield, photosynthetic efficiency after light saturation, flavonoid content, and antioxidant activity, indicating that moderate light stress may promote both plant growth and medicinal quality formation (Zhao et al., 2024). Therefore, in constructing understory ecological cultivation models, attention should be paid to the influence of canopy-filtered light environments on the quality formation of *T. hemsleyanum*.

Temperature and humidity are also important ecological factors affecting the growth and development of *T. hemsleyanum*. This species is suitable for growth in warm and humid environments, with an optimal growth temperature of approximately 25°C. When winter temperature drops to about 10°C, plant growth tends to stagnate, indicating that although it is adapted to warm-temperate evergreen forest environments, it remains sensitive to low temperatures (Guo et al., 2019; Zhu et al., 2020). Higher air humidity helps maintain leaf physiological activity and vine growth, while moderate soil moisture facilitates root absorption of water and nutrients. However, *T. hemsleyanum* prefers humid conditions but does not tolerate long-term waterlogging. If drainage is poor under forest canopies and the soil remains waterlogged for a long period, root hypoxia may occur, increasing the risk of soil-borne diseases such as root rot. Therefore, understory ecological cultivation should make full use of the forest canopy to buffer high temperature, strong light, and water evaporation, while maintaining a rhizosphere environment that is “moist but not waterlogged” through drainage ditches, slope planting, and organic mulching.

2.3 Characteristics of tuberous root formation and medicinal part accumulation in *Tetrastigma hemsleyanum*

The tuberous root of *T. hemsleyanum* is its main medicinal organ and the most economically valuable part in artificial cultivation. Tuberous root formation is not completed at once, but undergoes a continuous developmental process from fibrous roots to bar-shaped roots and then to calabash-shaped tuberous roots (Guo et al., 2019; Ji et al., 2020). Anatomical studies have shown that fibrous roots retain relatively intact vascular bundle structures and contain fewer intracellular inclusions. In the bar-shaped root stage, partial vascular bundle degeneration occurs, accompanied by the initial accumulation of inclusions. Mature calabash-shaped tuberous roots retain only traces of vascular bundles but contain abundant intracellular inclusions, which are considered important storage forms of medicinal substances (Xiang et al., 2021). Therefore, the enlargement of tuberous roots in *T. hemsleyanum* is essentially the result of root morphogenesis, vascular tissue changes, and storage substance accumulation.

Tuberous root formation is closely related to vegetative growth, photosynthate transport, and underground nutrient accumulation. In the early growth stage, *T. hemsleyanum* mainly enhances photosynthesis through the expansion of aboveground stems and leaves, providing a material basis for subsequent underground growth. As the plant enters a relatively stable growth stage, part of the nutrients is gradually transported to the underground organs, promoting tuberous root enlargement and dry matter accumulation. Transcriptome studies have found that tuberous root enlargement in *T. hemsleyanum* is associated with changes in the expression of genes related to cell wall modification, hormone signaling, and membrane components, indicating that root thickening and storage substance accumulation are regulated by complex regulatory networks (Xiang et al., 2021). Because *T. hemsleyanum* grows slowly and requires multiple years to form fully developed tuberous roots, its cultivation cycle is relatively long. Premature harvesting should therefore be avoided in production, as it may affect medicinal material yield and quality (Zhu et al., 2020; Hu et al., 2021).

In terms of medicinal part accumulation, active constituents in *T. hemsleyanum* show obvious tissue specificity. Studies have shown that the tuberous roots are rich in flavonoids, phenolic acids, terpenoids, polysaccharides, and other metabolites. Key indicator compounds such as polydatin, piceatannol, resveratrol, and kaempferol can be stably detected and are often used for medicinal material quality evaluation (Hu et al., 2021; Hu et al., 2023). Integrated metabolomic and transcriptomic studies further show that flavonoids, glycosides, alkaloids, and terpenoids are highly accumulated in tuberous roots, while leaves and fibrous roots are rich in certain flavonols and organic acids, indicating functional differentiation among different tissues in medicinal compound accumulation (Luo et al., 2022; Peng et al., 2025). Spatial metabolomics has also confirmed that some flavonoids, such as vitexin-2″-O-glucoside, are concentrated in the epidermis and xylem of tuberous roots, further supporting the status of tuberous roots as the core medicinal part (Fu et al., 2019; Chen et al., 2024). Therefore, understory ecological cultivation of *T. hemsleyanum* should establish a balance among light regulation, soil improvement, water and fertilizer management, and harvesting age, so as to promote stable tuberous root formation and active compound accumulation.

3 Analysis of the Understory Habitat Adaptability of *Tetrastigma hemsleyanum*

3.1 Adaptability of *Tetrastigma hemsleyanum* to low-light understory environments

Tetrastigma hemsleyanum is naturally distributed mostly in mountain forest margins, valley shrublands, and shaded, humid understory environments, showing strong adaptability to low-light conditions. Compared with open areas exposed to strong light, understory environments can effectively reduce direct solar radiation and create light conditions dominated by diffuse and filtered light, which is highly consistent with the ecological characteristics of *T. hemsleyanum*, namely its preference for shade and moisture and sensitivity to strong sunlight. Light-gradient experiments showed that under full light and 30%, 50%, 70%, and 90% shading treatments, the contents of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids in *T. hemsleyanum* increased with increasing shading intensity. Most photosynthetic parameters, including net photosynthetic rate, stomatal conductance, transpiration rate, apparent quantum efficiency, and maximum net photosynthetic rate, reached their highest values under approximately 70% shading and then decreased under stronger shading conditions (Xu et al., 2018). This indicates that moderate shading helps *T. hemsleyanum* maintain relatively high photosynthetic activity, whereas excessive light or excessive shading is unfavorable for plant growth.

A low-light understory environment does not mean that less light is always better. Although *T. hemsleyanum* has a certain degree of shade tolerance, its stem and leaf growth, photosynthesis, and tuberous root enlargement still require an appropriate amount of light energy. Earlier studies using 10%, 15%, and 30% of full sunlight showed that under moderate low-light conditions, namely 15% of full sunlight, *T. hemsleyanum* had higher photosynthetic capacity and yield, further indicating that it is adapted to diffuse and moderately weak light under forest canopies rather than full light or extremely dark environments. If stand canopy closure is too high and understory light transmittance is insufficient, plants are prone to vine overgrowth, thin leaves, and elongated internodes, leading to reduced accumulation of photosynthetic products and ultimately affecting underground tuberous root formation. Therefore, understory cultivation of *T. hemsleyanum* should emphasize “moderate shading” rather than “complete shading”. Stable and sufficient diffuse light should be provided by regulating canopy density, pruning branches and leaves, and arranging planting spacing properly.

From the perspective of ecological adaptation, low-light understory environments can provide *T. hemsleyanum* with light conditions close to its natural habitat, helping reduce environmental stress in artificial cultivation. Especially during periods of high temperature and strong light in summer, canopy shading can reduce leaf water loss and the risk of photoinhibition, thereby improving plant survival and growth continuity. Further studies have shown that *T. hemsleyanum* also has strong plasticity in response to changes in light quality. Continuous low-intensity blue light supplementation can significantly increase tuberous root yield, flavonoid content, and antioxidant activity, and enhance photosynthetic efficiency after light saturation, indicating that *T. hemsleyanum* can efficiently utilize limited light by optimizing photochemical processes and antioxidant systems (Zhao et al., 2024). In greenhouse photovoltaic systems, exogenous nitric oxide and phytohormones such as salicylic acid and jasmonic acid can restore photosynthetic parameters, reduce reactive oxygen species accumulation, and enhance plant adaptability to low-light and heterogeneous light environments (Figure 1) (Xie et al., 2022). Therefore, the rational use and regulation of understory light environments constitute an important basis for constructing ecological cultivation models for *T. hemsleyanum* and are also key to coordinating medicinal material yield and quality improvement.

3.2 Adaptability of *Tetrastigma hemsleyanum* to understory soil and moisture conditions

T. hemsleyanum has certain requirements for soil conditions and is suitable for growth in deep, loose, humus-rich, and well-drained soils. Understory soils usually have relatively high organic matter content due to long-term litter return, and their relatively favorable aggregate structure can provide a suitable rhizosphere environment for root extension and tuberous root enlargement. Understory environments are also characterized by strong soil structural heterogeneity, variable moisture conditions, and distinctive microbial communities, all of which jointly affect root development, nutrient absorption, and medicinal component accumulation in *T. hemsleyanum*. Studies have shown that intercropping *T. hemsleyanum* under moso bamboo forests and applying biochar-based organic fertilizer can significantly increase plant biomass, improve soil pH and soil organic carbon content, and alter bacterial community structure, indicating that improvements in soil physicochemical properties and microbial communities can jointly promote the growth of *T. hemsleyanum* (Zhang et al., 2019a).

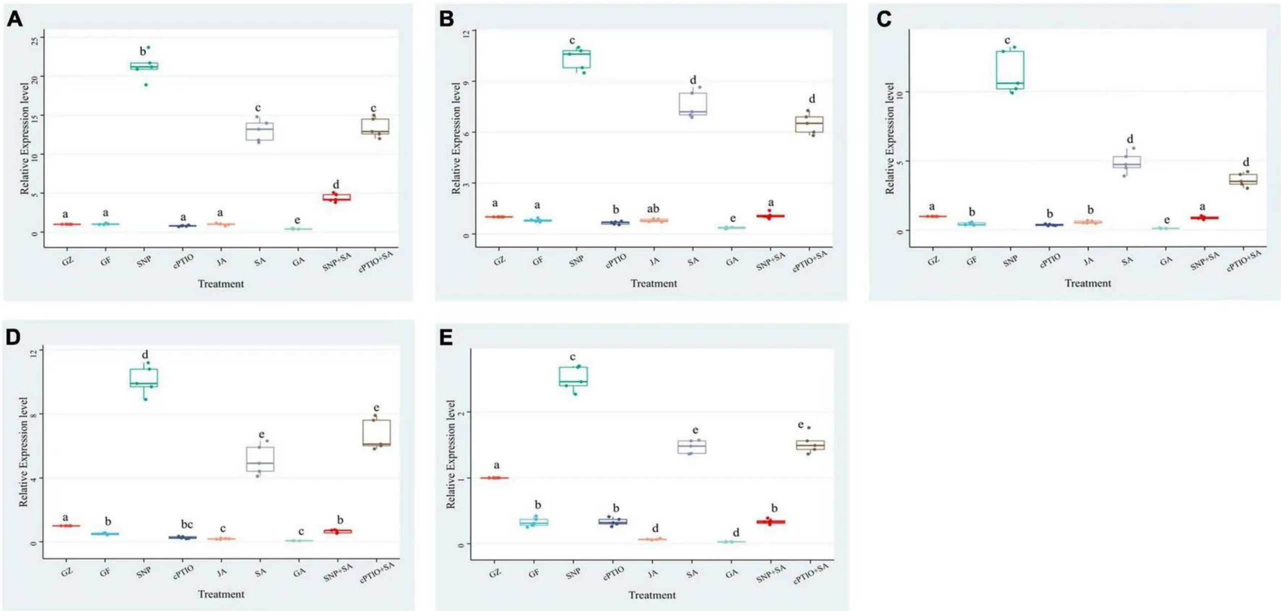


Figure 1 Effect of NO effectors and/or phytohormones on expression levels of (A) *psaL*, (B) *CHIL*, (C) *petF1*, (D) *psbQ*, and (E) *psaE,* of *T. hemsleyanum* under photovoltaic condition (GF) and normal light condition (GZ) (Adopted from Xie et al., 2022)
Image caption: Data are means±SE of the three technical replicates from five seedlings for each treatment; Means that do not share a same letter are significantly different at $p \le 0.05$ level through Tukey's test (Adopted from Xie et al., 2022)

However, understory soil environments also show variability and limiting factors. In some forestlands, well-developed tree roots may compete with *T. hemsleyanum* for water and nutrients; in low-lying or poorly drained plots, waterlogging may occur during the rainy season, resulting in root hypoxia and tuberous root decay. If understory land lacks long-term management, soil compaction, acidification, or pathogen accumulation may also occur. Therefore, understory cultivation of *T. hemsleyanum* should not rely solely on natural forestland conditions. Instead, soil fertility, permeability, pH, drainage status, and the rhizosphere microbial environment should be comprehensively assessed before planting. Pot experiments showed that pyrolytic organic matter, namely biochar, and organic fertilizer can both increase fresh root weight in *T. hemsleyanum*, with biochar being particularly effective in increasing plant height and total flavonoid content. These effects are associated with increases in soil available nitrogen, available phosphorus, available potassium, organic matter content, and enhanced activities of soil enzymes such as urease, protease, and cellobiohydrolase (Jiang et al., 2023). Therefore, in understory ecological cultivation, soil conditions can be optimized through the application of well-decomposed organic fertilizer, biochar-based fertilizer, drainage ditch construction, and mulching improvement.

Moisture conditions are an important factor affecting the growth of *T. hemsleyanum*. This species prefers humid conditions but does not tolerate long-term waterlogging, and it is suitable for growth in environments with relatively high air humidity, moderate soil moisture, and good drainage. Due to shading and litter coverage, understory environments can usually maintain relatively high humidity and reduce drought stress. However, during the plum rain season or periods of heavy rainfall, an inadequate drainage system may also induce root diseases. Soil microbial communities and rhizosphere conditions in different habitats also play an important role in the quality formation of *T. hemsleyanum*. Stony soils commonly found in mountainous forest terrain can support distinctive bacterial communities and enrich specific groups such as Actinobacteria and Rhizobiales. After two consecutive years of growth in such soils, *T. hemsleyanum* can form larger tuberous roots, and correlation analyses suggest that these microorganisms may promote tuberous root growth by releasing nutrients from rocks and regulating pathways related to phytohormone biosynthesis and stress resistance. Comparative studies of wild and cultivated populations have also shown that higher available phosphorus and potassium levels and distinctive rhizosphere microbial structures in wild habitats are associated with higher total flavonoid content and phenylalanine ammonia-lyase activity in roots. In addition, an appropriate amount of nitrogen is beneficial to the growth of *T. hemsleyanum*, whereas excessive nitrogen suppresses growth and reduces flavonoid and phenolic contents, indicating that high-quality understory production requires balanced nutrient supply rather than simply increasing fertilizer input (Fu et al., 2019). Therefore, understory ecological cultivation of *T. hemsleyanum* should follow the principles of "moisture retention without waterlogging" and "balanced fertilization" to create a stable rhizosphere environment for tuberous root formation and medicinal substance accumulation.

3.3 Growth performance of *Tetrastigma hemsleyanum* in different forest stand environments

Different forest stand environments vary markedly in shading degree, soil fertility, root competition, ventilation conditions, and management convenience, thereby affecting the growth performance of *T. hemsleyanum*. Field and controlled-environment studies have shown that intercropping *T. hemsleyanum* under moso bamboo stands combined with the application of biochar-based organic fertilizer can significantly increase plant biomass, indicating that *T. hemsleyanum* can grow well under relatively dense bamboo canopies when soil conditions are improved (Zhang et al., 2019a). Bamboo understories are characterized by relatively high humidity and stable shading, making them suitable for vine growth in *T. hemsleyanum*. However, dense bamboo rhizomes may compete with *T. hemsleyanum* for nutrients and space, and poor ventilation in some bamboo forests may increase disease risk. Therefore, when cultivating *T. hemsleyanum* under bamboo forests, bamboo culms should be appropriately thinned to improve light transmission and ventilation, while soil fertility supplementation and water drainage should be strengthened.

Cultivating *T. hemsleyanum* under fruit forests offers good advantages in spatial utilization. Fruit tree spacing is relatively regular, which facilitates land preparation, trellising, fertilization, and harvesting management. Understory light can also be regulated through canopy pruning, making this model suitable for the development of forest-medicine compound management. Although systematic trials on fruit forest-*T. hemsleyanum* cultivation remain relatively limited, fruit forests can be regarded as an important potential type for understory ecological cultivation of *T. hemsleyanum* based on its requirements for moderate shading, humid conditions, and vertical space utilization. However, fertilization, pesticide application, and irrigation measures in fruit tree management may affect the growth and medicinal material safety of *T. hemsleyanum*. Therefore, water and fertilizer management as well as pest and disease control for fruit trees and *T. hemsleyanum* should be coordinated to avoid interference between management practices.

Broad-leaved forests or near-natural stands are closer to the wild habitats of *T. hemsleyanum*, with advantages such as abundant litter, higher soil humus content, and stronger ecological stability, making them suitable for the development of simulated wild ecological cultivation models. In mixed broad-leaved forests with approximately 70% canopy density, soils containing a relatively high proportion of gravel can support the formation of larger tuberous roots and distinctive microbial communities in *T. hemsleyanum*, indicating that broad-leaved forest stands with moderate canopy closure, stony soils, and stable microclimates can provide a suitable ecological niche for cultivation. Seasonal climate analysis showed that moderate temperatures of 17.5°C~24.1°C, humidity of approximately 67%~80%, relatively low precipitation, and shorter sunshine duration are conducive to the formation of higher total flavonoid content in tuberous roots (Shi et al., 2022). Overall, different forest stands can provide certain conditions for understory cultivation of *T. hemsleyanum*, but suitable models should be selected according to stand structure, canopy closure, soil conditions, and management objectives. At the same time, regulation experience from greenhouse and stereoscopic planting systems can be used as a reference to further optimize understory ecological cultivation schemes (Xie et al., 2022; Hu et al., 2023).

4 Construction of Understory Ecological Cultivation Models for *Tetrastigma hemsleyanum*

4.1 *Tetrastigma hemsleyanum*-bamboo forest compound cultivation model

The *Tetrastigma hemsleyanum*-bamboo forest compound cultivation model is a forest-medicine compound model that uses the relatively stable shaded environment and humid microclimate under bamboo forests to cultivate *T.*

hemsleyanum ecologically within bamboo forest spaces. Moso bamboo (*Phyllostachys edulis*) forests usually have relatively high canopy closure and a stable microclimate, forming a cool, humid, and shaded understory environment. This is highly consistent with the ecological requirements of *T. hemsleyanum*, which prefers warm-temperate evergreen forest habitats and moderately low-light conditions. Light-treatment studies have shown that approximately 70% shading is beneficial to photosynthesis and growth in *T. hemsleyanum*. Therefore, when constructing a compound cultivation model under bamboo forests, canopy shading regulation should be regarded as one of the key technical links (Xu et al., 2018). Bamboo forest floors usually contain abundant litter, which can increase soil organic matter content and improve soil structure after decomposition, thereby providing a certain basis for root development and tuberous root enlargement in *T. hemsleyanum*. However, long-established bamboo forest soils are usually acidic, and nutrient supply and pH regulation should be strengthened after intensive understory cultivation is introduced (Zhang et al., 2019a).

In constructing this model, planting areas should be reasonably determined according to bamboo forest canopy closure, bamboo stand density, rhizome distribution, and topographic conditions. *T. hemsleyanum* can be intercropped between bamboo rows, using bamboo culms, simple mesh frames, or understory support structures to support its climbing growth, so that the vines are distributed upward in an orderly manner and poor ventilation and disease occurrence caused by long-term creeping along the ground can be avoided. In plots with overly dense bamboo stands and insufficient understory light, weak, old, and overly dense bamboo culms should be thinned appropriately to improve understory ventilation and light transmission. In areas with dense bamboo rhizomes and strong root competition, ditch isolation, localized land preparation, and the application of well-decomposed organic fertilizer and biochar-based organic fertilizer can be used to reduce water and nutrient competition between bamboo rhizomes and *T. hemsleyanum*. Studies have shown that, compared with pure moso bamboo forests, moso bamboo-*T. hemsleyanum* systems can increase soil organic carbon and available nitrogen contents, but soil pH and available potassium contents are lower. This suggests that potassium supplementation should be emphasized in production, and alkaline amendments should be applied when necessary (Zhang et al., 2019b).

The advantages of the *T. hemsleyanum*-bamboo forest compound cultivation model lie in its stable ecological environment, suitable shading conditions, and relatively high utilization efficiency of forestland space, making it suitable for promotion in mountainous areas rich in bamboo resources. Related studies have shown that applying biochar-based organic fertilizer under moso bamboo forests can increase soil pH and organic carbon content, significantly increase *T. hemsleyanum* biomass, and reshape bacterial community structure at the phylum and genus levels. At the same time, bamboo forest-medicinal plant systems can increase soil bacterial diversity and alter dominant bacterial groups, with soil pH, organic carbon, and available phosphorus being closely related to microbial community structure (Zhang et al., 2019c). Therefore, this model should comprehensively integrate reasonable plant and row spacing, organic fertilizer or biochar-based fertilizer application, potassium supplementation, pH regulation, drainage management, and green pest and disease control measures, so as to maintain habitat conditions characterized by “moderate shading, good ventilation, loose soil, and moisture without waterlogging” and improve the survival rate, tuberous root yield, and medicinal material quality of *T. hemsleyanum*.

4.2 *Tetrastigma hemsleyanum*-fruit forest compound cultivation model

The *Tetrastigma hemsleyanum*-fruit forest compound cultivation model refers to planting *T. hemsleyanum* between fruit tree rows or in the lower spaces beneath fruit tree canopies, thereby realizing compound management of fruit trees and medicinal plants. Fruit forests can provide certain shading, diverse litter inputs, and a relatively stable understory microclimate for *T. hemsleyanum*. At the same time, fruit tree spacing is usually relatively regular, and the understory space is relatively open, facilitating land preparation, trellising, fertilization, irrigation, and harvesting management. Compared with bamboo forests, fruit forest understories have stronger management controllability. They can reduce the adverse effects of strong summer light and high temperature on *T. hemsleyanum* while improving land-use efficiency and comprehensive output per unit area by utilizing the lower spaces under fruit trees.

Although specialized studies on fruit tree-*T. hemsleyanum* compound systems remain relatively limited, fruit tree-herb intercropping and other orchard agroforestry models can provide important references. In karst rocky desertification control areas, intercropping fruit trees with herbaceous legumes significantly improved economic returns compared with monoculture orchards and enhanced ecosystem services such as groundwater recharge, soil and water conservation, and carbon sequestration. This indicates that a “fruit tree + understory herb” structure can coordinate ecological protection and economic benefits (Cheng et al., 2022). Global studies on horticultural intercropping and fruit tree agroforestry also show that well-designed tree-crop combinations can improve land-use efficiency, yield stability, and the ability to resist climate stress (Burgess et al., 2022; Paut et al., 2024). Therefore, from the perspective of agroforestry management principles, cultivating *T. hemsleyanum* under fruit forests has a sound theoretical basis and promotion potential.

In model design, fruit forests with open crowns, moderate canopy closure, and stable management intensity, such as citrus, bayberry, and loquat orchards, should be prioritized. For shade-loving and climbing medicinal plants such as *T. hemsleyanum*, fruit tree species and planting densities should be reasonably selected so that the understory environment approaches the moderate light and humidity conditions favorable for flavonoid accumulation, such as temperatures of approximately 17.5°C~24.1°C, air humidity of approximately 67%~80%, and shorter sunshine duration (Shi et al., 2022). During planting, areas where fruit tree main roots are concentrated should be avoided, *T. hemsleyanum* planting belts should be reasonably arranged, and supports or mesh frames should be configured to guide vines to climb in an orderly manner, thereby reducing spatial, water, and nutrient competition with fruit trees. Existing studies have shown that, compared with simple creeping cultivation, stereoscopic cultivation can increase tuberous root yield and enhance the contents of key quality markers such as polydatin, piceatannol, resveratrol, and kaempferol in *T. hemsleyanum* (Hu et al., 2023). Therefore, in fruit forest understory cultivation of *T. hemsleyanum*, fertilization, pruning, pest and disease control, and harvesting arrangements for fruit trees and medicinal plants should be coordinated. Organic fertilizers, green control measures, and low-residue management practices should be adopted as much as possible to form a fruit-medicine compound cultivation system that is coordinated and non-interfering.

4.3 *Tetrastigma hemsleyanum*-broad-leaved forest simulated wild cultivation model

The *Tetrastigma hemsleyanum*-broad-leaved forest simulated wild cultivation model is a low-intervention and ecological cultivation model carried out under natural or semi-natural warm-temperate evergreen broad-leaved forests, subtropical broad-leaved forests, or near-natural mixed forests, with the core aim of simulating the natural habitat of *T. hemsleyanum*. The native habitats of *T. hemsleyanum* are mostly humid shrublands, valleys, and mountain slopes at elevations of 300~1 300 m. Broad-leaved forest understories usually have abundant litter, relatively high air humidity, favorable soil humus content, and strong ecosystem stability, which can provide growth conditions relatively close to its wild state. Ecological niche modeling and phylogeographic analyses show that *T. hemsleyanum* is closely associated with warm-temperate evergreen forests, and its highly suitable habitats are controlled by climatic variables such as mean diurnal temperature range and precipitation during the warmest quarter. Under future climate warming scenarios, the highly suitable areas of *T. hemsleyanum* may shrink significantly, highlighting the importance of near-native habitat cultivation in existing suitable forest patches for protecting genetic resources and maintaining ecological functions (Wang et al., 2023).

In the specific construction process, broad-leaved forestlands with stable stand structures, moderate canopy closure, good drainage, deep soil layers, and relatively low human disturbance should be selected. Before planting, large-scale excavation and destructive land preparation should be avoided. Hole preparation, strip preparation, or localized soil improvement can be adopted to reduce disturbance to the forest ecosystem. *T. hemsleyanum* seedlings can be planted at low to moderate densities along forest margins, forest gaps, slopes, valley edges, or understory areas with better light transmission. Existing shrubs and trees can be used as natural supports, or simple supports and ecological mesh frames can be combined for vine guidance. Management should mainly rely on microhabitat selection, low-disturbance land preparation, litter retention, and limited inputs, so as to maintain local soil microbial communities, litter cycling, and water regulation mechanisms, while highlighting ecological cultivation and simulated wild-quality characteristics.

Seasonal field studies have shown that under cool, humid spring conditions with shorter sunshine duration, the total flavonoid content and antioxidant activity of *T. hemsleyanum* tuberous roots are relatively high, and its flavonoid biosynthesis pathway is closely coupled with environmental factors throughout the annual cycle (Figure 2) (Shi et al., 2022). Light-intensity experiments further demonstrate that excessive radiation and high temperature reduce photosynthetic activity in *T. hemsleyanum*, whereas approximately 70% shading can optimize pigment content and photosynthesis (Xu et al., 2018). Therefore, in the broad-leaved forest simulated wild model, understory locations with moderate canopy shading, stable microclimates, and moist but non-waterlogged soils should be prioritized, so that the ecological conditions can approximate those required for the natural growth of *T. hemsleyanum*. The outstanding advantage of this model is that the ecological environment is close to nature and the medicinal material has a favorable quality image, making it suitable for the development of ecological medicinal materials, geo-authentic medicinal materials, and branded products. However, its management and harvesting are relatively difficult, and yield stability may be lower than that of intensive cultivation models. Therefore, in promotion and application, the model should be positioned according to production objectives. If ecological quality and resource conservation are prioritized, a low-density and low-intervention simulated wild model can be adopted. If stable yield and large-scale management are the goals, cultivation management should be moderately strengthened on the basis of simulated wild cultivation to balance ecological value and productivity.

5 Key Cultivation Techniques for Understory Planting of *Tetrastigma hemsleyanum*

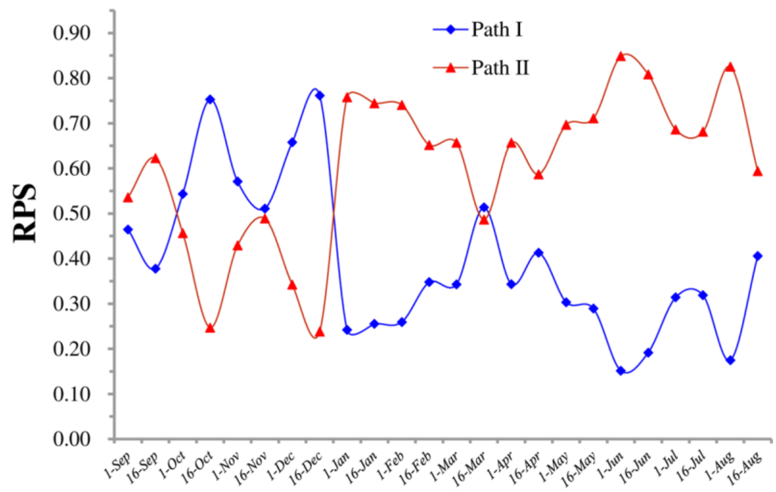
5.1 Propagation and planting of high-quality *Tetrastigma hemsleyanum* seedlings

The foundation of understory ecological cultivation of *Tetrastigma hemsleyanum* lies in obtaining high-quality seedlings and carrying out standardized planting. Seedling quality directly affects plant survival rate, later growth vigor, tuberous root formation, and the stability of medicinal material quality. Therefore, seedlings with clear provenance, stable traits, no pests or diseases, complete root systems, and vigorous growth should be selected as cultivation materials. Traditional seed propagation and cutting propagation are limited by low natural fruiting rate and restricted propagation quantity, making it difficult to fully meet the demand for large-scale understory cultivation. As a result, rapid propagation technologies have attracted increasing attention (Hu et al., 2021). In production, tuberous root propagation, cutting propagation, and tissue culture can be used for seedling propagation, among which tissue culture is conducive to the rapid propagation of seedlings with uniform morphology, genetic stability, and a high degree of disease-free quality (Pang et al., 2024).

Tissue culture is an important direction for the large-scale propagation of high-quality *T. hemsleyanum* seedlings. Tissue culture techniques based on axillary bud proliferation or shoot organogenesis can produce a large number of tissue-cultured seedlings with stable morphology, relatively stable flavonoid content, and high uniformity, thereby meeting both resource conservation needs and commercial production requirements. Studies have shown that when leaves and petioles are used as explants and induced on Murashige and Skoog (MS) medium supplemented with appropriate combinations of 6-benzylaminopurine and auxins, a relatively high adventitious shoot proliferation rate can be obtained within 30 days. Optimized rooting media can achieve a 100% rooting rate, and the survival rate of tissue-cultured seedlings after acclimatization in a peat-sand substrate can exceed 98% (Pang et al., 2024).

For large-scale seedling production suitable for understory transplantation, cutting propagation remains a practical and relatively low-cost method. Cutting propagation experiments have shown that when 2- to 3-year-old cuttings are treated with 1 000 mg/L indole-3-butyric acid for 10 s and then planted in loess, rooting performance is relatively good, providing a technical basis for standardized production of robust seedlings. Both tissue-cultured seedlings and cutting-derived seedlings should be fully hardened before transplantation into understory environments, so that they can gradually adapt to understory temperature, humidity, low-light, and ventilation conditions, thereby reducing transplanting stress and improving establishment speed (Zhang et al., 2019a; Hu et al., 2021). Before planting, localized land preparation or hole preparation should be carried out, and well-decomposed organic fertilizer should be applied as basal fertilizer. After planting, root-setting water should be applied promptly, and mulching or other moisture-retention measures should be adopted according to understory light and humidity conditions.

A



B

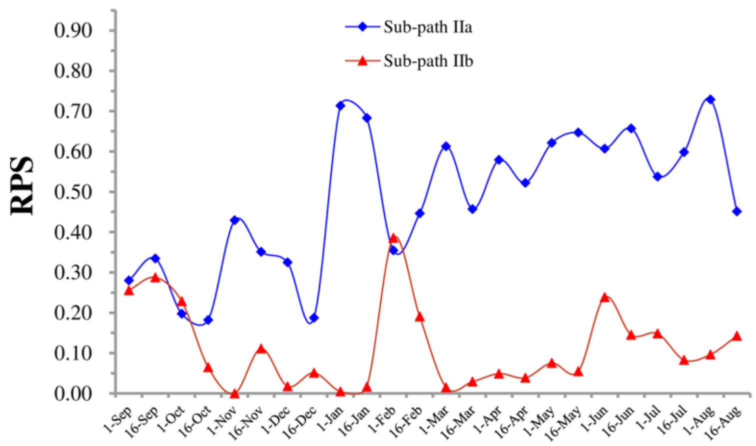


Figure 2 Reaction path selectivity (RPS) of flavonnoid biosynthesis in *T. hemsleyanum* and their seasonal variations (Adopted from Shi et al., 2022)

Image caption: (A): Path I: producing Ap, IsoO and Or; Path II: producing Km, Qu, IsoQ, Rut, Ast and Km3rut; (B) Sub-path IIa: producing Qu, IsoQ and Rut; Sub-path IIb: producing Ast and Km3rut (Adopted from Shi et al., 2022)

5.2 Vine guidance, trellising, and plant management of *Tetrastigma hemsleyanum*

T. hemsleyanum is a climbing vine with obvious twining and climbing growth characteristics in its aboveground parts. It requires support structures to make full use of vertical space, improve ventilation and light penetration, and reduce lodging. If allowed to creep naturally, plants are likely to become entangled with one another, causing excessive canopy closure within the crop layer, increasing disease risk, and hindering the transport of photosynthetic products to tuberous roots. Comparative studies of different planting models have shown that, compared with creeping cultivation, stereoscopic cultivation can significantly improve the quality of tuberous roots and increase the contents of compounds such as polydatin, piceatannol, resveratrol, and kaempferol. Greenhouse cultivation combined with stereoscopic planting can also produce higher aboveground and underground biomass, indicating that vertical support and spatial stratification are conducive to biomass accumulation and medicinal quality improvement (Hu et al., 2023).

Trellising management should follow the principle of not affecting normal tree growth or damaging the ecological structure of the forestland. Under bamboo forests and fruit forests, low supports, bamboo-pole supports, mesh frames, or simple hedge frames can be used to guide *T. hemsleyanum* vines upward or along the support surface, reducing ground contact and moisture accumulation. In simulated wild cultivation under broad-leaved forests, natural tree trunks, shrubs, or ecological supports can be appropriately used for climbing. Although systematic studies on dedicated understory trellising systems for *T. hemsleyanum* remain limited, experience from other medicinal climbing plants and vines can provide useful references. For example, trellised cultivation of *Codonopsis javanica* can increase plant height and leaf size compared with non-trellised treatment, showing certain practical application value (Son and Giang, 2026). Broader studies on climbing plants have shown that supports with small diameters and close spacing are important for climbers to form stable support networks (Figure 3) (Soffiatti et al., 2022; Yu et al., 2025).

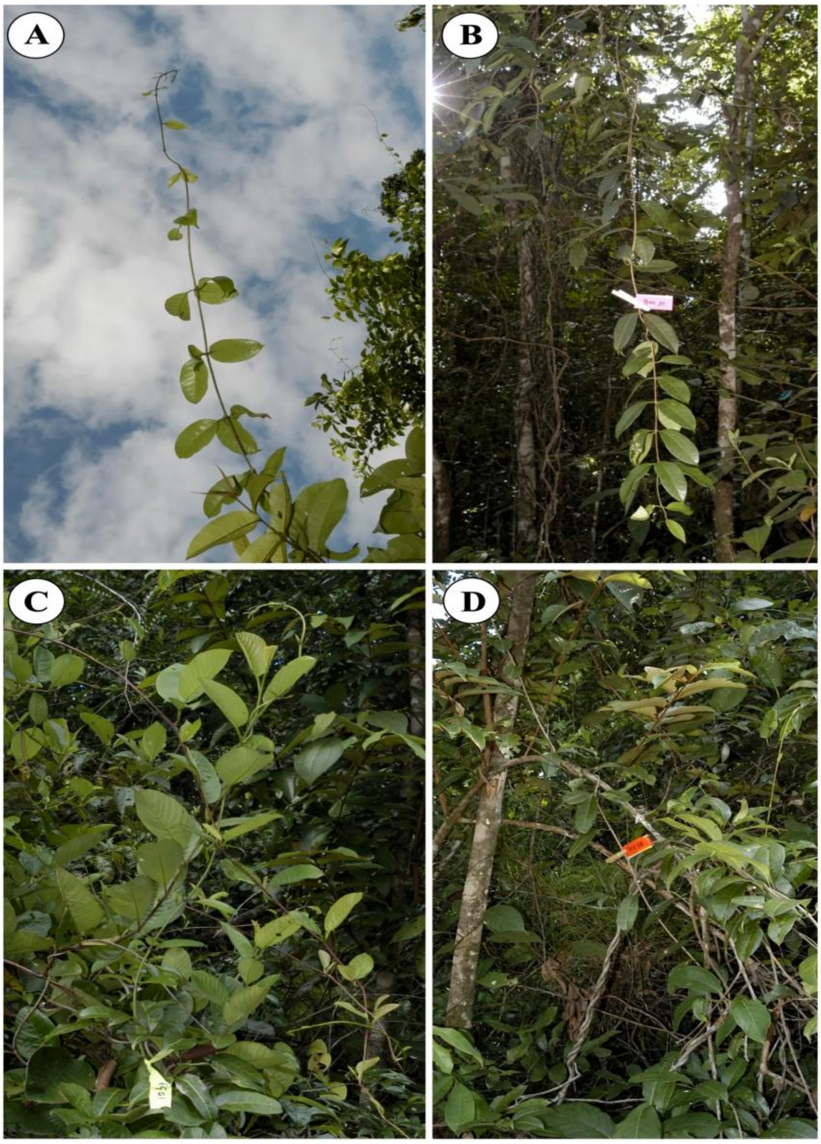


Figure 3 Four phases of stem growth that make up a trellis and which were sampled for mechanical properties and structural development (Adopted from Soffiatti et al., 2022)

Image caption: (A) Self-supporting stem, a young stem that has not yet encountered a support. (B) Pendulous stem that has not encountered a support. (C) Climbing stem represented by a young shoot, which has encountered a support and which has developed twining on that support. (D) A "fixed stem", a stem that shows the upper and lower phases of twining so that the segment in between the two attachment points is completely fixed between two sections of twining onto a host stem (Adopted from Soffiatti et al., 2022)

Plant management also includes pinching, vine thinning, removal of diseased and weak branches and leaves, and regulation of vegetative growth. Vine guidance should be carried out in the early growth stage to prevent stems and vines from becoming too entangled to manage. For overly vigorous plants, vine overgrowth may be moderately controlled to promote nutrient allocation to underground tuberous roots. For plants with overly dense branches and leaves, weak branches, diseased branches, and excessive foliage should be removed in time to improve understory ventilation and reduce pest and disease risk. Reasonable vine management can help maintain coordination between aboveground growth and underground tuberous root development, making it an important technical measure for improving yield and quality in understory cultivation.

5.3 Water and fertilizer management and green pest and disease control of *Tetrastigma hemsleyanum*

Understory cultivation of *T. hemsleyanum* should follow the fertilization principle of using organic fertilizer as the main source and appropriate topdressing as a supplement. Understory environments are characterized by strong heterogeneity in soil nutrients and moisture. Although litter decomposition can provide a certain humus foundation, nutrient supplementation is still required during long-term cultivation to meet the needs of vine growth and tuberous root enlargement. Basal fertilizer should mainly consist of fully decomposed farmyard manure, compost, commercial organic fertilizer, or biochar-based organic fertilizer, combined with appropriate phosphorus and potassium fertilizers to improve root development and tuberous root fullness. Related studies have shown that when *T. hemsleyanum* is intercropped under moso bamboo forests, the application of biochar-based organic fertilizer can significantly increase plant biomass, improve soil pH and organic carbon content, and alter bacterial community composition (Zhang et al., 2019a).

Organic, slow-release, and ecological fertilization methods are more suitable for maintaining soil fertility and medicinal material quality in understory systems. Related studies have shown that biochar and organic fertilizer can increase root weight, plant height, total flavonoid content, and soil enzyme activity in *T. hemsleyanum*, indicating that improved soil fertility and enhanced rhizosphere activity help promote tuberous root formation and active compound accumulation. At the same time, excessive nitrogen input is associated with decreased flavonoid and phenolic contents, suggesting that the fertilization regime for *T. hemsleyanum* should be designed around medicinal material quality rather than simply pursuing maximum biomass or yield (Fu et al., 2019; Hu et al., 2021). Water management should follow the principle of "maintaining moisture while avoiding waterlogging". Drainage should be strengthened during the rainy season, while drip irrigation, sprinkler irrigation, or organic mulching can be used for water supplementation and moisture retention during dry seasons.

In terms of pest and disease control, prevention should be prioritized, and a green control system combining agricultural, physical, biological, and low-risk chemical measures should be established. In high-humidity understory environments, *T. hemsleyanum* is prone to diseases such as root rot and leaf spot. Therefore, healthy seedlings, improved ventilation and light transmission, appropriate planting density, timely removal of diseased plant residues, and prevention of waterlogging should be used to reduce disease risk. For pests such as aphids and grubs, trapping, manual removal, biological agents, or low-toxicity and low-residue pesticides can be adopted. Studies have shown that endophytic fungi associated with the roots of *T. hemsleyanum* can promote root development and enhance plant vigor and stress resistance by secreting phytohormones and other substances. In the future, green understory management of *T. hemsleyanum* should integrate organic fertilizer and biochar-based fertilizer application, beneficial microbial utilization, rational density design, and low-residue control measures, so as to form an integrated ecological cultivation technology system that balances yield, medicinal material quality, and forest ecological environment protection (Li et al., 2025; Guo et al., 2026).

6 Effects of the Understory Environment on the Yield and Quality of *Tetrastigma hemsleyanum*

6.1 Effects of Light conditions on the plant growth of *Tetrastigma hemsleyanum*

Light is an important ecological factor affecting the understory growth of *Tetrastigma hemsleyanum*. Light intensity and light quality jointly determine plant morphogenesis, photosynthetic efficiency, and biomass allocation. *T. hemsleyanum* prefers shaded and humid conditions and is sensitive to strong light. In understory environments with diffuse light, it can better maintain leaf water status and physiological activity. Shading experiments have shown that, as shading intensity gradually increases from full light to 30%~90%, chlorophyll and carotenoid contents in *T. hemsleyanum* gradually increase, while most photosynthetic parameters, such as net photosynthetic rate, stomatal conductance, transpiration rate, and maximum net photosynthetic rate, reach their peaks at approximately 70% shading and then decline. This indicates that excessive light inhibits photosynthetic activity and normal growth in *T. hemsleyanum* (Xu et al., 2018). Under lower light conditions, namely 10%~30% of full sunlight, plants under 15% sunlight show higher photosynthetic capacity and yield than those under 10% and 30% sunlight, further indicating that *T. hemsleyanum* is better adapted to moderate diffuse light environments and is not suitable for strong direct light conditions.

However, the low-light adaptability of *T. hemsleyanum* does not mean that it can remain in excessively shaded environments for long periods. If stand canopy closure is too high and understory light transmission is insufficient, the plants may show rapid vine elongation, but this growth is often characterized by etiolation, including thinner leaves, elongated internodes, reduced tissue firmness, and insufficient accumulation of photosynthetic products, ultimately affecting underground tuberous root enlargement. Conversely, if understory shading is insufficient, strong light and high temperature may cause leaf scorching, wilting, and damage to the photosynthetic system, reducing plant survival. Therefore, understory cultivation should create a diffuse-light environment suitable for *T. hemsleyanum* growth by pruning tree canopies, adjusting planting locations, and controlling stand density, so that plants can avoid strong light stress while obtaining sufficient photosynthetically active radiation.

From the perspective of yield and quality formation, suitable light conditions can promote coordinated growth between the aboveground and underground parts of *T. hemsleyanum*. Healthy leaves are the basis for photosynthate formation, and only when the aboveground parts maintain moderate growth can sufficient nutrient sources be provided for tuberous root enlargement and medicinal substance accumulation. Light quality also significantly regulates growth and biomass allocation in *T. hemsleyanum*. Experiments using different colored films showed that blue film promoted plant height growth, leaf expansion, specific leaf weight, and fresh root weight, and increased soluble amino acid content and chalcone isomerase activity, thereby improving yield. Red film reduced root biomass but enhanced phenylalanine ammonia-lyase activity and total flavonoid content, indicating a certain trade-off between vegetative growth and secondary metabolism under different spectral conditions (Bai et al., 2021). In vitro regeneration studies also showed that when light intensity increased from 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, shoot proliferation and chlorophyll content increased, suggesting that young tissues can utilize higher light levels when other stress factors are controlled (Pang et al., 2024). Therefore, in the understory ecological cultivation of *T. hemsleyanum*, the light environment should be dynamically regulated according to stand type, seasonal changes, and plant growth stage, so that light conditions can protect plants from strong light stress while meeting their needs for photosynthesis and substance accumulation.

6.2 Effects of soil fertility on tuberous root yield of *Tetrastigma hemsleyanum*

The main medicinal part of *T. hemsleyanum* is the underground tuberous root, and soil fertility directly affects root development, tuberous root enlargement, and yield formation. Loose, fertile, and organic matter-rich soils can provide good extension space and nutrient supply for the roots of *T. hemsleyanum*, which helps enhance root absorption capacity and promote nutrient transport to underground parts. Because understory soils accumulate litter over long periods, they usually have a certain humus foundation, which can improve soil structure and enhance water and fertilizer retention to some extent, thereby creating a suitable rhizosphere environment for tuberous root formation. Pot experiments have shown that both low and high additions of pyrolytic organic matter, namely biochar, can significantly increase plant height and fresh root weight in *T. hemsleyanum*. Compared with the unfertilized control, fresh root weight and total flavonoid content increased by 1.60~2.70 times (Jiang et al., 2023).

Soil fertility is reflected not only in nutrient content but also in comprehensive conditions such as soil aeration, water retention, microbial activity, soil enzyme activity, and pH. The study by Jiang et al. (2023) showed that the yield- and quality-enhancing effects of biochar were associated with increases in soil available nitrogen, available phosphorus, available potassium, and organic matter levels, as well as enhanced activities of soil enzymes such as urease, protease, and cellobiohydrolase and increased chalcone isomerase activity. This indicates that improvements in soil fertility and microbial activity can jointly promote biomass accumulation and secondary metabolism in *T. hemsleyanum*. Application of organic fertilizer alone can also increase fresh root weight, but its promoting effect on total flavonoid content is relatively weaker, and its yield-increasing effect is mainly related to available potassium, available phosphorus, and protease activity (Jiang et al., 2023). Therefore, during understory cultivation, soil structure should be improved through the application of well-decomposed organic fertilizer, compost, biochar, and humus soil, and nutrients should be supplemented reasonably according to plant growth stages.

Field studies further emphasize the role of soil structure and microbial communities in tuberous root enlargement of *T. hemsleyanum*. After two consecutive years of cultivation in stony soils, *T. hemsleyanum* produced significantly larger tuberous roots than plants grown in similar soils from which stones had been removed. Stony soils had distinctive bacterial communities, higher microbial diversity, and enrichment of groups such as Actinobacteria and Rhizobiales. These differential bacteria were associated with host plant pathways related to phytohormone biosynthesis, photosynthesis, and stress resistance, indicating that microbial communities driven by stony soils can promote tuberous root initiation and enlargement in *T. hemsleyanum* (Hong et al., 2021). Comparative analysis of wild and cultivated rhizosphere environments also showed that higher available phosphorus and potassium contents and specific bacterial genera in wild soils were associated with increased total flavonoid content and phenylalanine ammonia-lyase activity in roots. Therefore, understory cultivation of *T. hemsleyanum* should establish a fertility management model based on organic fertilizer, balanced nitrogen, phosphorus, and potassium supply, and soil ecological health, so that soil conditions can truly support the simultaneous improvement of tuberous root yield and medicinal material quality.

6.3 Effects of cultivation years on the medicinal quality of *Tetrastigma hemsleyanum*

T. hemsleyanum is a perennial medicinal plant, and its tuberous root formation and accumulation of active substances follow an obvious temporal process. Generally, the shorter the cultivation period, the less sufficient the accumulation in the underground parts, resulting in smaller tuberous roots and underdeveloped dry matter content and medicinal quality. As the growth period extends, *T. hemsleyanum* continuously accumulates photosynthates and transports nutrients, leading to gradual enlargement of underground tuberous roots and improvements in the weight, fullness, and commercial value of the medicinal parts. Field observations have shown that larger tuberous roots of *T. hemsleyanum* usually begin to form in the later stage of the second growth year, and many cultivation systems also use tuberous roots of the same growth age for quality evaluation (Shi et al., 2022). Therefore, reasonably extending the cultivation cycle is one important way to improve the yield and quality of *T. hemsleyanum* medicinal materials.

However, a longer cultivation period is not always better. As cultivation time increases, problems such as nutrient depletion in understory soils, pathogen accumulation, root aging, and increased management costs may gradually emerge. If plants are continuously cultivated in the same plot for a long time without soil improvement or pest and disease control, plant vigor may decline, the rate of tuberous root decay may increase, and the stable supply of medicinal materials may be affected. Therefore, when determining the appropriate harvesting age for *T. hemsleyanum*, plant growth status, tuberous root size, medicinal material quality, market demand, and input-output ratio should be comprehensively considered, rather than using cultivation years as the sole criterion.

From the perspective of quality regulation, cultivation years and seasonal environments jointly affect the accumulation level and stability of medicinal components in *T. hemsleyanum*. A three-year trial with sampling every half month showed that the total flavonoid content and antioxidant activity in tuberous roots changed dynamically within a year and across different growth cycles, indicating that its secondary metabolism undergoes continuous adjustment. Seasonal analysis showed that under spring conditions with precipitation of 2.0~6.6 mm, temperature of 17.5°C~24.1°C, humidity of 67.3%~80.2%, and sunshine duration of 3.4~5.8 h, total flavonoid content in tuberous roots reached a relatively high level of 281.3~392.8 μg/g, suggesting that cool and moderately humid conditions are conducive to flavonoid enrichment (Shi et al., 2022). In addition, metabolomic and origin-tracing studies have identified catechin, darendoside B, resveratrol derivatives, and other compounds as key quality markers. These compounds differ among production areas and may be related to cultivation environments and cultivation history (Hu et al., 2023; Chu et al., 2024). Therefore, in production practice, age-specific management and timely harvesting systems should be established, and harvesting standards suitable for different understory cultivation models should be gradually developed based on production area conditions and quality testing results.

7 Benefit Analysis of Understory Ecological Cultivation of *Tetrastigma hemsleyanum*

7.1 Ecological benefits of understory cultivation of *Tetrastigma hemsleyanum*

Understory ecological cultivation of *Tetrastigma hemsleyanum* can make full use of forestland space and form a compound ecological structure integrating the tree layer, shrub-herb layer, and medicinal plant layer. Compared with monoculture open-field cultivation, understory cultivation is closer to the natural growth environment of *T. hemsleyanum* and can reduce the adverse effects of strong light, high temperature, and drought on plants, allowing *T. hemsleyanum* to grow in a relatively stable understory microclimate. Meanwhile, canopy shading, litter cover, and soil humus accumulation help maintain soil moisture, regulate surface temperature, and enhance the stability of forestland ecosystems. Existing studies have pointed out that understory vegetation plays an important role in forest ecosystem functioning by promoting ecosystem productivity, nutrient cycling, organic matter decomposition, and ecosystem self-renewal (Deng et al., 2023).

During understory cultivation, *T. hemsleyanum* causes relatively little disturbance to the original forestland structure. It does not require large-scale land clearing or intensive tillage, thereby helping reduce soil erosion and surface exposure. Especially in mountainous, hilly, and sloping forest areas, developing understory ecological cultivation of *T. hemsleyanum* can improve land-use efficiency while protecting forest vegetation and avoid ecological damage caused by blind land reclamation. Meta-analyses and review studies have shown that maintaining diverse understory plants helps preserve soil organic carbon, total nitrogen, soil water content, pH, and microbial biomass, whereas removing understory vegetation increases soil temperature and significantly reduces multiple soil properties (Zhang et al., 2022). In oil palm plantations, increasing understory cover, namely avoiding herbicide use, can improve the diversity and abundance of soil macrofauna and enhance litter decomposition rates, without obvious negative effects on soil fertility. This indicates that retaining and utilizing the understory vegetation layer has positive significance for maintaining soil ecological functions.

In addition, understory cultivation of *T. hemsleyanum* contributes to the conservation of medicinal plant resources. In the past, *T. hemsleyanum* resources depended largely on wild harvesting, and overharvesting could easily lead to the decline of wild populations and habitat degradation. Artificial understory ecological cultivation can reduce dependence on wild resources to a certain extent and promote a shift from “wild resource harvesting” to “conservation-oriented artificial cultivation”. Studies on mixed forests and agroforestry systems further show that diversified understory layers can improve ecosystem functions. A global meta-analysis of mixed plantations showed that, compared with monocultures, tree species mixing significantly increased understory plant biomass, cover, and species richness by approximately 30%~55%, while also improving soil nutrients, nutrient availability, microbial biomass, and carbon sequestration capacity (Guo et al., 2025). On the Loess Plateau, higher taxonomic and phylogenetic diversity of understory plants was positively correlated with ecosystem multifunctionality, especially in terms of nitrogen and phosphorus cycling, water conservation, and productivity enhancement (Sha et al., 2024). As a shade-tolerant medicinal vine with relatively deep roots, *T. hemsleyanum* can serve as a structural and functional understory component in bamboo forests, fruit forests, or broad-leaved forests, improving biodiversity and promoting soil processes while reducing herbicide use and the need for intensive surface disturbance.

7.2 Economic benefits of understory cultivation of *Tetrastigma hemsleyanum*

T. hemsleyanum has high medicinal development value and market utilization potential, and its tuberous roots, as the main medicinal part, have considerable economic value. *T. hemsleyanum* is widely regarded as a high-value medicinal plant with pharmacological activities such as anti-tumor, anti-inflammatory, antiviral, antipyretic, and immunomodulatory effects. In clinical and folk applications, it is also known as a "plant antibiotic" (Zhu et al., 2020; Pang et al., 2024). At present, more than 140~150 compounds have been identified from *T. hemsleyanum,* especially flavonoids and polysaccharides. Related studies support its development and utilization in areas associated with fever, pneumonia, hepatitis, liver injury, and other diseases (Ji et al., 2020; Hu et al., 2021). Relevant reviews suggest that *T. hemsleyanum* has high economic and social value and is an important rare resource with promising prospects for the development of new drugs, functional foods, and health products (Wang et al., 2025).

Planting *T. hemsleyanum* in the understory spaces of bamboo forests, fruit forests, or broad-leaved forests can increase medicinal material income without substantially affecting the management of existing forest trees or fruit trees, thereby improving the comprehensive output per unit forestland area. For mountainous areas and regions rich in forestland resources, understory cultivation of *T. hemsleyanum* can transform idle or inefficiently used understory space into a sustainable management resource and enhance the economic returns of forestland management. Resource investigations in Zhejiang Province show that wild populations of *T. hemsleyanum* are scarce and endangered, while the artificial planting area has expanded rapidly with increasing market demand, reaching approximately 104.55 hm^2, with an expected output of about 173.91 t. This indicates a clear commercial driving force for artificial cultivation. From the broader experience of medicinal plant production, although medicinal plants are often considered "minor crops" in terms of production scale, their trade value is relatively high. They can provide important income sources for rural households and offer opportunities for farmers to shift from low-value crop management to diversified production (Mofokeng et al., 2022).

From the perspective of production input and income stability, understory cultivation can make use of natural shading conditions and reduce the cost of constructing artificial shading facilities. Understory litter and humus resources can also improve soil fertility to some extent and reduce part of the cost of soil improvement. Although *T. hemsleyanum* has a relatively long cultivation cycle, once a stable cultivation system is established, standardized management can improve survival rate and tuberous root yield, thereby generating relatively sustained returns. A profitability analysis of high-value medicinal plants in smallholder systems in South Africa showed that such cultivation generated positive net farm income, with a return on investment of 0.77 per growing period, indicating that the cultivation of high-value medicinal plants has certain profitability potential (Mbelebele et al., 2024). However, the economic benefits of understory cultivation of *T. hemsleyanum* do not depend solely on yield; they are also affected by seedling costs, management level, harvesting age, market price, medicinal material grade, and sales channels. Therefore, economic stability and sustainable resource utilization in understory cultivation of *T. hemsleyanum* should be improved through high-quality seedlings, ecological cultivation, quality control, contract sales, and origin-based brand building (Zhu et al., 2020; Pang et al., 2024).

7.3 Industrial promotion value of understory cultivation of *Tetrastigma hemsleyanum*

Understory ecological cultivation of *T. hemsleyanum* has strong industrial promotion value and is especially suitable for demonstration and application in regions with forestland resources, humid climates, and a foundation in Chinese medicinal herb cultivation. This model can integrate forestry resources, medicinal plant resources, and local specialty industries, forming a forest-medicine compound management pathway and providing a new option for agricultural transformation and understory economic development in mountainous areas. The rapid progress of phytochemical and pharmacological research on *T. hemsleyanum* also provides important support for its industrial development potential. Comprehensive studies have shown that *T. hemsleyanum* has broad pharmacological activities, including anti-tumor, antioxidant, anti-inflammatory, antiviral, hepatoprotective, immunomodulatory, and analgesic effects, and is considered a potential high-quality source for the development of new drugs and health products (Ji et al., 2020; Zhu et al., 2020; Hu et al., 2021).

From the perspective of industrial chain extension, understory cultivation of *T. hemsleyanum* can not only provide raw medicinal materials but also drive the development of related sectors such as seedling propagation, primary processing at the production site, quality testing, brand packaging, and functional product development. *T.*

hemsleyanum polysaccharides have antioxidant, anti-tumor, anti-inflammatory, immunomodulatory, and metabolic regulatory effects, showing clear application prospects in food, medicine, and cosmetics (Wang et al., 2025). New extraction and processing technologies, such as GA-BPNN-optimized flavonoid extraction and nanoparticle delivery systems, can significantly improve extraction efficiency, antioxidant capacity, anti-inflammatory activity, and bioavailability, helping promote the development of standardized preparations and functional foods. In addition, pectic polysaccharide fractions and freeze-dried products with enhanced hepatoprotective and immunomodulatory effects further expand the application space of *T. hemsleyanum* in high-end medicine and health products.

During promotion, attention should be paid to the construction of technical standards and quality control systems. The scarcity of wild resources and increasing market demand have promoted the expansion of artificial cultivation of *T. hemsleyanum*, but problems such as backward processing technology, storage difficulties, and imperfect detection methods still exist (Zhu et al., 2020). Reviews on medicinal plant commercialization point out that formalizing value chains, improving quality control, and strengthening the connection among cultivation, processing, and sales can promote rural economic development, create employment opportunities, and drive small and micro-enterprises in the transportation and processing chain (Mofokeng et al., 2022). Therefore, systematic technical protocols should be established in the future around high-quality seedling propagation, understory cultivation techniques, green pest and disease control, timely harvesting, primary processing at the production site, active compound detection, and quality traceability. Only by forming a positive linkage among ecological conservation, quality control, and market development can the understory ecological cultivation model of *T. hemsleyanum* achieve stable promotion and sustainable development (Ji et al., 2020; Hu et al., 2021; Wang et al., 2025).

8 Summary and Analysis

Understory ecological cultivation of *Tetrastigma hemsleyanum* is an important pathway for alleviating pressure on wild resources, improving the comprehensive utilization efficiency of forestland, and promoting the development of characteristic medicinal plant industries. With the rapid expansion of *T. hemsleyanum* cultivation, problems related to seedling quality control and provenance standardization have become increasingly prominent. Because *T. hemsleyanum* has a low natural fruiting rate, traditional cutting propagation produces a limited number of plants, while long-term tissue culture may induce somaclonal variation and affect genetic stability and flavonoid composition profiles. Therefore, establishing a stable and traceable seedling propagation system is particularly important. In the future, micropropagation, controlled subculture, slow-growth conservation, and stress-resistance-oriented strain selection should be integrated to screen, fix, and register superior strains, thereby constructing standardized seedling and provenance systems and providing cultivation materials with clear genetic backgrounds, stable quality, and strong adaptability for understory ecological cultivation.

From the perspective of production practice, understory cultivation of *T. hemsleyanum* still faces problems such as immature technical systems, insufficient standardization, and weak extension services. Light, temperature, humidity, soil fertility, pH, and microbial communities in understory environments are complex and variable. If canopy density, planting density, water and fertilizer management, and stand conditions are not properly matched, yield and quality fluctuations can easily occur. At present, there are still considerable differences among different cultivation bases and planting models in biomass and in the contents of key indicator compounds such as polydatin, piceatannol, resveratrol, and kaempferol. The fact that greenhouse plus stereoscopic cultivation outperforms some understory cultivation models in both yield and quality also indicates that a technical gap remains between understory ecological systems and intensive systems. Therefore, systematic technical protocols should be established for understory cultivation of *T. hemsleyanum* in terms of suitable stand selection, canopy density regulation, stereoscopic trellising, soil improvement, ecological fertilization, rhizosphere microbial regulation, and quality certification, so as to improve the reproducibility, stability, and promotion value of cultivation models.

Overall, the optimization of understory ecological cultivation of *T. hemsleyanum* should achieve coordinated integration of germplasm resources, field techniques, and industrial organization. At the technical level, experience from controlled-environment and greenhouse systems can be used as a reference to promote biomass accumulation and active compound formation through the regulation of light intensity and spectrum, temperature and humidity, nutrient supply, and moderate abiotic stress. Meanwhile, canopy-density zoning, stereoscopic trellising, the application of organic amendments such as biochar, and rhizosphere microbial management can be used to gradually construct an understory ecological cultivation environment close to a "semi-controlled" system. At the industrial level, a coordinated management mechanism between forestry and traditional Chinese medicine sectors should be established, the quality certification and regulatory system for understory-cultivated medicinal materials should be improved, and regional standardized demonstration bases should be developed to benchmark understory ecological cultivation against greenhouse and vertical farming models in terms of quality. Through the integration of contract farming, quality traceability, brand building, and processing and marketing systems, understory ecological cultivation of *T. hemsleyanum* is expected to form a sustainable development pathway from technical optimization to large-scale promotion and from resource conservation to industrial value enhancement.

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.

References

Bai Y., Chen W., Liu S.Z., Xu L.Y., Li Z., and Liu B., 2021, Physiological responses of the *Tetrastigma hemsleyanum* plant under different color films, HortScience, 56(6): 672-677.
https://doi.org/10.21273/hortsci15690-21

Burgess A.J., Cano M.E., and Parkes B., 2022, The deployment of intercropping and agroforestry as adaptation to climate change, Crop and Environment, 1(2): 145-160.
https://doi.org/10.1016/j.crope.2022.05.001

Chen S.J., Zhang H., Wang X.S., Xu Y.S., Li X.S., Jiang Y., Lu Y.Y., and Tu P.F., 2024, Spatial distribution of differential metabolites in different parts of *Tetrastigma hemsleyanum* Diels et Gilg by ultrahigh-performance liquid chromatography/mass spectrometry and desorption electrospray ionization mass spectrometry imaging, Arabian Journal of Chemistry, 17: 105900.
https://doi.org/10.1016/j.arabjc.2024.105900

Cheng H., Hu W., Zhou X., Dong R., Liu G., Li Q., and Zhang X., 2022, Fruit tree-legume-herb intercropping orchard system is an effective method to promote the sustainability of systems in a karst rocky desertification control area, Forests, 13(10): 1536.
https://doi.org/10.3390/f13101536

Chu C., Lv Y., Yao X., Ye H., Li C., Peng X., Gao Z., and Mao K., 2024, Revealing quality chemicals of *Tetrastigma hemsleyanum* roots in different geographical origins using untargeted metabolomics and random-forest based spectrum-effect analysis, Food Chemistry, 449: 139207.
https://doi.org/10.1016/j.foodchem.2024.139207

Deng J., Fang S., Fang X., Jin Y., Kuang Y., Lin F., Liu J., Nie Y., Ouyang S., Ren J., Tie L., Tang S., Tan X., Wang X., Fan Z., Wang Q., Wang H., and Liu C., 2023, Forest understory vegetation study: current status and future trends, Forestry Research, 3: 6.
https://doi.org/10.48130/fr-2023-0006

Fu L., Zhao L., Lyu H., Yan M., Zheng Y., Liu Q., Jin L., Cheng J., Lu T., and Wang L., 2019, Effects of nitrogen level on growth of *Tetrastigma hemsleyanum* and phytochemical content and antioxidant activity in stems and leaves, Zhongguo Zhong Yao Za Zhi, 44(4): 696-702.
https://doi.org/10.19540/j.cnki.cjcmm.20181204.006

Guo B., Mao Y., Yang L., Li D., Zhang H., and Zhang W., 2026, Problems and development recommendations for understory medicinal herb cultivation, Zhongguo Zhong Yao Za Zhi, 51(2): 596-600.
https://doi.org/10.19540/j.cnki.cjcmm.20250815.401

Guo J., Kneeshaw D., Peng C., Wu Y., Feng L., Qu X., Wang W., Pan C., and Feng H., 2025, Positive effects of species mixing on biodiversity of understory plant communities and soil health in forest plantations, Proceedings of the National Academy of Sciences of the United States of America, 122(11): e2418090122.
https://doi.org/10.1073/pnas.2418090122

Guo W., Yang Z., Hou Z., Hou Z., Qi Z., Sun Y., Ding X., Hu S., and Hu J., 2019, A comprehensive review of a Chinese folk herbal species *Tetrastigmae hemsleyanum* with multiplicity of pharmacological effects, Chinese Traditional Medicine Journal, 2(1): 1-19.

Hong C., Shao Q., Qin W., Zhang J., Wei B., Shen D., Zheng B., and Guo H., 2021, Bacterial communities are associated with the tuber size of *Tetrastigma hemsleyanum* in stony soils, Biology and Fertility of Soils, 57: 373-388.
https://doi.org/10.1007/s00374-020-01530-4

Hu W.Y., Jiang M.D., Liang Z.S., and Xia P.G., 2023, The stereoscopic planting mode improved the quality and yield of *Tetrastigma hemsleyanum*, South African Journal of Botany, 157: 44-52.
https://doi.org/10.1016/j.sajb.2023.03.048

Hu W.Y., Zheng Y.J., Xia P.G., and Liang Z.S., 2021, The research progresses and future prospects of *Tetrastigma hemsleyanum* Diels et Gilg: a valuable Chinese herbal medicine, Journal of Ethnopharmacology, 271: 113836.
https://doi.org/10.1016/j.jep.2021.113836

Ji T., Ji W., Wang J., Chen H., Peng X., Cheng K., Qiu D., and Yang W., 2020, A comprehensive review on traditional uses, chemical compositions, pharmacology properties and toxicology of *Tetrastigma hemsleyanum*, Journal of Ethnopharmacology, 264: 113247.
https://doi.org/10.1016/j.jep.2020.113247

Jiang L.T., Zhang S.B., Liu S.Z., Geng D.J., Li M.M., Xia J.Q., Gu Y.W., Huang C.C., Li S., Wang H.Z., and Yan B., 2023, Linking soil fertility, enzyme activity, and flavonoid-related enzymes to growth and quality of *Tetrastigma hemsleyanum* Diels et Gilg amended with pyrogenic organic matter and organic fertilizer, Journal of Soils and Sediments, 24: 1183-1193.
https://doi.org/10.1007/s11368-023-03696-4

Li X., Liang H., Liang J., Huang Y., and Liang Y., 2025, Understory cultivation of medicinal plants promotes sustainable forestry development, Agroforestry Systems, 99(2): 39.
https://doi.org/10.1007/s10457-025-01141-8

Luo Y., Yang Y., Yang X., Sun C., and Chen H., 2022, Quality evaluation of *Tetrastigma hemsleyanum* different parts based on quantitative analysis of 42 bioactive constituents combined with multivariate statistical analysis, Phytochemical Analysis, 33(5): 754-765.
https://doi.org/10.1002/pca.3127

Mbelebele Z., Mdoda L., and Ntlanga S., 2024, Growing wealth from nature: Analyzing the profitability and determinants of high-value medicinal plants in smallholder production systems, Cogent Economics and Finance, 12(1): 2426536.
https://doi.org/10.1080/23322039.2024.2426536

Mofokeng M.M., Du Plooy C.P., Araya H.T., Amoo S.O., Mokgehle S.N., Pofu K.M., and Mashela P.W., 2022, Medicinal plant cultivation for sustainable use and commercialisation of high-value crops, South African Journal of Science, 118(7/8): 1-7.
https://doi.org/10.17159/sajs.2022/12190

Pang J.H., Xiong Y.P., Zeng Y.J., Chen X.H., Li J.R., Zhang X.H., Li Y., Wu K.L., Zeng S.J., da Silva J.A.T., and Ma G.H., 2024, Shoot organogenesis from *Tetrastigma hemsleyanum* leaf and petiole explants, and subsequent plant regeneration and acclimatization, Journal of Plant Growth Regulation, 43: 4782-4795.
https://doi.org/10.1007/s00344-024-11433-5

Paut R., Garreau L., Ollivier G., Sabatier R., and Tchamitchian M., 2024, A global dataset of experimental intercropping and agroforestry studies in horticulture, Scientific Data, 11: 5.
https://doi.org/10.1038/s41597-023-02831-7

Peng L.X., Li H.J., Yang L.J., Liang Z.S., and Zhang X.D., 2025, Exploring the metabolic and transcriptomic profiles of *Tetrastigma hemsleyanum* for tissue-specific compound accumulation, Frontiers in Plant Science, 16: 1478061.
https://doi.org/10.3389/fpls.2025.1478061

Sha G.L., Yu H., Chen Y.X., Ren K., Xin P.C., Guo X., Xiao J., and Fu Y.C., 2024, Understory plant diversity supports the delivery of ecosystem multifunctionality on the *Loess Plateau*: a comparative of plantations and natural forests, Journal of Environmental Management, 371: 123191.
https://doi.org/10.1016/j.jenvman.2024.123191

Shi Y., Yang L., Yu M., Li Z., Ke Z., Qian X., Ruan X., He L., Wei F., Zhao Y., and Wang Q., 2022, Seasonal variation influences flavonoid biosynthesis path and content, and antioxidant activity of metabolites in *Tetrastigma hemsleyanum* Diels & Gilg, PLOS ONE, 17(4): e0265954.
https://doi.org/10.1371/journal.pone.0265954

Soffiatti P., Fort E., Heinz C., and Rowe N., 2022, Trellis-forming stems of a tropical liana *Condylocarpon guianense* (Apocynaceae): A plant-made safety net constructed by simple “start-stop” development, Frontiers in Plant Science, 13: 1016195.
https://doi.org/10.3389/fpls.2022.1016195

Son C., and Giang D., 2026, Effects of using trellis work on survival and growth of medicinal plant (*Codonopsis javanica*), International Journal of Forestry and Horticulture, 12(1): 12-17.
https://doi.org/10.20431/2454-9487.1201002

Wang L.H., Wang Q., Dong C.Q., Teng C.C., Wang L., Zhou Y.Y., Yang B.Y., Kuang H.X., and Sun Y.P., 2025, Exploring *Tetrastigma hemsleyanum* polysaccharides: a recent advance in preparation, structural features, bioactivities, and potential application prospects, International Journal of Biological Macromolecules, 310(4): 143477.
https://doi.org/10.1016/j.ijbiomac.2025.143477

Wang Y.H., Zhang L., Zhou Y.C., Ma W.X., Li M.Y., Guo P., Feng L., and Fu C.X., 2023, Using landscape genomics to assess local adaptation and genomic vulnerability of a perennial herb *Tetrastigma hemsleyanum* (Vitaceae) in subtropical China, Frontiers in Genetics, 14: 1150704.
https://doi.org/10.3389/fgene.2023.1150704

Xiang T.H., Li J.S., Bao S.Y., Xu Z.X., Wang L.Z., Long F.Z., and He C.J., 2021, Digital RNA-seq transcriptome plus tissue anatomy analyses reveal the developmental mechanism of the calabash-shaped root in *Tetrastigma hemsleyanum*, Tree Physiology, 41(9): 1729-1748.
https://doi.org/10.1093/treephys/tpab024

Xie Z., Yang C., Li M., Zhang Z., Wu Y., Gu L., and Peng X., 2022, Nitric oxide crosstalk with phytohormone is involved in enhancing photosynthesis of *Tetrastigma hemsleyanum* for photovoltaic adaptation, Frontiers in Plant Science, 13: 852956.
https://doi.org/10.3389/fpls.2022.852956

Xu L.Y., Liu S.Z., Bai Y., Ding H.M., Hu X., Wu X.Y., Xu H.L., and Zheng B., 2018, Effects of light intensity treatments on photosynthetic characteristics in *Tetrastigma hemsleyanum*, Journal of Zhejiang A&F University, 35(3): 467-475.
https://doi.org/10.11833/j.issn.2095-0756.2018.03.010

Yu P., Weng S., Zhang B., Huang Y., and Xu F., 2025, Diverse climbing strategies in aroid vines: functional adaptations and environmental drivers, Frontiers in Plant Science, 16: 1692444.
https://doi.org/10.3389/fpls.2025.1692444

Zhang S., Yang X., Li D., Li S., Chen Z., and Wu J., 2022, A meta-analysis of understory plant removal impacts on soil properties in forest ecosystems, Geoderma, 426: 116116.
https://doi.org/10.1016/j.geoderma.2022.116116

Zhang X.P., Gao G.B., Wu Z.Z., Wen X., Bian F.Y., and Yang C., 2019a, Biochar-based organic fertilizer application rates for *Tetrastigma hemsleyanum* planted under Moso bamboo, Journal of Forestry Research, 31: 1813-1821.
https://doi.org/10.1007/s11676-019-00965-2

Zhang X.P., Gao G.B., Wu Z.Z., Wen X., Zhong H., Zhong Z.K., Bian F.Y., and Gai X., 2019b, Agroforestry alters the rhizosphere soil bacterial and fungal communities of moso bamboo plantations in subtropical China, Applied Soil Ecology, 143: 192-200.
https://doi.org/10.1016/j.apsoil.2019.07.019

Zhang X., Gao G., Wu Z., Wen X., Zhong H., Zhong Z., Yang C., Bian F., and Gai X., 2019c, Responses of soil nutrients and microbial communities to intercropping medicinal plants in moso bamboo plantations in subtropical China, Environmental Science and Pollution Research, 27: 2301-2310.
https://doi.org/10.1007/s11356-019-06750-2

Zhao G., Liu W.L., Zhu H., Duan H.P., Nie J.N., Hong S.R., and Wen J., 2024, The influence of prolonged but low intensity blue light on the physiological properties of root tubers and the accumulation of flavonoids in *Tetrastigma hemsleyanum* Diels et Gilg, Plant Physiology and Biochemistry, 213: 108824.
https://doi.org/10.1016/j.plaphy.2024.108824

Zhu R.Y., Xu X.F., Ying J.L., Cao G., and Wu X., 2020, The phytochemistry, pharmacology, and quality control of *Tetrastigma hemsleyanum* Diels and Gilg in China: a review, Frontiers in Pharmacology, 11: 550497.
https://doi.org/10.3389/fphar.2020.550497

Medicinal Plant Research 2026, Vol.16, No.1, 52-68
http://hortherbpublisher.com/index.php/mpr

Research Insight Open Access

Hangbaiju Tea Beverages and Industrial Chain Extension

Weiying Gao [1,2]
1 Tongxiang Lukang Chrysanthemum Industry Co. Ltd., Tongxiang 314501, Zhejiang, China
2 Zhejiang Agronomist College, Hangzhou, 310021, Zhejiang, China
Corresponding email: 1304837229@qq.com
Medicinal Plant Research, 2026, Vol.16, No.1 doi: 10.5376/mpr.2026.16.0004
Received: 25 Jan., 2026
Accepted: 10 Mar., 2026
Published: 24 Mar., 2026

Preferred citation for this article:
Gao W.Y., 2026, Hangbaiju tea beverages and industrial chain extension, Medicinal Plant Research, 16(1): 52-68 (doi: 10.5376/mpr.2026.16.0004)

Abstract This study explores the development of Hangbaiju tea beverage products and the extension of the industrial chain. Hangbaiju is a traditional medicinal and edible plant in China and a characteristic agricultural product of Zhejiang Province, with significant medicinal, beverage, cultural, and economic value. With the growing popularity of health-conscious consumption and the rapid development of the new-style tea beverage market, the development of Hangbaiju tea beverage products and industrial chain extension have become important directions for promoting industrial transformation and upgrading. This paper systematically analyzes the upgrading of traditional Hangbaiju tea beverage products, the development of compound tea beverages, and the innovation of new-style tea beverage products. It also summarizes key processing technologies, including raw material quality control, tea beverage processing and flavor preservation, and product quality and safety control. On this basis, the paper further discusses the extension models of the Hangbaiju industrial chain toward upstream standardized cultivation bases, midstream deep-processed products, and downstream sales channels and consumption scenarios. It also proposes development pathways involving regional public brand building, differentiated product positioning, diversified marketing model innovation, and integrated development with agriculture, culture, tourism, health and wellness, educational programs, and cultural communication. The study suggests that the Hangbaiju tea beverage industry should be supported by technological innovation, standardized production, brand building, and industrial integration, so as to promote the transformation of Hangbaiju resources from traditional dried flower products into standardized, functional, branded, and high-value tea beverage products, thereby providing a reference for the development of characteristic medicinal and edible resources and the high-quality development of regional agricultural industries.
Keywords Hangbaiju; tea beverage product development; industrial chain extension; deep processing; brand building

1 Introduction

Hangbaiju (*Chrysanthemum morifolium* Ramat.) is an important representative of traditional medicinal and edible plants in China and one of Zhejiang Province's characteristic agricultural products. As a chrysanthemum variety with a long history of cultivation and application, Hangbaiju has long been consumed as flower tea and used in folk medicine and nutritional health products, reflecting considerable cultural, health-related, and economic value. Studies have shown that Hangbaiju is rich in flavonoids and possesses strong antioxidant and anti-inflammatory activities, making it an important plant resource for the development of functional foods and tea beverage products (Lu and Liu, 2025). Meanwhile, the quality of Hangbaiju is closely related to its geographical origin. Technologies such as hyperspectral imaging combined with chemometrics have been used for rapid and non-destructive origin identification, providing technical support for quality control and brand building of geographical indication products. In recent years, with the continuous advancement of the rural revitalization strategy and high-quality development of characteristic agriculture, major producing areas such as Tongxiang, Zhejiang, have relied on ecological conditions, cultivation foundations, and regional brand advantages to gradually form a Hangbaiju industry integrating cultivation, processing, sales, and cultural communication. However, overall, the Hangbaiju industry still mainly relies on raw material sales and traditional dried flower products, and its product added value and market competitiveness still need to be further improved.

With the improvement of living standards and the popularization of health-conscious consumption, consumer demand for natural, green, and functional beverages has continued to grow. China's tea beverage industry has developed into a large-scale modern consumer sector, and the tea beverage market is shifting from traditional thirst-quenching consumption toward standardization, branding, quality orientation, and globalization. New-style tea beverage chains are also expanding in both domestic and overseas markets. Tea beverages have become an important part of leisure consumption, especially among young consumers, and the industry is characterized by intensified competition, rapid product iteration, and increasing demand for differentiated ingredients and flavors (Huang, 2025). At the same time, the tea industry is also facing the need to transform toward low-carbon, ecological, and deep-processing development. Policy and market forces are jointly promoting the extension of the tea industrial chain and the development of health drinks, functional ingredients, and related derivative products (Zhang et al., 2024). Currently, consumer demand is gradually shifting from traditional hot-brewed tea toward convenient, standardized, and ready-to-drink tea beverage products, while still emphasizing health attributes and natural sources (Lu and Liu, 2025; Yang, 2025). Against this background, Hangbaiju, which combines medicinal value, beverage value, and regional cultural characteristics, has ushered in an important opportunity for transformation from traditional flower tea to modern functional tea beverages.

Hangbaiju has the characteristics of relatively high safety, refreshing flavor, and clear functional components, which align well with consumer demand for natural antioxidant, anti-inflammatory, and plant-based health beverages (Lu and Liu, 2025). In addition to traditional chrysanthemum tea, new products such as compound herbal teas, cold-brew teas, ready-to-drink tea beverages, and chrysanthemum functional drinks have continued to emerge, further expanding the consumption scenarios and market space of Hangbaiju. Scholars have pointed out that Chinese herbal teas and flower teas should transform from loose and traditional forms into fast, convenient, and standardized beverage formats, and reach young consumers and international markets through modern channels such as e-commerce and social media (Yang, 2025). Therefore, the development of Hangbaiju tea beverage products is not only a modern utilization of traditional medicinal and edible resources, but also an important pathway connecting traditional herbal culture, modern lifestyles, and global health consumption trends. Although market demand continues to expand, the Hangbaiju industry still faces problems such as insufficient product development depth, obvious product homogenization, limited deep-processing capacity, weak coordination between upstream and downstream sectors, and insufficient influence of regional public brands. These factors restrict, to some extent, the value enhancement and sustainable development of the Hangbaiju industry.

This study explores the development of Hangbaiju tea beverage products and industrial chain extension. On the basis of analyzing Hangbaiju's resource advantages, industrial foundation, and changes in market demand, it systematically reviews the development directions of Hangbaiju tea beverage products, key processing technologies, industrial chain extension pathways, and strategies for brand promotion and integrated development. Existing studies on Hangbaiju have mostly focused on component analysis, extraction technologies, and functional evaluation, and have verified its application value in food forms such as tea beverages and nutritional drinks. However, research integrating these technical foundations with industrial chain upgrading remains relatively insufficient, particularly in areas such as standardized raw material base construction, low-carbon processing, diversified product development, brand building, and domestic and international market expansion. Therefore, this study aims to clarify feasible pathways for transforming Hangbaiju from traditional dried flower products into standardized, functional, and branded tea beverage products, promote the high-value utilization of Hangbaiju resources, support the development of regional characteristic industries, enrich the functional tea beverage product system, and provide a reference for the transformation, upgrading, and global expansion of Chinese traditional tea and herbal beverage industries.

2 Development Directions of Hangbaiju Tea Beverage Products

2.1 Upgrading traditional hangbaiju tea beverage products

Traditional Hangbaiju tea beverages are mainly consumed by brewing dried flowers and are characterized by simple preparation, a broad consumer base, and an elegant floral flavor. However, with growing consumer demand for high-quality, convenient, branded, and functional products, single-form flower tea products can no longer fully reflect the comprehensive value of Hangbaiju resources. Studies on functional beverages indicate that consumers are increasingly concerned with natural bioactive compounds, health benefits, and product stability. Therefore, traditional herbal beverages need to enhance their market competitiveness through clarification of functional components, standardization of processing technologies, and innovation in product forms (Gupta et al., 2023). Hangbaiju is rich in flavonoids and exhibits strong antioxidant and anti-inflammatory activities, making it an important raw material for developing functional foods and tea beverages (Lu and Liu, 2025). Consequently, while retaining its natural floral aroma and health-promoting properties, the upgrading of traditional Hangbaiju tea beverages should focus on defining active compounds, quality markers, and processing standards, thereby transforming conventional brewed flower tea into modern tea beverages with clear functional attributes and technological support.

In terms of product forms, portable products such as individually packaged tea bags, pyramid tea bags, freeze-dried flower tea, and ready-to-drink (RTD) Hangbaiju tea can be developed to meet the diverse needs of office, travel, household, and gift-giving scenarios. Research has shown that green extraction technologies, including ultrasonic-assisted extraction and enzymatic extraction, can increase flavonoid yields from Hangbaiju while helping maintain the stability of active compounds, thereby providing technical support for the development of high-content, low-additive Hangbaiju tea beverages (Gupta et al., 2023; Lu and Liu, 2025). Meanwhile, modern extraction methods, non-thermal sterilization, improved packaging, and flavor optimization technologies can further enhance sensory quality, shelf life, and brewing convenience (Tong et al., 2019; Liu et al., 2024; Qin and Zhou, 2024). Through raw material grading, packaging design, geographical indication certification, and traceability system construction, traditional Hangbaiju tea can be transformed from a low-value bulk product into a high-value beverage characterized by regional identity, quality assurance, and brand recognition (Zhang et al., 2022).

2.2 Development of compound hangbaiju tea beverage products

Compound tea beverages represent an important development direction in the functional beverage market. Beverages combining multiple plant resources and functional ingredients can integrate bioactive substances such as polyphenols, vitamins, minerals, and amino acids, enriching sensory characteristics while providing synergistic health benefits (A'yuni et al., 2022; Gupta et al., 2023; Onsun et al., 2025; Munarso et al., 2026). With its mild floral aroma and rich flavonoid content, Hangbaiju is suitable as a core ingredient in compound tea beverages. It can be blended with green tea, white tea, oolong tea, matcha, herbal extracts, or fruit ingredients to develop functional beverages targeting antioxidant, liver-protective, soothing, or immune-support functions (Yang et al., 2022; Najman et al., 2023; Lu and Liu, 2025). For example, blending Hangbaiju with green tea or white tea can enhance flavor complexity, while combining it with medicinal and edible ingredients such as goji berries, cassia seeds, honeysuckle, and monk fruit can create eye-care, soothing, and wellness-oriented tea beverages.

From a technological perspective, the development of compound Hangbaiju beverages requires not only appropriate ingredient combinations but also solutions to issues related to solubility, stability, and flavor compatibility among multiple active compounds. Research has demonstrated that the rational blending of plant extracts can increase total phenolic content, antioxidant capacity, and consumer acceptance of color, aroma, and taste, providing valuable guidance for Hangbaiju beverage formulation (A'yuni et al., 2022; Maulida et al., 2024). Encapsulation and embedding technologies can improve the dispersion of active ingredients and protect heat-sensitive flavonoids, helping maintain stability in aqueous systems and during storage (Gupta et al., 2023; Munarso et al., 2026). In addition, selecting suitable sweeteners, acidulants, and natural flavorings can harmonize the floral aroma and slight bitterness of Hangbaiju with fruity, tea-like, or spicy flavor profiles. In the future, product lines such as beauty-enhancing teas for women, eye-care teas for office workers, wellness teas for older adults, and recovery beverages for athletes can be developed according to seasonal trends, consumer preferences, and target demographics, thereby enhancing product segmentation and market competitiveness.

2.3 Innovation of new-style hangbaiju tea beverages

With the rapid development of new-style tea beverages and functional drinks, the application scenarios of Hangbaiju have expanded from traditional brewed tea to ready-to-drink beverages, cold-brew tea, sparkling beverages, functional shots, instant powdered drinks, and fermented beverages. Related studies suggest that the new-style tea beverage market is evolving toward personalization, fashion, health orientation, and scenario-based consumption, with consumers paying greater attention to low-sugar formulations, natural ingredients, functionality, and cultural expression (Liu et al., 2024; Qin and Zhou, 2024; Huang, 2025; Yang, 2025). The high-value utilization of Hangbaiju flavonoids has enabled its application not only in traditional RTD teas but also in functional beverages, nutritional drinks, and cross-category beverage products (Lu and Liu, 2025). For example, cold-brew Hangbaiju tea can better preserve its fresh floral aroma and align with the trend of light wellness consumption; low-sugar or sugar-free RTD Hangbaiju beverages can meet consumer demands for sugar control; and sparkling Hangbaiju beverages can enhance drinking experiences through flavor innovation and appeal to younger consumers.

In terms of processing and product innovation, Hangbaiju beverages can draw inspiration from products such as matcha, kombucha, and fermented teas to create a more diversified product portfolio. Studies have shown that matcha can be combined with proteins, inulin, and other functional ingredients to develop convenient nutritional beverages, while kombucha and novel fermented teas can generate distinctive flavors and potentially increase levels of organic acids and γ-aminobutyric acid (GABA) through fermentation (Tong et al., 2019; Najman et al., 2023; Onsun et al., 2025). Therefore, Hangbaiju can be explored for use in instant powders, plant-based mixed beverages, chrysanthemum-fermented drinks, and low-sugar functional beverages. Moreover, technologies such as ultra-high-temperature sterilization, aseptic filling, microencapsulation, and nanoencapsulation can improve the stability and bioavailability of active compounds in RTD products, ensuring flavor quality and functional properties during storage and transportation (A'yuni et al., 2022; Gupta et al., 2023; Munarso et al., 2026).

In the future, innovation in Hangbaiju tea beverages should also be closely integrated with digital consumption models and cultural storytelling. Through co-branded product development, customized packaging design, online interactive marketing, and regional cultural IP creation, brand communication can be strengthened, transforming Hangbaiju beverages from traditional herbal infusions into scenario-based functional drinks with modern consumer appeal and international market potential (Qin and Zhou, 2024; Huang, 2025; Yang, 2025). At the same time, continuous development of new products featuring antioxidant, soothing, anti-fatigue, and light wellness functions should be pursued based on advances in functional ingredient research and evolving consumer demands, thereby enhancing technological content and market value while providing new growth drivers for the transformation and upgrading of the Hangbaiju industry.

3 Key Processing Technologies for Hangbaiju Tea Beverages

3.1 Raw material quality control technologies

The quality of Hangbaiju tea beverage products first depends on the quality of raw materials. Therefore, establishing a scientific, stable, and standardized raw material quality control system is the foundation for ensuring product quality and industrialized production. The contents of flavonoids, polyphenols, amino acids, pigments, and volatile aromatic compounds in Hangbaiju flowers are greatly affected by variety, cultivation environment, harvest period, and primary processing methods (Aaqil et al., 2023; Tang et al., 2025). In production, high-quality local varieties should be prioritized, standardized cultivation techniques should be adopted, and water-fertilizer management, pest and disease control, and harvesting standards should be unified to improve raw material quality stability. At the same time, standardized cultivation bases should be established to control the use of pesticides and chemical fertilizers at the source, reduce exogenous contamination risks, and ensure that raw materials meet the requirements for green food, functional beverages, and deep-processed product development.

With the development of quality control technologies for tea and floral raw materials, rapid and non-destructive detection methods such as spectroscopy, computer vision, chromatographic analysis, and electrochemical detection are increasingly being used for real-time evaluation of raw material appearance, chemical composition, and contaminant levels (Bhargava et al., 2022; Moreira et al., 2024). Among them, spectroscopy and improved chromatographic techniques can rapidly determine polyphenols, amino acids, pigments, and inorganic/organic contaminants, improving detection sensitivity and accuracy. Computer vision combined with deep learning can classify chrysanthemum tea according to type and flowering stage, providing technical support for appearance grading, authenticity identification, and pre-processing screening of Hangbaiju flower buds (Figure 1) (Liu et al., 2020; Yu et al., 2020). Therefore, Hangbaiju raw material quality control should shift from traditional sensory judgment to a comprehensive evaluation model integrating "sensory evaluation+physicochemical testing + intelligent identification."

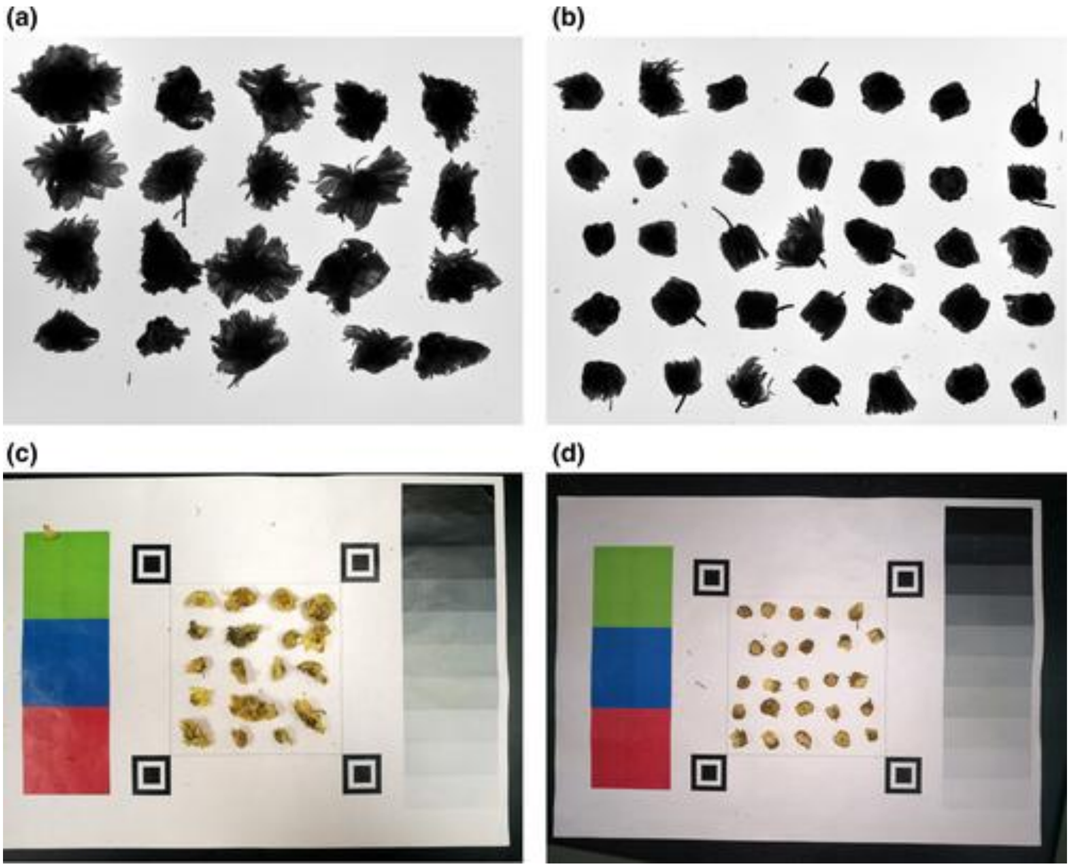


Figure 1 Representative contour images of chrysanthemum teas (Adopted from Liu et al., 2020)
Image caption: (a) Hangbaiju by a gel imager, (b) Hangtaiju by a gel imager, (c) Hangbaiju by a smartphone, and (d) Hangbaiju by a smartphone (Adopted from Liu et al., 2020)

Harvest period and primary processing conditions have important effects on Hangbaiju quality formation. Generally, harvesting at an appropriate flowering stage can yield higher active ingredient contents and better appearance quality. After harvesting, grading should be carried out promptly according to flower diameter, flower integrity, color, impurity content, and active component levels, so as to achieve differentiated utilization of high-quality and ordinary raw materials. Studies have shown that optimized kill-green and drying processes can shorten drying time, improve color, and enhance the retention of phenolics, sugars, amino acids, volatile compounds, and antioxidant activity (Prabawa et al., 2023; Xu et al., 2024; Leelapattana and Asavarachan, 2025). Therefore, standardized cultivation, timely harvesting, graded primary processing, intelligent detection, and quality traceability should be integrated to build a raw material quality control system covering cultivation and processing, thereby laying a foundation for the development of high-quality Hangbaiju tea beverage products.

3.2 Tea beverage processing and flavor preservation technologies

Processing technology is an important factor determining the quality of Hangbaiju tea beverage products. Traditional Hangbaiju processing mainly involves steaming, kill-green treatment, and drying, aiming to preserve flower shape, color, and aroma characteristics. With increasing market demand for high-quality tea beverage products, modern processing technologies are gradually moving toward precision, low-temperature operation, and intelligence. Studies on tea beverage processing technologies have shown that non-thermal or mild processing methods, such as cold extraction and ultrasonic extraction, help improve the extraction efficiency of active components while reducing the degradation of polyphenols and aroma compounds (Liang et al., 2021; Liang et al., 2022). For Hangbaiju tea beverages, extraction temperature, extraction time, solid-liquid ratio, and concentration conditions should be reasonably optimized according to product type, so as to ensure sufficient release of functional components such as flavonoids and polyphenols while maintaining elegant floral aroma and a mild taste.

Drying and flavor preservation are key technologies in Hangbaiju tea beverage processing. Studies have shown that the developmental stage of floral materials and drying methods significantly affect the levels of polyphenols, amino acids, and volatile compounds in floral beverages, and suitable drying conditions contribute to better sensory quality (Xu et al., 2024). Hot-air drying, vacuum freeze-drying, and medium- to low-temperature drying can reduce damage caused by high temperatures to active components and aromatic substances to varying degrees, improving color retention, rehydration performance, and aroma stability. Among them, freeze-drying can better preserve the original structure and natural aroma of flowers, making it suitable for high-end Hangbaiju tea beverages and premium flower tea products. Hot-air drying is more suitable for large-scale production, where the balance between cost and quality can be achieved through temperature and time optimization.

Flavor preservation is also important during tea beverage production and storage. The characteristic fragrance of Hangbaiju mainly comes from volatile aromatic compounds, which are prone to loss through oxidation, light exposure, and temperature fluctuations during processing, concentration, sterilization, and storage. Research indicates that extraction temperature, extraction time, tea-to-water ratio, and mixing procedures are core parameters affecting the sensory quality of tea beverages; improper control may weaken characteristic aroma and lead to an imbalance among bitterness, sweetness, and umami (Moreira et al., 2024). Therefore, microencapsulation, low-temperature concentration, aseptic filling, antioxidant protection systems, and improved packaging can be used to reduce aroma loss and enhance clarity, color, and flavor stability during shelf life (Liang et al., 2021; Liang et al., 2022). In the development of compound Hangbaiju tea beverage products, analytical chemistry and sensory evaluation should also be combined to optimize the ratio of Hangbaiju with tea leaves, fruit juice, or medicinal and edible ingredients, thereby forming a rich and stable flavor system (Geng et al., 2026).

3.3 Product quality and safety control technologies

As consumers pay increasing attention to food safety and the quality of functional beverages, establishing a complete quality and safety control system has become an important guarantee for the development of the Hangbaiju tea beverage industry. High-value Hangbaiju tea beverages should meet multidimensional quality requirements covering chemical composition, microbiological indicators, contaminant levels, and sensory quality. At the raw material stage, testing for pesticide residues, heavy metals, microorganisms, and exogenous contaminants should be strengthened to ensure compliance with food safety standards. Emerging methods such as spectroscopy, electrochemical detection, nanozymes, computer vision, and chromatography can rapidly, cost-effectively, and non-destructively or minimally destructively determine physical, chemical, and contaminant indicators in tea products, and can be applied throughout the whole process from fresh raw material intake to final product evaluation (Yu et al., 2020; Bhargava et al., 2022). Among them, advanced chromatographic techniques can precisely quantify pesticides, heavy metals, and other exogenous risks, providing technical support for the safety control of Hangbaiju tea beverages.

At the processing stage, Good Manufacturing Practices (GMP), Sanitation Standard Operating Procedures (SSOP), and the Hazard Analysis and Critical Control Point (HACCP) management system should be strictly implemented to monitor key links such as raw material acceptance, pretreatment, extraction, concentration, blending, filling, sterilization, packaging, storage, and transportation throughout the process. Studies have shown that HACCP can identify critical control points and critical limits through hazard analysis, and control biological, chemical, and physical risks through monitoring and corrective measures, making it an important tool for tea-producing enterprises to improve food safety management (Kristiningrum et al., 2023). For Hangbaiju tea beverages, key control points should include raw material contamination, microbial load of extracts, sterilization intensity, packaging sealability, and storage and transportation temperature. Automated production equipment should also be used to reduce human contamination and improve product consistency.

At the circulation and consumption stages, digital technologies such as QR-code traceability systems, the Internet of Things, big data, blockchain, and online sensors can be used to enable full-process product information inquiry and real-time quality monitoring. Research on intelligent technologies shows that big data, the Internet of Things, and blockchain can support the development of transparent, traceable, and sustainable tea industrial chains, enabling quality information connectivity from plantation to end product. Consumers can use traceability systems to understand the source of Hangbaiju raw materials, cultivation processes, processing techniques, and quality test results, thereby enhancing consumer trust. In the future, with the continuous improvement of intelligent detection technologies and digital management platforms, the Hangbaiju tea beverage industry should gradually establish a quality and safety management system covering cultivation, processing, and sales, providing solid support for high-quality industrial development and brand building.

4 Industrial Chain Extension Models for the Hangbaiju Industry

4.1 Construction of standardized upstream cultivation bases

The foundation of industrial chain extension lies in the stable, high-quality, and sustainable supply of raw materials, while the construction of standardized cultivation bases is an important link in enhancing the competitiveness of the Hangbaiju industry. At present, some Hangbaiju cultivation still relies on fragmented operations, with differences in seedling selection, field management, harvesting standards, and primary processing methods, resulting in insufficient stability of raw material quality. Studies on the tea industry and ecological tea industrial chains indicate that fragmented smallholder production restricts quality control and modern management, whereas integrating scattered plots through land transfer, trusteeship management, or cooperative models helps achieve intensive operation, effective pest and disease control, and efficient resource utilization (Zhang et al., 2024). Therefore, upstream Hangbaiju base construction should promote large-scale production through organizational models such as “enterprise+cooperative+farmers,” establish unified cultivation technical specifications, quality standard systems, and harvesting management systems, and improve the consistency of raw material quality.

In the construction of cultivation bases, efforts should be made to strengthen the breeding of superior varieties and the establishment of seedling propagation systems, so as to improve varietal purity, stress resistance, and the stability of active components in Hangbaiju. Related studies have shown that low-carbon ecological tea production can reduce environmental burdens while enhancing product value and ecological resilience by expanding plantation scale, optimizing planting density, and promoting organic or reduced-input production systems (Zhang et al., 2024). For Hangbaiju, green cultivation technologies should be promoted, the use of chemical pesticides and fertilizers should be reduced, and integrated pest management, water-fertilizer integration, ecological certification, and low-carbon production methods should be adopted to improve raw material safety and market recognition. Meanwhile, the stable supply of functional components such as Hangbaiju flavonoids is an important foundation for subsequent functional tea beverage development; therefore, upstream bases should also establish quality control standards based on raw material specifications for functional beverages (Lu and Liu, 2025).

With the development of digital agriculture, information-based management technologies are increasingly being applied in standardized cultivation bases. Research on whole agricultural industrial chains shows that agricultural production capacity, technology extension, informatization, marketization, and risk protection jointly affect industrial chain performance (Ying et al., 2022). Internet of Things sensors, drone monitoring, big data platforms, and intelligent management systems can be used to monitor soil conditions, meteorological factors, input use, crop growth, and yield levels in real time, thereby realizing precision cultivation management (Zhang et al., 2024). Therefore, the construction of standardized Hangbaiju cultivation bases should integrate agronomic standards, digital traceability, ecological certification, and low-carbon practices, providing a stable, traceable, and high-quality resource foundation for midstream processing and downstream brand building (Lu and Liu, 2025).

4.2 Expansion of midstream deep-processed products

Deep processing is an important pathway for increasing the added value of the Hangbaiju industry and enhancing market competitiveness. For a long time, the Hangbaiju industry has mainly relied on dried flower sales and simple packaged products, with a relatively low level of processing and obvious product homogenization, making it difficult to fully release the functional value of this medicinal and edible resource. Studies on Hangbaiju flavonoid extraction show that green technologies such as ultrasonic-assisted extraction and enzymatic extraction can significantly increase the yield of active substances and improve their stability, providing technical support for the application of Hangbaiju in tea beverages, capsules, nutritional supplements, and other products. Research on tea product diversification also indicates that transforming low-value primary tea into high-value-added products such as liquid beverages, instant powders, concentrates, fermented drinks, and nutraceuticals is an important way to increase industrial returns and cope with rising production costs (Liang et al., 2021; Zohora and Arefin, 2022).

In terms of product development, comprehensive utilization research can be carried out around flavonoids, polyphenols, and volatile components in Hangbaiju to develop diversified products such as ready-to-drink tea beverages, instant granules, functional concentrates, plant-based beverages, and compound herbal drinks. At the same time, in line with the development trend of medicinal and edible resources, Hangbaiju can be applied to functional foods, solid beverages, substitute teas, healthy snacks, and cross-category bakery products, forming a multi-level product system centered on functional positioning such as “soothing,” “eye care,” “antioxidant,” and “light wellness” (Liang et al., 2021; Huda et al., 2024; Lu and Liu, 2025). Developing low-sugar, sugar-free, highly functional, and portable products according to the needs of different consumer groups can also improve market adaptability and product coverage.

In addition, processing enterprises should strengthen cooperation with universities and research institutes to promote the development of new processes, new equipment, and new products. Low-carbon ecological tea research emphasizes that midstream technological innovation should focus on energy-saving equipment, by-product recycling, and derivative product development (Zhang et al., 2024). For Hangbaiju, regional processing centers or industrial innovation platforms integrating flower drying, active component extraction, beverage manufacturing, by-product utilization, and quality testing can be established. Clean energy, intelligent equipment, and resource utilization of by-products can be used to improve industrial chain efficiency. For example, Hangbaiju processing residues can be used in fertilizers, feed, or plant-based raw material development, thereby improving resource utilization and reducing environmental pressure. Research on advanced tea beverage processing also shows that cold extraction, ultrasonic extraction, enzymatic treatment, and fermentation are important technical tools for enhancing the flavor and functionality of tea beverages (Liang et al., 2021; Liu et al., 2024). Embedding these technologies into the Hangbaiju deep-processing system can help promote the transformation of Hangbaiju from a primary agricultural product into branded, functional, and high-value products.

4.3 Extension of downstream sales channels and consumption scenarios

Sales channel innovation is an important link in realizing industrial chain value. In the downstream sector, the focus of Hangbaiju industrial chain extension lies in expanding sales channels for tea beverage products and enriching consumption scenarios. With the development of the Internet economy and digital consumption models, Hangbaiju product sales have gradually shifted from traditional wholesale and physical retail toward integrated online and offline models. Studies on the herbal tea and new-style tea beverage markets show that consumer demand for convenient, standardized, health-oriented, and naturally functional beverages is growing rapidly (Figure 2) (Huda et al., 2024; Carbone et al., 2025). Research on the globalization of Chinese herbal tea also points out that transforming loose traditional tea into fast, convenient, and standardized beverages is an important pathway for entering international markets and building sustainable value networks. Therefore, Hangbaiju tea beverages should further expand from traditional agricultural product sales channels into diversified channels such as specialty tea shops, cafés, supermarkets, convenience stores, e-commerce platforms, cross-border e-commerce, and functional beverage shelves.

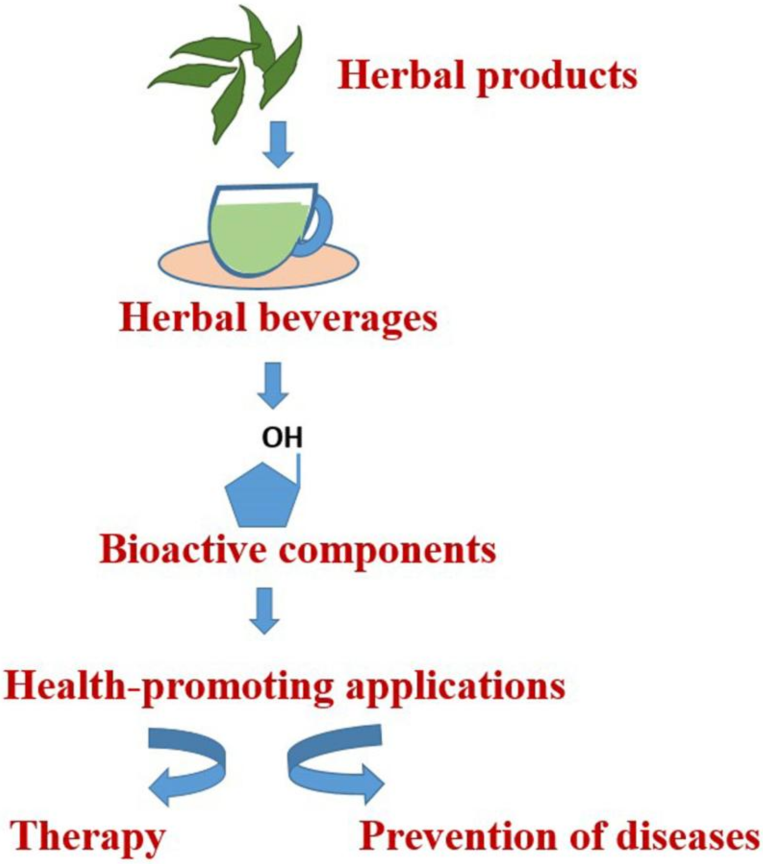


Figure 2 Herbal beverages promote health benefits via bioactive compounds (Adopted from Huda et al., 2024)

In terms of consumption scenario expansion, Hangbaiju should be promoted from household brewing toward diversified scenarios such as office leisure, business gifting, health and wellness, sports recovery, cultural tourism experiences, and new-style tea beverage stores. Studies on China's new-style tea beverage industry and leading brands show that multi-channel strategies, including offline stores, e-commerce, delivery platforms, overseas market expansion, and cultural IP development, are important pathways for attracting traffic and meeting diverse lifestyle needs (Cheng, 2025; Yang, 2025; Zhou, 2026). Therefore, enterprises can develop specialty Hangbaiju beverages in new-style tea beverage stores, promote portable tea beverage products in office and leisure tourism scenarios, and develop high-end gift boxes for festival consumption and business gifting, thereby increasing product added value and brand exposure.

Digitalization and "Internet+" models are profoundly reshaping the marketing of agricultural products and food supply chains. Big data-driven e-commerce platforms can improve logistics efficiency, brand building, and the deep processing level of agricultural products, thereby enhancing overall marketing performance (Xiao et al., 2021). Food supply chain research further shows that relying on e-commerce, the Internet of Things, and business model innovation helps enterprises better match consumer demand with product quality (Nosratabadi et al., 2020). Meanwhile, case studies of new-style tea beverage brands emphasize that "third-space" consumption scenarios, emotional and cultural marketing, and community-based communication are important ways to achieve differentiation in a homogenized market (Lu, 2022; Fu and Song, 2024). Therefore, Hangbaiju tea beverages can build an integrated downstream network through online content communication, live-streaming marketing, cultural storytelling, seasonal limited products, and cross-scenario applications, feeding consumer demand back into upstream cultivation and midstream processing optimization. Relying on chrysanthemum landscapes and chrysanthemum cultural resources in major producing areas, sightseeing and picking gardens, themed experience centers, and educational practice bases can also be developed to integrate product sales with cultural experiences, further extending the industrial chain and improving comprehensive benefits.

5 Brand Building and Marketing Promotion of Hangbaiju Tea Beverages

5.1 Development of regional public brands

Regional public brands are important carriers for enhancing the market influence and industrial competitiveness of characteristic agricultural products. As an agricultural product with distinctive regional characteristics, the brand value of Hangbaiju is reflected not only in product quality, but also in local culture, historical heritage, and industrial image. Studies on regional public brands of agricultural products show that government support, resource endowment, industrial clusters, and regional culture jointly influence brand reputation, with regional culture often playing an important role (Zhang et al., 2024). Therefore, the brand building of Hangbaiju tea beverages should make full use of geographical indication advantages and resources from major producing areas. Supported by high-quality raw material bases, distinctive ecological resources, and chrysanthemum culture, a unified regional public brand should be created to enhance market recognition and consumer awareness.

In the process of brand building, the historical and cultural connotations as well as the wellness value of Hangbaiju should be deeply explored, integrating regional characteristics, traditional cultivation techniques, and health concepts into brand development. Research indicates that brand trust in regional public brands of agricultural products can significantly improve consumer attitudes, purchase intentions, and actual purchasing behavior, while stable product quality and reliable sales channels are important conditions for strengthening brand trust. At the same time, embedding traditional culture into regional brand products helps enhance consumers' perceived functional, emotional, and social value, thereby increasing customer loyalty. Therefore, Hangbaiju tea beverages should build a brand image that integrates regional, cultural, and functional attributes through cultural storytelling, origin narratives, health concepts, and visual identity systems.

In addition, brand protection and intellectual property management should be strengthened, and geographical indication certification, green food certification, organic product certification, and brand authorization management should be actively promoted to enhance consumer trust in product quality. Studies on regional brands in urban and e-commerce contexts further point out that public marketing, market maintenance, and digital channels are of great significance to regional brand development, and regional public agricultural brands supported by e-commerce tend to gain higher online reputation (Xu et al., 2024). Therefore, the construction of a regional public brand for Hangbaiju should form a collaborative mechanism of "government guidance + industry association coordination + enterprise operation+digital platform communication." Through unified quality standards, standardized brand authorization, and traceability system construction, coordinated development of "regional brand + enterprise brand" can be promoted, thereby enhancing the overall competitiveness of the industry.

5.2 Differentiated product positioning

As competition in the tea beverage market becomes increasingly intense, product homogenization has become an important factor restricting product development. To gain competitive advantages in the market, Hangbaiju tea beverage products must adopt differentiated positioning based on the needs of different consumer groups. Conjoint analysis of Chinese tea consumption shows that tea type is an important attribute affecting consumer choice, followed by brand and packaging, while price plays a relatively less decisive role. This suggests that Hangbaiju tea beverages should not rely solely on low-price competition, but should highlight their raw material and cultural attributes, such as "medicinal and edible chrysanthemum," "regional specialty flower tea," and "natural functional beverage," and form differentiated advantages through distinctive brand expression and packaging design.

In terms of functional positioning, Hangbaiju tea beverages can rely on active components such as flavonoids and polyphenols to emphasize concepts such as eye care, soothing effects, light wellness, and antioxidation, thereby meeting consumer demand for healthy beverages. Case studies of new-style tea beverage brands show that successful differentiation often combines "Chinese-style tea beverages+cultural symbols," transforming regional culture into a brand moat and increasing consumer repurchase intention (Cheng, 2025). Therefore, Hangbaiju tea beverages can be positioned around concepts such as “regional functional flower tea,” “Chinese herbal wellness tea,” and “Oriental floral ready-to-drink health beverage,” integrating local stories, cultural IP, and health concepts into the product system to form a clear value proposition.

In terms of product image design, packaging style, product specifications, and brand expression should be optimized according to the characteristics of the target market. For middle-aged and elderly consumers, traditional wellness and health-preserving value can be emphasized through classic and functional tea beverage products. For younger consumers, fashionability, convenience, low-sugar features, and personalization can be highlighted through compound fruit-flower teas, cold-brew teas, and ready-to-drink tea beverages. Research on precision marketing for tea beverages shows that market segmentation, product pricing, and communication methods should be matched with consumers' needs for health, brand experience, and emotional resonance (Huang, 2025; Yang, 2025). Therefore, Hangbaiju tea beverages can establish a layered product system: daily affordable products for mass health consumption, mid- to high-end boutique products for the gift market, and culturally co-branded or innovative products for younger consumers. This can help occupy multiple market segments while maintaining the core brand identity of Hangbaiju.

5.3 Innovation in diversified marketing models

The development of Internet technologies and digital consumption models has brought new opportunities for the marketing of Hangbaiju tea beverage products. Traditional sales models relying on distributors and physical channels can no longer fully meet modern market demands, so enterprises should actively build an integrated online and offline marketing system. Research on localized marketing of tea beverages emphasizes that brand stories integrating local culture and emotional narratives can enhance brand recognition and consumer loyalty while supporting regional market expansion. Studies of Chinese-style tea beverage brands based on the AISAS model also find that physical stores remain important touchpoints for brand awareness, while digital platforms and applications are also crucial for brand discovery, user engagement, and purchase conversion. Therefore, Hangbaiju marketing should combine offline themed stores, tourism festivals, and product tasting experiences with online storytelling, short video promotion, livestreaming sales, and interactive marketing to increase brand exposure and market coverage.

In brand communication, cooperation with new-style tea beverage brands, cultural and creative brands, healthy lifestyle platforms, and local cultural tourism institutions can be strengthened to carry out co-branded product development and cross-boundary marketing activities. Case studies of new-style tea beverages show that co-branding, social media communication, O2O integration, and diversified promotion are important ways to break through market homogenization (Yang, 2025). At the same time, treating “products as content and consumption as communication” and connecting brands with city IP, cultural scenes, or festival activities can create strong user stickiness at relatively low cost (Cheng, 2025). Therefore, Hangbaiju tea beverages can launch seasonal limited products, themed gift boxes, cultural and creative derivatives, and co-branded drinks to enhance consumer interaction and brand topic visibility.

Offline experiential marketing is also an important means of enhancing brand influence. Enterprises can establish experience zones in supermarkets, scenic areas, tea culture museums, specialty agricultural product exhibition centers, and major Hangbaiju producing areas, enhancing consumer experience through product tasting, cultural displays, tea beverage preparation experiences, and educational activities. Research on agricultural enterprise brands shows that innovation capacity, digital marketing, and “Internet+” strategies can significantly promote brand visibility and growth. Therefore, Hangbaiju tea beverages should build a diversified marketing model integrating “online flagship stores+livestreaming e-commerce+offline experience spaces+cultural tourism scenarios+community operation.” By integrating traditional culture, digital tools, and multi-channel distribution, a sustainable brand communication system can be established to promote the healthy development of the Hangbaiju tea beverage industry.

6 Integrated Development Pathways for the Hangbaiju Tea Beverage Industry

6.1 Integration of Agriculture, Culture, and Tourism

The integration of agriculture, culture, and tourism is an important pathway for promoting the transformation and upgrading of the Hangbaiju industry and improving its overall benefits. Hangbaiju not only has economic value, but also contains rich historical, cultural, and ornamental value. Studies on agro-cultural-tourism integration and agritourism show that combining agricultural production, local culture, and leisure experiences can promote county-level sustainable development, optimize industrial structure, and stimulate consumption and investment vitality (Qiu et al., 2021; Wang et al., 2023; Wang et al., 2025). Therefore, relying on large-scale cultivation bases in major Hangbaiju producing areas such as Tongxiang, Zhejiang, distinctive agricultural landscapes themed around chrysanthemum culture can be created, integrating traditional agricultural production with cultural display and leisure tourism. During the flowering season, large areas of blooming chrysanthemum fields can form unique rural landscape resources, attracting tourists for sightseeing and injecting new vitality into local tourism development.

In the process of agro-cultural-tourism integration, cultural theme parks, sightseeing bases, and characteristic towns centered on Hangbaiju culture can be developed, along with chrysanthemum viewing festivals, tea beverage experience activities, and traditional cultural exhibitions. Relevant case studies show that “agriculture as the foundation, culture as the core, and tourism as the engine” is an important logic for agro-cultural-tourism integration; that is, integrated industrial bases and differentiated products can be built by relying on characteristic agricultural products and cultural symbols (Bin, 2023; Qin et al., 2025). Studies related to the tea industry also indicate that tea culture tourism and tea garden tourism can promote industrial upgrading and form practical models such as “tea culture+basic tourism,” “tea culture+participatory experience,” “tea culture+health and wellness,” and “tea culture+knowledge-seeking study” (Zhang et al., 2022; Huali, 2023; Yang et al., 2025). Drawing on the experience of tea-tourism integration, the Hangbaiju industry can strengthen tourists’ understanding of its products and brands by showcasing cultivation history, processing techniques, tea beverage preparation, and wellness culture.

In addition, digital technologies should be integrated with the cultural tourism industry. Short videos, livestreaming platforms, digital exhibition halls, and online interactive activities can be used to promote Hangbaiju culture and industrial characteristics, thereby expanding brand influence. Research has pointed out that building themed routes, experience-oriented tea gardens, and tea tourism brands, while strengthening publicity platforms, helps deepen integration in terms of functions, culture, talent, and branding (Yang et al., 2025). Therefore, Hangbaiju can develop an industrial model of “cultivation base+cultural experience + leisure tourism + product sales,” combining flower landscapes, tea beverage experiences, cultural and creative products, and souvenir sales to achieve coordinated development of primary, secondary, and tertiary industries, promote rural economic growth, and increase farmers’ income.

6.2 Integration with the health and wellness industry

With the deep implementation of the Healthy China strategy and the acceleration of population aging, the health and wellness industry has become a new economic growth point. As a medicinal and edible plant, Hangbaiju is associated with soothing and wellness-related qualities and is highly compatible with the development needs of the modern health and wellness industry. Studies on agritourism and tea tourism emphasize that health, ecology, and sustainability are important competitive advantages and consumption drivers of agritourism and tea culture tourism (Huali, 2023). Agritourism, by utilizing natural, organic, and ecological attributes, can not only meet people’s health needs but also help improve the “health” of rural settlements and ecological environments (Ciolac et al., 2019). Therefore, Hangbaiju tea beverage products can be deeply integrated with health management, wellness services, rehabilitation and healthcare, and ecological tourism, thereby expanding industrial development space.

In terms of product development, a series of health and wellness tea beverages can be developed for different age groups and health needs. For example, wellness-oriented tea beverages can be launched for middle-aged and elderly consumers, fatigue-relieving and eye-care products for office workers, and low-sugar, refreshing, light-wellness functional beverages for younger consumers. Studies on tea tourism and rural tourism suggest that green, health-oriented, and wellness concepts should be incorporated into tourism products and route design to enhance tourism value and meet wellness-oriented consumption demand (Huali, 2023). Research on tea-related intangible cultural heritage in Anhui also proposes integrating tea culture with health and wellness to develop "tea wellness tourism products," satisfying healthy lifestyle needs and expanding the market space for tea products (Jia et al., 2025). This indicates that Hangbaiju tea beverages can serve not only as daily health drinks, but also as core consumer products in wellness tourism and health services.

At the same time, the Hangbaiju industry can be integrated with wellness tourism, ecological vacations, and health services to build comprehensive service platforms that combine wellness experiences, health consultation, tea beverage tasting, and leisure vacations. Studies show that agriculture-tourism integration can improve agricultural green productivity and ecological efficiency, especially when combined with rural human capital enhancement and green practices (Jiang, 2022; Wang et al., 2023). Therefore, the Hangbaiju industry can be embedded into a low-carbon, ecological, and wellness-oriented development model, in which organic cultivation, ecological landscapes, and functional tea beverage supply reinforce one another. By connecting cultivation bases, processing enterprises, wellness institutions, and tourism service providers, an integrated industrial chain of "Hangbaiju cultivation-tea beverage processing-health experience-wellness consumption" can be formed, thereby improving overall industrial benefits and market competitiveness.

6.3 Integration of educational programs and cultural communication

Educational programs have become an important form of promoting agricultural cultural communication, improving public scientific literacy, and cultivating industrial talent. The Hangbaiju industry has rich agricultural production practices and traditional cultural resources, making it capable of providing high-quality educational resources for primary and secondary school students, university students and teachers, and the general public. Studies on tea-tourism integration include indicators such as the number of higher education institutions and tea culture museums in evaluating the level of integration, indicating that educational institutions and cultural exhibition spaces play important roles in cultural communication, visitor experience, and innovation support (Yang et al., 2025). Research on the innovative management path of integrating tea culture with rural tourism also emphasizes the need to build routes with functions such as "visiting, learning, popular science education, and recreation," highlighting science popularization and knowledge-seeking functions (Huali, 2023).

In terms of educational content design, a Hangbaiju-themed curriculum system can be developed by integrating labor education, ecological education, traditional culture education, and food processing science popularization. For example, activities such as flowering-stage observation, harvesting experience, primary processing practice, tea beverage preparation, product packaging design, and cultural interpretation can be organized to improve students' understanding of modern agriculture, medicinal and edible resources, and rural industrial development. The "tea culture + knowledge-seeking" model has been identified as an important practical form in tea garden tourism, indicating that educational experiences can be institutionally embedded into agricultural tourism products (Huali, 2023). Therefore, major Hangbaiju producing areas can build educational practice bases, agricultural science demonstration parks, Hangbaiju cultural centers, and field internship bases, forming an educational platform that integrates production practice, scientific education, and cultural experience.

Cultural communication is an important support for enhancing the influence of the Hangbaiju industry. Research on industry-education integration in the tea industry suggests that mechanisms such as connecting facilities with job positions, transforming standards, strengthening cultural integration, building dual-qualified teaching teams, and integrating platforms can improve industrial technical skills, brand marketing, and cross-cultural communication capacity (Ou and Chen, 2025). Studies on tea-related intangible cultural heritage also emphasize that cultural and creative industries, film and television works, and cultural products can be used to extend industrial and value chains and increase the visibility and influence of tea culture (Jia et al., 2025). For Hangbaiju, historical documents, folk traditions, and wellness culture resources can be systematically collected and integrated to develop thematic courses, popular science publications, cultural and creative products, short-form video content, and digital exhibition projects. Through the coordinated advancement of educational programs and cultural communication, the industry can not only strengthen its cultural soft power but also cultivate potential consumer groups and professional talent, thereby providing sustained momentum for the long-term sustainable development of the Hangbaiju industry.

7 Strategies for the Development of the Hangbaiju Tea Beverage Industry

For Hangbaiju tea beverages, strengthening technological innovation and product research and development means drawing on the development experience of both the traditional tea industry and new-style tea beverage brands. Studies on the Japanese tea industry have shown that long-term survival in a disruptive environment depends on continuous product development based on technological innovation, transforming tea from a bulk commodity into branded, high-value products, and protecting innovation achievements through patents and trademarks. Research on Chinese herbal tea beverages suggests that the industry must increase investment and accelerate the transition from traditional loose tea to fast, convenient, and standardized tea beverage products to meet global demand. Case studies of leading new-style tea beverage brands such as HEYTEA and CHAGEE show that product innovation, health-oriented formulations such as low-sugar products, and original-leaf tea bases or functional bases are core drivers for enhancing competitiveness and promoting international expansion. For Hangbaiju, this means establishing an R&D system that integrates flower-derived functional components into diversified product forms such as ready-to-drink teas, instant beverages, and compound herbal drinks, while using standardized processes and intellectual property protection as support to build a sustainable innovation engine.

Improving the industrial chain coordination mechanism of Hangbaiju requires strengthening supply chain capabilities and promoting effective connections among upstream, midstream, and downstream actors. Quantitative analysis of Chinese tea beverage brands has found that improving supply chain capabilities, including cold-chain coverage and inventory turnover efficiency, can significantly improve brand competitiveness indicators such as store profitability and new product iteration speed. However, resource-constrained regional brands benefit less, indicating that industrial upgrading cannot rely on isolated breakthroughs but requires coordinated advancement. Studies on Mixue and other chain brands emphasize that vertically integrated industrial chains combining R&D, production, warehousing, logistics, and chain operations help reduce costs and support rapid expansion. Research on the global development strategy of herbal tea stresses that standardized and normalized beverage production chains should be established instead of relying on raw material exports, as this is the foundation for sustainable internationalization. For Hangbaiju, establishing industrial alliances, order-based agriculture, shared cold-chain and logistics platforms, and industrial chain information-sharing mechanisms can help transform ecological and cultural advantages into stable supply, efficient cost control, and rapid responsiveness to market changes.

To enhance brand influence and market competitiveness, Hangbaiju tea beverages can draw on proven brand-building and marketing strategies from the new-style tea beverage sector. Case studies and SWOT analyses of leading brands show that strong brand reputation, differentiated cultural positioning, and immersive offline experiences are core elements for standing out in a homogenized market. Brands such as HEYTEA, Nayuki, CHAGEE, and Mixue have built competitive advantages through co-branding, festival and music marketing, “third-space” experiential stores, and integrated multi-channel distribution, while gradually shifting toward omnichannel models and moderate pricing strategies to expand their customer bases. Research on Chinese herbal tea and tea exports further emphasizes that improving international brand visibility, standardizing quality, and using social media and digital tools to attract younger consumers are key to global expansion. For Hangbaiju, this means constructing clear regional and functional brand narratives, leveraging digital marketing and e-commerce, promoting co-branded and culturally themed products, and continuously launching innovative SKUs to maintain market freshness. At the same time, these efforts should be combined with reliable quality assurance to build long-term trust and consumer loyalty.

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.

References

A'yuni Q., Wijaya C.H., Mastuti T.S., and Sukarno, 2022, Sensory and bioactive properties response to reformulation and processing of java-tea-based functional drink: a review, Journal of Functional Food and Nutraceutical, 4(1): 17-35.
https://doi.org/10.33555/jffn.v4i1.99

Aaqil M., Peng C., Kamal A., Nawaz T., Zhang F., and Gong J.S., 2023, Tea harvesting and processing techniques and its effect on phytochemical profile and final quality of black tea: a review, Foods, 12(24): 4467.
https://doi.org/10.3390/foods12244467

Bhargava A., Bansal A., Goyal V., and Bansal P., 2022, A review on tea quality and safety using emerging parameters, Journal of Food Measurement and Characterization, 16: 1291-1311.
https://doi.org/10.1007/s11694-021-01232-x

Bin S., 2023, Exploration on the development path of agricultural, cultural and tourism industry integration under the background of rural revitalization: a case study of chaxi village, Hongjiang City, Hunan Province, Frontiers in Business, Economics and Management, 11(2): 22-27.
https://doi.org/10.54097/fbem.v11i2.12157

Carbone R., Caracciolo F., Di Vita G., D'Amico M., and Spina D., 2025, Consumer trends in the herbal tea market: a systematic literature review, Food Reviews International, 41: 2634-2652.
https://doi.org/10.1080/87559129.2025.2493224

Cheng Z., 2025, Case analysis of the marketing strategy of tea yan yue se, Highlights in Business, Economics and Management, 60: 287-292.
https://doi.org/10.54097/e561k370

Ciolac R., Adamov T., Iancu T., Popescu G., Lile R., Rujescu C., and Marin D., 2019, Agritourism: a sustainable development factor for improving the "health" of rural settlements, case study Apuseni Mountains area, Sustainability, 11(5): 1467.
https://doi.org/10.3390/su11051467

Fu Y., and Song X., 2024, Market strategy analysis of traditional Chinese medicine tea replacement drinks based on corporate strategic management, Academic Journal of Business and Management, 6(5): 199-204.
https://doi.org/10.25236/ajbm.2024.060527

Geng J.Y., Cui H.C., Wang Y.W., Sun H.W., Xu J., Wang W.W., Chen F., Zhao Y., Yin J.F., and Zhang J., 2026, Deciphering the flavor chemistry, processing and quality evaluation methods of milk tea: a comprehensive review, Foods, 15(4): 681.
https://doi.org/10.3390/foods15040681

Gupta A., Sanwal N., Bareen M.A., Barua S., Sharma N., Olatunji O.J., Nirmal N.P., and Sahu J., 2023, Trends in functional beverages: functional ingredients, processing technologies, stability, health benefits, and consumer perspective, Food Research International, 170: 113046.
https://doi.org/10.1016/j.foodres.2023.113046

Huali L., 2023, Research on the integration trend of tea industry and tea garden tourism in China, Journal of Agriculture and Forestry, 2(2): 47.
https://doi.org/10.57237/j.jaf.2023.02.002

Huang Y., 2025, The path of low-cost differentiation for the new tea beverage industry: a case study of Mixue Bingcheng based on producer-consumer dual perspectives, Advances in Economics, Management and Political Sciences, 223: 167-171.
https://doi.org/10.54254/2754-1169/2025.gl27920

Huda H.S.A., Majid N.B.A., Chen Y., Adnan M., Ashraf S.A., Roszko M., Bryła M., Kieliszek M., and Sasidharan S., 2024, Exploring the ancient roots and modern global brews of tea and herbal beverages: a comprehensive review of origins, types, health benefits, market dynamics, and future trends, Food Science and Nutrition, 12(10): 6938-6955.
https://doi.org/10.1002/fsn3.4346

Jia B.Y., Zhu Q.Q., and Lu J., 2025, Study on promoting rural revitalization through the integrated development of Anhui's tea industry and tea-related intangible cultural heritage from the perspective of new quality productive forces, Journal of Humanities, Arts and Social Science, 9(2): 251-257.
https://doi.org/10.26855/jhass.2025.02.007

Jiang G., 2022, How does agro-tourism integration influence the rebound effect of China's agricultural eco-efficiency? an economic development perspective, Frontiers in Environmental Science, 10: 921103.
https://doi.org/10.3389/fenvs.2022.921103

Kristiningrum E., Setyoko A.T., Adinugroho T.P., Susanto D.A., Isharyadi F., and Ayundyahrini M., 2023, Improvement of the food safety management system for tea-producing SMEs based on HACCP, E3S Web of Conferences, 465: 02039.
https://doi.org/10.1051/e3sconf/202346502039

Leelapattana W., and Asavarachan R., 2025, Enhancing technology transfer and innovation for processing of dried yellow chrysanthemum (*Chrysanthemum indicum*) flowers: a case study of the mae wang lao community enterprise group, Chiang Rai Province, Journal of Food Processing and Preservation, 2025(1): 3541701.
https://doi.org/10.1155/jfpp/3541701

Liang S., Gao Y., Fu Y.Q., Chen J., Yin J.F., and Xu Y., 2022, Innovative technologies in tea beverage processing for quality improvement, Current Opinion in Food Science, 47: 100870.

Liang S., Granato D., Zou C., Gao Y., Zhu Y., Zhang L., Yin J.F., Zhou W., and Xu Y., 2021, Processing technologies for manufacturing tea beverages: from traditional to advanced hybrid processes, Trends in Food Science and Technology, 118: 431-446.
https://doi.org/10.1016/j.tifs.2021.10.016

Liu C.L., Lu W.Y., Gao B.Y., Kimura H., Li Y.F., and Wang J., 2020, Rapid identification of chrysanthemum teas by computer vision and deep learning, Food Science and Nutrition, 8(4): 1968-1977.
https://doi.org/10.1002/fsn3.1484

Liu X., Zhao Y., and Zhao D., 2024, Next-generation tea beverages: innovations in formulation and processing, Journal of Tea Science Research, 14(2): 112-122.
https://doi.org/10.5376/jtsr.2024.14.0011

Lu D., 2022, Analyze the marketing strategies of new-tea drinks industry by the SWOT and PEST tools: take Nayuki as an example, Proceedings of the 2022 7th International Conference on Social Sciences and Economic Development (ICSSED 2022), 2022: 98-101.
https://doi.org/10.2991/aebmr.k.220405.019

Lu J., and Liu C., 2025, Research on the extraction of flavonoids from Hangbaiju (*Chrysanthemum morifolium*) and the development of functional foods, Medicinal Plant Research, 15(2): 88-98.
https://doi.org/10.5376/mpr.2025.15.0010

Maulida I.D., Marsam M.R.A., Purnama I., and Mutamima A., 2024, A novel beverage with functional potential incorporating cascara (*Coffea arabica*), roselle (*Hibiscus sabdariffa*), and red ginger (*Zingiber officinale* Rosc. var. *rubrum*) extracts: chemical properties and sensory evaluation, Discover Food, 4(1): 94.
https://doi.org/10.1007/s44187-024-00180-x

Moreira J., Aryal J., Guidry L., Adhikari A., Chen Y., Sriwattana S., and Prinyawiwatkul W., 2024, Tea quality: an overview of the analytical methods and sensory analyses used in the most recent studies, Foods, 13(22): 3580.
https://doi.org/10.3390/foods13223580

Munarso S.J., Elmatsani H.M., Djafar M.J., Kailaku S.I., Lukas A., Susetyo E.B., Setianto W.B., and Warsono S.Y., 2026, Global trends and innovations in anti-inflammatory functional beverages: a bibliometric and consumer insights analysis (2006-2025), Beverages, 12(1): 7.
https://doi.org/10.3390/beverages12010007

Najman K., Sadowska A., Wolińska M., Starczewska K., and Buczak K., 2023, The content of bioactive compounds and technological properties of matcha green tea and its application in the design of functional beverages, Molecules, 28(20): 7018.
https://doi.org/10.3390/molecules28207018

Nosratabadi S., Mosavi A., and Lakner Z., 2020, Food supply chain and business model innovation, Foods, 9(2): 132.
https://doi.org/10.3390/foods9020132

Onsun B., Toprak K., and Şanlıer N., 2025, Kombucha tea: a functional beverage and all its aspects, Current Nutrition Reports, 14(1): 69.
https://doi.org/10.1007/s13668-025-00658-9

Ou L.T., and Chen Y., 2025, Research on the strategy of constructing an efficient model of integration of industry and education in Guangxi tea industry based on the "five integration" mechanism, Journal of Asia Social Science Practice, 1(1): 57-72.
https://doi.org/10.71411/jassp.2025.10

Prabawa S., Raida A., Hartanto R., and Yudhistira B., 2023, The physicochemical quality of yellow chrysanthemum flower (*Chrysanthemum indicum*) brewed drink, Food Research, 7(3): 12-21.
https://doi.org/10.26656/fr.2017.7(3).840

Qin K., and Zhou L., 2024, Analysis of the high-quality development path of China's tea export, PLOS ONE, 19(10): e0311629.
https://doi.org/10.1371/journal.pone.0311629

Qin R., Zhong X., and Tang L., 2025, A study on the integrated development model of agriculture, culture, and tourism in Guangxi: based on a case study of four locations in three cities, Journal of Education, Humanities, and Social Research, 2(2): 65-76.
https://doi.org/10.71222/gc8s7829

Qiu P., Zhou Z., and Kim D., 2021, A new path of sustainable development in traditional agricultural areas from the perspective of open innovation: a coupling and coordination study on the agricultural industry and the tourism industry, Journal of Open Innovation: Technology, Market, and Complexity, 7(1): 16.
https://doi.org/10.3390/joitmc7010016

Tang Y., Han X., Zhao N., Chen X., Zheng X., and Yan F., 2025, From forest to cup: a comprehensive review of health benefits and quality control of *Cyclocarya paliurus* tea, Food Reviews International, 42: 988-1013.
https://doi.org/10.1080/87559129.2025.2509867

Tong T., Liu Y., Kang J., Zhang C., and Kang S.G., 2019, Antioxidant activity and main chemical components of a novel fermented tea, Molecules, 24(16): 2917.
https://doi.org/10.3390/molecules24162917

Wang Q., Dang X., Song T., Xiao G., and Lu Y.Z., 2025, Agro-tourism integration and county-level sustainability: Mechanisms and regional heterogeneity in China, Sustainability, 17(10): 4549.
https://doi.org/10.3390/su17104549

Wang Y., Zhao Z., Xu M., Tan Z., Han J., Zhang L.C., and Chen S., 2023, Agriculture-tourism integration's impact on agricultural green productivity in China, Agriculture, 13(10): 1941.
https://doi.org/10.3390/agriculture13101941

Xiao J., Wang W., and Tsai S.B., 2021, Coupling of agricultural product marketing and agricultural economic development based on big data analysis and "Internet+", Mobile Information Systems, 2021: 3702064.
https://doi.org/10.1155/2021/3702064

Xu H., Wu M., Wei W., Ren W., and Zheng Z., 2024, *Chrysanthemum morifolium* Ramat. as a traditional tea material: unraveling the influence of kill-green process on drying characteristics, phytochemical compounds, and volatile profile, Food Research International, 200: 115478.
https://doi.org/10.1016/j.foodres.2024.115478

Yang M.X., Tian X., Zhang M.T., Wei J.H., Niu Y.K., Hou J.L., Jin Y.R., and Du Y.F., 2022, A holistic comparison of flavor signature and chemical profile in different harvesting periods of *Chrysanthemum morifolium* Ramat. based on metabolomics combined with bioinformatics and molecular docking strategy, RSC Advances, 12(52): 34971-34989.
https://doi.org/10.1039/d2ra05698d

Yang Y., 2025, Analysis of overseas investments of China's new tea beverage industry, Advances in Economics, Management and Political Sciences, 167(1): 132-138.
https://doi.org/10.54254/2754-1169/2025.21175

Yang Z.D., Wang X.Y., and Xiao J.W., 2025, Measurement of the development level of tea tourism integration, spatiotemporal evolution and obstacle factors in China, PLOS ONE, 20(7): e0329974.
https://doi.org/10.1371/journal.pone.0329974

Ying S., He T., and Wu C., 2022, Intelligent evaluation model based on index system of agricultural industrial chain, IEEE Access, 10: 133720-133732.
https://doi.org/10.1109/access.2022.3231749

Yu X.L., Sun D., and He Y., 2020, Emerging techniques for determining the quality and safety of tea products: a review, Comprehensive Reviews in Food Science and Food Safety, 19(5): 2613-2638.
https://doi.org/10.1111/1541-4337.12611

Zhang J., Lu M., Song Z., and Zhang Z., 2022, Research on the development of tea culture tourism products under the background of cultural and tourism integration, Frontiers in Humanities and Social Sciences, 2(11): 243-252.
https://doi.org/10.54691/fhss.v2i11.2813

Zhang W.E., Zhao M.Y., Chen Y.C., Xu Y.L., Ma Y.Q., and Fan S.S., 2024, Low-carbon ecological tea: the key to transforming the tea industry towards sustainability, Agriculture, 14(5): 722.
https://doi.org/10.3390/agriculture14050722

Zhou J.Y., 2026, A study on the profit model of mixue bingcheng driven by value chain, Advances in Economics, Management and Political Sciences, 258(1): 1-15.
https://doi.org/10.54254/2754-1169/2026.ld31795

Zohora K.F.T., and Arefin M.R., 2022, Tea and tea product diversification: a review, Turkish Journal of Agriculture-Food Science and Technology, 10(12): 2334-2353.
https://doi.org/10.24925/turjaf.v10i12.2334-2353.5280

Review and Progress Open Access

Effects of Cultivation Environment on the Yield of *Fritillaria thunbergii* and the Accumulation of Peimine

Xiaoying Li [1], Jianhua Wang [2]
1 Songyang Xiaoying Family Farm, Songyang, 323400, Zhejiang, China
2 Songyang Shuimoshicang Agricultural Products Co. Ltd., Songyang, 323499, Zhejiang, China
Corresponding author: wjianhua2009@vip.qq.com
Medicinal Plant Research, 2026, Vol.16, No.1 doi: 10.5376/mpr.2026.16.0005
Received: 29 Jan., 2026
Accepted: 13 Mar., 2026
Published: 28 Mar., 2026

Preferred citation for this article:
Li X.Y., and Wang J.H., 2026, Effects of cultivation environment on the yield of *Fritillaria thunbergii* and the accumulation of peimine, Medicinal Plant Research, 16(1): 69-91 (doi: 10.5376/mpr.2026.16.0005)

Abstract *Fritillaria thunbergii* Miq. is a commonly used traditional Chinese medicinal herb and a representative geo-authentic medicinal material of Zhejiang Province. Its underground bulb is the main medicinal part, and steroidal alkaloids such as peimine and peiminine are important indicators for evaluating its medicinal quality. With the transition of *F. thunbergii* production from traditional experience-based cultivation to standardized, large-scale, and high-quality cultivation, improving bulb yield while maintaining stable peimine accumulation has become a key issue in industrial development and quality control. This study focuses on the effects of cultivation environment on the yield of *F. thunbergii* and peimine accumulation, and analyzes the regulatory effects of light, temperature, water, soil, regional ecological conditions, and different cultivation patterns on plant growth, bulb enlargement, dry matter accumulation, and secondary metabolism. The results indicate that suitable light and temperature conditions, stable water supply, favorable soil structure, rational nutrient management, and a healthy rhizosphere microecology are important foundations for promoting high-quality and high-yield cultivation of *F. thunbergii*. In contrast, unfavorable environmental factors, such as excessive shading, high temperature, drought, waterlogging, soil compaction, and continuous cropping obstacles, may affect photosynthesis, root absorption, and bulb development, thereby causing yield reduction or quality fluctuation. Meanwhile, moderate environmental regulation can promote peimine accumulation by influencing carbon assimilation, hormone signaling, rhizosphere microecology, and pathways related to steroidal alkaloid biosynthesis. Future cultivation of *F. thunbergii* should aim to achieve the coordinated improvement of yield and quality by integrating ecological suitability zoning, comprehensive light-temperature-water-fertilizer management, soil environment optimization, and the construction of a quality evaluation system, thereby promoting the standardized, green, and sustainable development of the *F. thunbergii* industry.
Keywords *Fritillaria thunbergii*; Cultivation environment; Bulb yield; Peimine; Quality formation

1 Introduction

Fritillaria thunbergii Miq., a perennial herb of the genus *Fritillaria* in the family Liliaceae, is used medicinally as its dried bulb. It is one of the commonly used traditional Chinese medicinal materials in China and a representative geo-authentic medicinal material of Zhejiang Province. *F. thunbergii* has a long history of medicinal use and is clinically applied mainly for clearing heat and resolving phlegm, relieving cough and promoting expectoration, dissipating nodules, and resolving carbuncles. It has shown important application value in the intervention of respiratory diseases, pneumonia, inflammatory diseases, and related metabolic disorders (Nile et al., 2021). Modern pharmacological and phytochemical studies have shown that the bulbs of *F. thunbergii* contain various active substances, including alkaloids, polysaccharides, saponins, flavonoids, and volatile components. Among them, steroidal alkaloids such as peimine and peiminine have received particular attention and constitute an important material basis for its antitussive, expectorant, anti-inflammatory, antitumor, and antioxidant pharmacological effects (Huang et al., 2024a; Zou et al., 2026). Because peimine-type components are often regarded as important quality markers of *F. thunbergii* medicinal materials and their preparations, their content directly affects clinical efficacy, quality evaluation, and commercial value (Sui et al., 2021; Cheng et al., 2023; Zhou et al., 2023). With the continuous advancement of traditional Chinese medicine modernization and quality standardization of Chinese medicinal materials, *F. thunbergii* not only maintains stable demand in the field of traditional decoction pieces, but is also increasingly applied in Chinese patent medicine development, functional product research, and the comprehensive utilization of medicinal plant resources. Its industrial value and market attention have therefore continued to increase.

From the perspective of industrial development, *F. thunbergii* has medicinal, economic, and regional specialty agricultural value, making it an important crop for promoting local Chinese medicinal material industries and increasing farmers' income. With growing market demand and ecological constraints on wild resources, the supply of *F. thunbergii* has gradually shifted from wild collection to artificial cultivation. Stable, high-yield, and high-quality cultivation has therefore become a key issue in current industrial development (Sui et al., 2021; Du et al., 2024; Liu et al., 2025a). Major production areas such as Zhejiang have developed a relatively mature cultivation foundation as well as processing and distribution systems. However, in production practice, *F. thunbergii* still faces problems such as yield fluctuation, uneven quality, and unstable contents of active components. Since the underground bulb is the medicinal part of *F. thunbergii*, yield formation is influenced not only by cultivar, seed bulb quality, and cultivation management, but also closely related to light, temperature, water, soil, and regional ecological conditions. Existing studies have shown that cultivation environments and agronomic measures, including fertilizer type and application rate, potassium nutrition, organic fertilizer and biochar amendment, shading intensity, soil disinfestation, and biological control, can significantly affect bulb biomass, peimine/peiminine contents, and levels of other steroidal alkaloids in *F. thunbergii* (Cheng et al., 2023; Huang et al., 2024a). Therefore, different cultivation environments may affect final yield and medicinal quality by changing plant growth rhythm, photosynthetic efficiency, dry matter accumulation, rhizosphere microecology, and bulb enlargement.

At present, *F. thunbergii* production has gradually shifted from traditional experience-based cultivation to standardized, large-scale, and high-quality cultivation. Simply pursuing bulb yield can no longer meet the requirements of the medicinal material market and quality evaluation systems. Studies have shown that yield-oriented intensive cultivation may be associated with a decline in the levels of medicinal components in bulbs, while the accumulation of peimine-type steroidal alkaloids varies with species, organs, developmental stages, and environmental conditions (Sui et al., 2021; Huang et al., 2024a). For example, appropriate potassium and organic fertilizer application can simultaneously increase bulb yield and peimine content, whereas shading or certain stress-mimicking measures may increase alkaloid concentrations but are often accompanied by reduced biomass (Liu et al., 2025a). This indicates that high yield does not necessarily equate to high quality. If cultivation environment regulation is inappropriate, plant growth may be restricted, disease incidence may increase, bulb marketability may decline, or peimine accumulation may be insufficient. Therefore, in *F. thunbergii* production, greater attention should be paid to the coordination between "yield formation" and "quality formation." On the one hand, optimizing light-temperature-water-fertilizer management, improving soil structure, regulating the field microclimate, and reducing continuous cropping obstacles can enhance plant growth stability and bulb yield. On the other hand, the promoting effects of suitable environmental conditions on peimine synthesis, transport, and accumulation should also be emphasized to provide a basis for improving the medicinal quality of *F. thunbergii*.

This study will explore the effects of cultivation environment on the yield of *Fritillaria thunbergii* and peimine accumulation. Focusing on the growth and developmental characteristics, yield formation process, and peimine accumulation patterns of *F. thunbergii*, this study will systematically analyze the regulatory effects of light, temperature, water, soil, regional ecological conditions, and cultivation patterns on its growth and quality formation. Existing studies have explored individual factors such as potassium application rate, organic fertilizer type, shading treatment, soil disinfestation, and biological control; however, comprehensive evaluations that simultaneously link specific cultivation environments with bulb yield and peimine accumulation remain relatively limited. In addition, transcriptomic and metabolomic studies have shown that the effects of cultivation environment on the growth and quality of *F. thunbergii* may be mediated by regulating hormone signaling, rhizosphere microecology, and the expression of key genes involved in steroidal alkaloid biosynthesis. Therefore, this study will further analyze the possible mechanisms by which environmental factors regulate photosynthesis, dry matter accumulation, and secondary metabolism. It aims to clarify the intrinsic relationships between cultivation environment, yield formation, and peimine accumulation in *F. thunbergii*, providing theoretical references for ecological suitability zoning, standardized cultivation, optimization of high-quality and high-yield cultivation techniques, and construction of a coordinated yield-quality evaluation system. It also offers practical insights for the green, standardized, and sustainable development of the *F. thunbergii* industry.

2 Growth and Development Characteristics of *Fritillaria thunbergii* and Features of Peimine Accumulation

2.1 Biological characteristics and growth cycle of *Fritillaria thunbergii*

Fritillaria thunbergii Miq. is a perennial geophyte of the genus *Fritillaria* in the family Liliaceae. Its underground bulb is used medicinally, serving not only as a storage organ for nutrients but also as the main site for the accumulation of steroidal alkaloids such as peimine and peiminine (Nile et al., 2021; Huang et al., 2024a). The plant usually develops aboveground stems and leaves from sprouting bulbs. The leaves perform photosynthesis, and the photosynthetic products are gradually allocated to the underground bulbs through assimilate transport, thereby supporting bulb enlargement and the accumulation of medicinal constituents. *F. thunbergii* is suitable for growth in mild, humid, cool, well-ventilated environments with loose soil and good drainage. It is relatively sensitive to high temperature, waterlogging, and soil compaction. At present, commercial production mainly relies on artificial cultivation systems, and some cultivation patterns regulate light and microclimate through field shading facilities to simulate its native shaded mountain habitats, thereby improving the plant growth environment and the conditions for bulb quality formation (Liu et al., 2025a).

In terms of growth cycle, *F. thunbergii* generally undergoes several stages, including bulb dormancy, dormancy release, sprouting and emergence, leaf expansion and vegetative growth, bulb enlargement, and aboveground withering. During dormancy, the bulb mainly undergoes physiological regulation and nutrient storage, laying the foundation for sprouting in the following growing season. Studies have shown that storing *F. thunbergii* bulbs at low temperatures of 4°C~10°C for several weeks can reduce the content of phenolic compounds and alter the activities of phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO), changes that are closely associated with dormancy release. In vitro and ex situ studies on *Fritillaria* bulbs have also shown that appropriate temperature regimes and gibberellin (GA) signaling contribute to fresh weight increase and sprouting, whereas unsuitable conditions may delay growth and prolong dormancy (Marković et al., 2020; Marković et al., 2021). In addition, micropropagation systems established using bulb scale sections can regenerate numerous bulblets within a short period, but these bulblets still require cold treatment to achieve synchronized sprouting. This indicates that the rhythm of “dormancy-cold induction-sprouting growth” is an important developmental pattern in *F. thunbergii* and related *Fritillaria* species.

Bulb development in *F. thunbergii* is also jointly regulated by plant hormones and genetic factors. Transcriptomic studies have found that the GGPS1 family gene FtGGPS can influence bulb development and differences in bulb size among cultivars by regulating the levels of gibberellin (GA) and abscisic acid (ABA) (Xu et al., 2026). Meanwhile, ABA-related signaling is also considered to be associated with increased bulb yield under certain fertilization regimes, indicating that the growth cycle of *F. thunbergii* is regulated not only by external environmental factors such as temperature, light, and water, but also by finely tuned endogenous hormone signaling (Huang et al., 2024a). Therefore, when understanding the growth and developmental patterns of *F. thunbergii*, it should be regarded as the result of the combined effects of environmental factors, hormonal regulation, photosynthate accumulation, and bulb storage function.

2.2 Major Factors influencing yield formation in *Fritillaria thunbergii*

The yield of *F. thunbergii* mainly depends on the number of effective plants per unit area, single-bulb weight, degree of bulb enlargement, and marketable traits. Among these factors, seed bulb quality is the fundamental condition for yield formation. Plump, healthy, disease-free seed bulbs usually have stronger sprouting capacity and growth vigor, which can improve emergence rate and population uniformity. In contrast, small, diseased, or improperly stored seed bulbs may easily cause uneven emergence, weakened growth, and disease transmission, ultimately affecting bulb enlargement and yield stability. Since the underground bulb is both the medicinal and commercial part of *F. thunbergii*, yield formation is essentially the result of a continuous process involving aboveground photosynthetic establishment, assimilate accumulation, and underground bulb enlargement. Therefore, production should emphasize germplasm selection, seed bulb grading, pre-sowing treatment, and population establishment quality to lay a foundation for high yield in later stages.

Cultivation environment is the core external factor affecting yield formation in *F. thunbergii*. Nutrient management, light conditions, and rhizosphere microecology are currently key research directions. Field experiments have shown that different types of basal fertilizers have significant effects on the yield and quality of *F. thunbergii*. Among them, organic fertilizer treatment can produce higher bulb yield and higher peimine and peiminine contents than raw chicken manure or plant ash, indicating that organic fertilizer has a better coordinating effect between biomass accumulation and alkaloid formation (Huang et al., 2024a). Potassium nutrition is also an important factor affecting dry matter formation. Within an appropriate application range, potassium fertilizer significantly increases bulb biomass and yield by approximately 4%~11% compared with the unfertilized control, suggesting that potassium contributes to assimilate transport, bulb filling, and yield formation (Liu et al., 2025a). Therefore, rational fertilization, especially the combination of organic fertilizer input and appropriate potassium application, is an important technical pathway for improving the yield and quality of *F. thunbergii*.

Light intensity and its associated microclimate exert dual effects on yield formation in *F. thunbergii*. Suitable light is beneficial for leaf photosynthesis and dry matter accumulation, whereas insufficient light limits carbon assimilation and reduces bulb biomass. However, moderate shading may also improve field temperature and humidity conditions and alleviate strong light and high-temperature stress. Studies have shown that strong shading can significantly increase the concentration of bioactive components in bulbs, but it reduces biomass and overall yield, and severe yield reduction may occur under extremely low light transmittance. Moderate shading combined with appropriate potassium supply can partially compensate for shading-induced yield reduction while maintaining or increasing active component content (Liu et al., 2025a). In addition, rhizosphere microbial communities are also involved in regulating the balance between yield and quality. Shading and potassium can jointly alter soil pH and available nutrient status, enriching bacterial and fungal groups positively correlated with bulb growth and medicinal constituent accumulation, such as *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*, *Burkholderia-Caballeronia-Paraburkholderia*, *Chryseobacterium*, *Brevundimonas*, and *Phoma*. This indicates that yield formation in *F. thunbergii* is not determined by a single factor, but by the coordinated effects of light, nutrients, rhizosphere microecology, and field management.

2.3 Types, accumulation characteristics, and quality evaluation significance of peimine

Peimine is an important steroidal alkaloid active component in *F. thunbergii* and serves as an important material basis for evaluating its medicinal quality. Among these components, peimine is a cevanine-type steroidal alkaloid and often coexists in *F. thunbergii* bulbs with peiminine, peimisine, imperialine, and other steroidal alkaloids (Nile et al., 2021; Shan et al., 2022). Metabolomic studies have shown that peimine, peiminine, and related cevanine-type alkaloids are relatively abundant alkaloid components in *Fritillaria* species, especially in bulb tissues, where their contents are usually higher than those in aboveground parts (Liao et al., 2023). In aqueous and hydroethanolic extracts of *F. thunbergii* bulbs, peimine, peiminine, peimisine, and their glycosides have been identified as major components using UPLC-QTOF-MS and other techniques, with characteristic fragmentation patterns further confirming the structures of these compounds (Huang et al., 2024a; Jeong et al., 2024; Zou et al., 2026). Therefore, peimine-type components are not only important constituents of the pharmacodynamic basis of *F. thunbergii*, but also provide detectable and quantifiable chemical indicators for modern quality evaluation.

Peimine accumulation shows obvious organ specificity and stage specificity. Since the bulb is the medicinal part of *F. thunbergii*, it is both the core site of yield formation and an important site of peimine accumulation. In the early growth stage, vegetative growth and leaf establishment predominate, and photosynthetic products are mainly used for the development of aboveground parts and roots. As growth progresses, assimilates are gradually transported to the underground bulbs, bulb enlargement and secondary metabolic activity are enhanced, and the accumulation of peimine and related steroidal alkaloids changes accordingly. Comparative metabolomic and time-series metabolomic studies on related *Fritillaria* species have shown that peimine and peiminine mainly accumulate in bulbs and often reach relatively high levels at later developmental stages or shortly after aboveground withering, indicating that alkaloid enrichment is closely associated with bulb maturation (Figure 1) (Duan et al., 2022; Duan et al., 2023). From the perspective of biosynthesis, peimine may originate from cholesterol metabolism and involve the terpenoid backbone pathway and downstream steroid pathways. Cytochrome P450 enzymes and glycosyltransferases may participate in its structural diversification, but the complete enzymatic biosynthetic route remains to be further clarified (Nile et al., 2021; Shan et al., 2022; Liao et al., 2023).

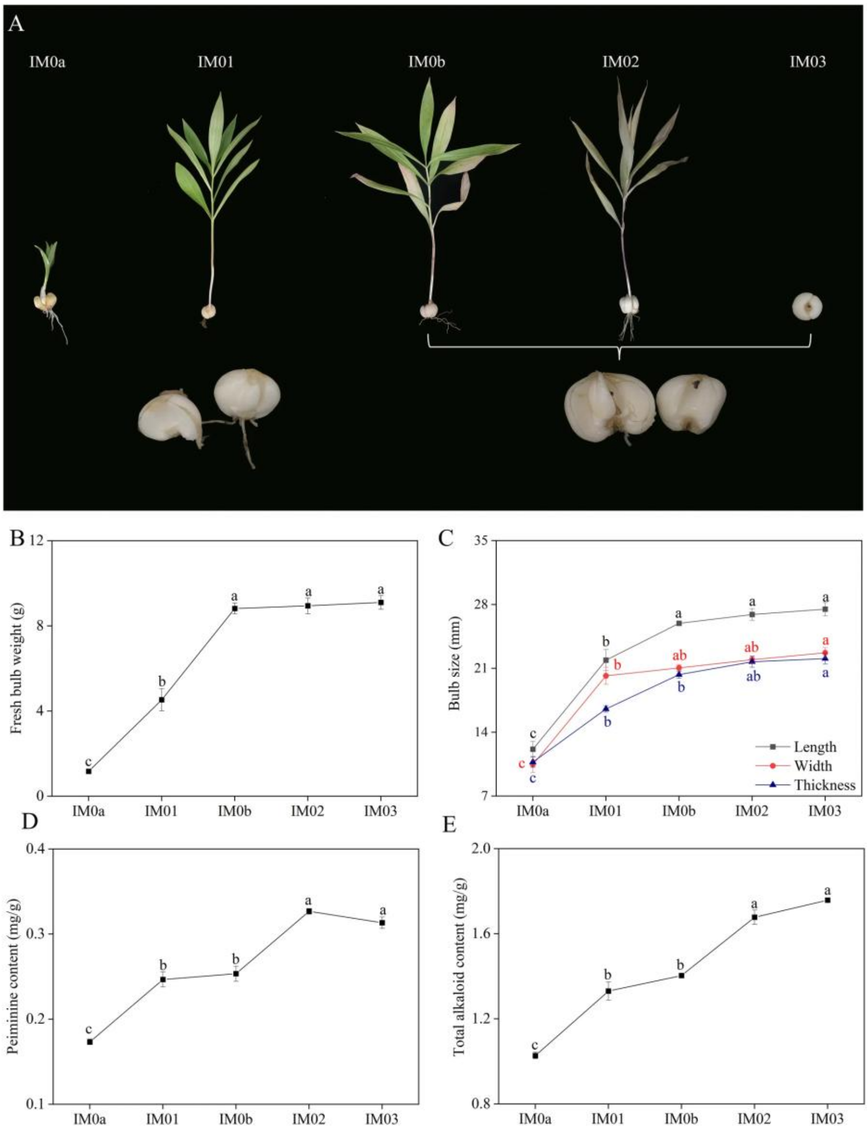


Figure 1 Dynamic phenotypic and biochemical variations in regenerated bulb development of *F. hupehensis* (Adopted from Duan et al., 2023)

Image caption: (A): Phenotypic changes in *(F) hupehensis* at five developmental stages; (B): Bulb size (length, width, and thickness) changes; (C): Details of changes in fresh bulb weight; (D): Details of changes in peiminine content; (E): Details of changes in total alkaloid content; All data in the Figure are represented as mean±standard error; Different letters in each system represent significant differences at $p<0.05$ (Adopted from Duan et al., 2023)

The accumulation of peimine and related steroidal alkaloids is sensitive to cultivation practices and environmental conditions. Studies have shown that, compared with less optimized treatments, organic fertilizer application and appropriate potassium supply under shading conditions can significantly increase peimine and peiminine levels in bulbs (Huang et al., 2024a; Liu et al., 2025a). The application of biocontrol agents during cultivation can not only improve plant growth, but also increase the contents of peimine, peiminine, and other steroidal alkaloids. This effect may be related to the regulation of key enzyme activities, oxidative phosphorylation, amino acid metabolism, cytochrome P450 enzymes, and transcription factors such as MYB and bHLH (Cheng et al., 2023). From the perspective of quality evaluation, the quality of *F. thunbergii* should not be judged solely by yield, but should be comprehensively evaluated based on bulb size, morphology, dry matter content, peimine and peiminine contents, safety, and pharmacological indicators. Given the central role of peimine, peiminine, and related steroidal alkaloids in antitussive, anti-inflammatory, and other pharmacological effects, they are widely regarded as core quality markers of *F. thunbergii*. They constitute an important basis for modern chromatographic quality evaluation systems and provide a foundation for linking cultivation environment with clinical efficacy (Nile et al., 2021; Zhou et al., 2023; Zou et al., 2026).

3 Effects of Light and Temperature Conditions on the Yield of *Fritillaria thunbergii* and Peimine Accumulation

3.1 Effects of light intensity and shading conditions on plant growth

Light is an important environmental factor affecting aboveground growth, photosynthesis, and dry matter accumulation in *Fritillaria thunbergii*. During growth, *F. thunbergii* relies on its leaves for photosynthesis, converting light energy into organic matter, which is subsequently transported to the underground bulbs for bulb enlargement and the accumulation of medicinal constituents. Appropriate light intensity helps improve leaf photosynthetic efficiency, promotes robust plant growth, and prolongs the functional duration of leaves, thereby providing sufficient material basis for subsequent bulb formation. Existing studies have shown that light intensity directly constrains photosynthesis and dry matter accumulation in *F. thunbergii*, and excessive shading significantly inhibits carbon assimilation and plant growth. Under strong shading conditions, namely approximately 5% light transmittance, bulb biomass and yield of *F. thunbergii* decline significantly; compared with full light, shading treatment can reduce bulb biomass and yield by approximately 17% and 9%, respectively (Liu et al., 2025a). Single-factor shading experiments have also shown that although shading can increase the content of active ingredients, shading alone can reduce bulb biomass by approximately 11%. This indicates that *F. thunbergii* still requires a certain light basis to achieve high yield, and yield loss increases when light intensity falls below its photosynthetic requirement.

However, *F. thunbergii* is not suitable for long-term growth under conditions of both strong light and high temperature. Excessively strong light can accelerate leaf water loss, damage the photosynthetic system, and promote premature senescence. Especially in late spring, when temperatures rise, strong light may aggravate heat stress, causing early withering of the aboveground parts and shortening the effective growth period. Since yield formation in *F. thunbergii* depends on the continuous transport of assimilates from the aboveground parts to the bulbs, premature leaf senescence directly affects underground bulb enlargement and dry matter accumulation. Therefore, in cultivation practice, light conditions should be reasonably regulated according to the climatic characteristics of the production area and the growth stage, so as to avoid growth imbalance caused by excessively weak or excessively strong light. Under low-light conditions, *F. thunbergii* exhibits certain morphological and physiological plasticity, such as enhancing light capture by adjusting leaf traits and chlorophyll content. This is similar to the phenomenon observed in crops such as strawberry, where low light reduces photosynthetic rate and growth but increases pigment content and alters leaf area (Liu et al., 2025a).

Moderate shading is an important measure for improving the field microclimate of *F. thunbergii*. Shading cultivation can reduce light intensity and surface temperature, alleviate damage caused by direct strong light to leaves, help maintain soil moisture, and improve the plant growth environment. Understory cultivation and sunshade-net cultivation can, to some extent, simulate the cool and humid ecological requirements of *F. thunbergii*, helping delay premature senescence of the aboveground parts and maintain relatively stable photosynthetic function. However, the degree of shading must be properly controlled, as excessive shading reduces photosynthetic accumulation and is unfavorable for bulb enlargement. Studies have shown that sufficient potassium supply can partially alleviate the adverse effects of shading on the growth of *F. thunbergii* and increase bulb biomass and yield under shading conditions, although these indicators still cannot fully recover to the level of the unshaded control (Liu et al., 2025a). Therefore, combining moderate shading with optimized nutrient supply is an important pathway for balancing light energy utilization, stress mitigation, and yield stability.

3.2 Effects of temperature changes on sprouting, leaf expansion, and bulb enlargement

Temperature is one of the core factors regulating the growth rhythm and phenological process of *F. thunbergii*. *F. thunbergii* has a biological preference for cool conditions, and its sprouting, emergence, leaf expansion, and bulb enlargement are closely related to temperature changes. Under suitable low-temperature and mild climatic conditions, seed bulbs can successfully break dormancy and sprout, aboveground growth is relatively uniform, and leaves expand fully, which is conducive to the formation of a good population structure. Studies have shown that temperature plays a key role in breaking bulb dormancy and initiating sprouting in *F. thunbergii*. Storage of *F. thunbergii* bulbs at 10°C for 30~45 days or at 4°C for 45~60 days is considered a critical period for dormancy release. During this process, the content of phenolic compounds decreases and related enzyme activities change, indicating that sprouting induction involves a temperature-dependent biochemical mechanism. Low-temperature pretreatment of in vitro-produced bulblets at approximately 5°C for several weeks can also promote uniform sprouting after transplantation, indicating that exposure to low temperature is important for successful emergence and population establishment (Marković et al., 2021).

Once dormancy is released, subsequent temperature conditions regulate leaf expansion and bulb enlargement by affecting carbon acquisition and assimilate allocation. Leaf expansion and vegetative growth stages are relatively sensitive to temperature. Suitable temperatures promote leaf expansion, root absorption, and photosynthesis, enabling plants to establish a strong vegetative growth foundation. When temperatures are too high, transpiration increases, water consumption accelerates, and leaves are prone to wilting, yellowing, or premature senescence, leading to decreased photosynthetic capacity. Meanwhile, high temperature may also alter the balance of carbon and nitrogen metabolism in plants, resulting in insufficient transport of assimilates to underground bulbs and ultimately affecting bulb enlargement and marketable yield. Studies on related *Fritillaria* species have shown that in geophytes such as *Fritillaria meleagris*, compared with 7°C, higher temperatures during post-dormancy growth, approximately 24°C, combined with gibberellin treatment can significantly increase bulb fresh weight and sprouting rate, whereas low-temperature conditions slow biomass accumulation (Figure 2) (Marković et al., 2020). Therefore, *F. thunbergii* does not require low temperatures throughout its entire growth cycle; rather, it requires appropriate low temperature to complete dormancy release, followed by moderately warm conditions to promote leaf expansion, photosynthesis, and bulb enlargement.

The bulb enlargement stage is the key period for yield formation in *F. thunbergii*, during which temperature conditions directly affect dry matter accumulation and underground organ development. A mild, stable environment with an appropriate diurnal temperature difference is conducive to the accumulation of organic matter through photosynthesis during the day and to reduced respiratory consumption at night, thereby promoting the transfer of more assimilates to the bulbs. If persistent high temperatures occur during this stage, the aboveground parts are prone to premature withering, the duration of bulb enlargement is shortened, and single-bulb weight decreases. In vitro culture studies have shown that under a 16 h light/8 h dark regime, approximately 25°C is the most favorable temperature for bulblet regeneration and early growth of *F. thunbergii*. Compared with continuous darkness at the same temperature, this condition better supports rapid leaf development and bulblet enlargement. Thus, temperature not only affects the progression of each growth stage of *F. thunbergii*, but also determines whether the plant can complete sufficient material accumulation within a limited growing period. Overall, the growth of *F. thunbergii* requires a “cool-warm” temperature sequence: sufficient low temperature to break dormancy, followed by moderately warm conditions to promote leaf establishment, photosynthesis, and bulb weight gain.

Figure 2 Sprouting of bulbs cultured *F. meleagris* bulbs cultured on medium with 10 μM GA3 and GA inhibitors (Adopted from Marković et al., 2020)

Image caption: (A,B) Bulbs grown for five weeks at 24 °C on culture medium supplemented with GA3 inhibitors: ancymidol (A) and paclobutrazol (B); (C) Bulb grown for five weeks at 7 °C on culture medium supplemented with and GA3. (D-F) Bulbs cultured on medium with GA3 after one (D), two (E) and five weeks (F) at 24 °C; Scale bars = 5 mm (Adopted from Marković et al., 2020)

3.3 Regulatory effects of light-temperature interaction on peimine accumulation

As an important secondary metabolite in *F. thunbergii*, peimine synthesis and accumulation are influenced not only by genetic factors but also by external environmental conditions such as light and temperature. Light provides the material basis for the synthesis of peimine and other secondary metabolites by affecting photosynthesis and carbon source supply, whereas temperature influences the formation and accumulation of active ingredients by regulating enzyme activity, respiratory metabolism, and growth processes. Existing studies have shown that light conditions not only regulate the growth of *F. thunbergii*, but also strongly affect the accumulation of steroidal alkaloids, including peimine. In field and shade-house experiments, shading generally increased the total active ingredient content in *F. thunbergii* bulbs by approximately 11%~21%, even though it reduced biomass (Liu et al., 2025a). Under the combined effects of shading and optimized potassium supply, the contents of peimine and related steroidal alkaloids, including imperialine, peiminine, and cyclopamine, were significantly higher than those under full light. Despite a certain yield penalty, the total alkaloid accumulation per unit area was still increased.

The effects of light and temperature on peimine accumulation are usually not independent, but rather show coordinated regulation. Appropriate light is conducive to dry matter accumulation, while suitable low temperature or a relatively large diurnal temperature difference may reduce respiratory consumption and promote the accumulation of active ingredients in bulbs. Within a certain range, mild environmental stress may also activate plant defense responses and secondary metabolic pathways, thereby promoting the synthesis of alkaloid components. Transcriptomic and metabolomic analyses have shown that shading under sufficient potassium supply can upregulate key genes and pathways involved in steroidal alkaloid biosynthesis, including farnesyl pyrophosphate synthase and multiple transcription factors, thereby linking changes in light microclimate with the molecular regulation of peimine synthesis (Liu et al., 2025a). These findings indicate that low to moderate light is not only an ecological environmental factor, but may also act as a quality-regulating “signal,” promoting the diversion of carbon flow from growth expansion toward secondary metabolism and thereby increasing peimine concentration.

Temperature integrates with light signals to jointly regulate developmental processes and metabolic allocation in *F. thunbergii*. Low-temperature treatment can regulate bulb dormancy and phenolic metabolism, indirectly affecting the length of the growth period available for alkaloid accumulation; subsequent moderately warm conditions help enhance photosynthetic capacity and biomass formation (Marković et al., 2020). Controlled-environment studies have shown that higher temperature can synergize with lower light intensity and extended photoperiod to promote leaf expansion and total photon capture, thereby increasing biomass without reducing secondary metabolite levels under suitable spectral conditions (Jeong et al., 2025). In *Fritillaria* systems, in vitro studies have shown that a defined temperature of approximately 25°C combined with controlled light quality can significantly increase the contents of peimine and related isosteroidal alkaloids in callus or seedlings (Chen et al., 2020; Peng et al., 2024). Therefore, in the cultivation of *F. thunbergii*, light and temperature management should take into account both yield formation and peimine accumulation. Through moderate shading, sufficient low-temperature treatment, suitable growing-season temperature, field ventilation, and microclimate regulation, high peimine content can be promoted while maintaining acceptable bulb yield.

4 Effects of Water Conditions on the Yield of *Fritillaria thunbergii* and Peimine Accumulation

4.1 Effects of soil moisture on root growth and bulb development

Water is an important ecological factor affecting the growth, development, and yield formation of *Fritillaria thunbergii*. *F. thunbergii* prefers moist conditions but is intolerant of waterlogging. Since both its roots and bulbs grow in the soil, they are sensitive to changes in soil water content and its spatial distribution. Appropriate soil moisture can maintain normal root extension and absorption functions, promote the uptake and transport of mineral nutrients, and provide necessary conditions for aboveground growth and underground bulb enlargement. Rhizobox and soil column studies have shown that root growth is mainly driven by the vertical distribution of soil moisture. Roots tend to proliferate in moist soil layers, whereas root elongation is inhibited when soil moisture falls below a critical threshold. After local soil rewetting, roots can dynamically adjust growth allocation within 48 h, showing a clear “hydromatching” phenomenon (Maan et al., 2023; Ceolin et al., 2025). This suggests that maintaining a suitable and relatively uniform moisture environment within the main rooting depth of *F. thunbergii* is conducive to continuous root exploration of the soil space, stable water and nutrient supply, and sustained bulb enlargement.

In the early growth stage of *F. thunbergii*, suitable soil moisture helps promote seed bulb sprouting, uniform emergence, and root establishment. Well-developed roots enhance plant utilization of water and nutrients and improve population growth uniformity. After entering the vegetative growth and bulb enlargement stages, the plant’s demand for water supply further increases. At this stage, if soil moisture is sufficient and aeration is good, leaves can maintain high photosynthetic efficiency, allowing assimilates to be continuously transported to underground bulbs and promoting bulb filling and dry matter accumulation. Studies have shown that as roots develop, they can alter soil structure and form subzones with high, medium, and low moisture levels. After irrigation, moisture changes rapidly in the near-root zone, whereas soil moisture farther from the roots remains relatively stable (Zhang et al., 2021). This indicates that water management in *F. thunbergii* should focus not only on overall field soil water content, but also on the spatiotemporal changes in moisture within the rhizosphere microenvironment.

It should be noted that the water requirement of *F. thunbergii* does not mean that more water is always better; instead, it emphasizes the coordination between moisture and aeration. Soil moisture stability is as important as absolute water content. Studies on tomato seedlings have shown that, compared with fluctuating moisture conditions, maintaining stable soil moisture through precise water replenishment can improve shoot and root morphology, photosynthesis, and water-use efficiency, even when the average water content is similar (Li et al., 2023). For *F. thunbergii*, which depends on a healthy fibrous root system to provide carbohydrates and precursors for steroidal alkaloid biosynthesis, avoiding large fluctuations between dry and wet soil conditions may be important for uniform bulb development and stable peimine accumulation. If soil moisture is excessive, soil pores become filled with water, restricting root respiration and reducing root vitality. Meanwhile, because the bulb tissue of *F. thunbergii* is relatively tender, it is more susceptible to pathogenic microbial infection under poor aeration and excessive humidity. Therefore, water management should follow the basic principles of maintaining moderate moisture, avoiding long-term waterlogging, and preserving rhizosphere aeration, so as to maintain a balance among root growth, bulb development, and soil aeration.

4.2 Effects of drought, waterlogging, and wet injury on yield formation

Drought stress directly restricts the normal growth of *F. thunbergii*. When soil moisture is insufficient, plants first exhibit difficulty in root water uptake, leaf water loss, stomatal closure, and reduced photosynthetic efficiency. As drought persists, leaves may wilt, yellow, or senesce prematurely, shortening the functional period of the aboveground parts and resulting in insufficient accumulation of photosynthetic products. Since the yield of *F. thunbergii* mainly derives from the enlargement and filling of underground bulbs, inhibited aboveground growth reduces the assimilates transported to the bulbs, ultimately causing a decline in single-bulb weight, marketability, and total yield. Studies on medicinal plants have also shown that drought stress usually suppresses biomass and yield. A meta-analysis covering 27 medicinal plant species found that moderate and severe drought stress significantly reduced plant relative water content and yield while strongly activating enzymatic antioxidant systems (Tan and Gören, 2024). In field experiments on Balangu (*Lallemantia* spp.), moderate and severe drought reduced seed yield and oil content, although phenolic compounds and antioxidant enzyme levels increased (Omidi et al., 2018). These results suggest that although drought may induce certain defensive metabolic responses, long-term water deficiency is generally unfavorable for bulb yield formation in *F. thunbergii*.

Compared with drought, waterlogging and wet injury are equally serious hazards in *F. thunbergii* production, and may be even more severe in some rainy or poorly drained regions. Long-term soil waterlogging causes rhizosphere hypoxia, inhibits root respiration, reduces nutrient absorption capacity, and induces root rot and bulb rot. Reviews on waterlogging stress indicate that soil oxygen depletion after saturation leads to enhanced anaerobic respiration, reduced dry matter accumulation, impaired nutrient uptake, especially potassium and calcium uptake, and significant yield losses in many crops (Manghwar et al., 2024). Species-specific experiments have shown that complete waterlogging significantly reduces fine-root growth and transpiration, whereas partial waterlogging may promote root proliferation in non-flooded upper soil layers to compensate for damaged deep roots (Fujita et al., 2021). For underground bulb crops such as *F. thunbergii*, prolonged saturation around the bulbs and main root zone can easily cause root decay, wet injury symptoms, and reduced population stability, thereby decreasing marketable bulb size and yield.

Although drought and wet injury differ in their manifestations, both disrupt the physiological basis required for yield formation in *F. thunbergii*. Drought mainly reduces dry matter accumulation by lowering water supply, inducing stomatal closure, and limiting photosynthetic capacity, whereas waterlogging affects plant growth mainly by inhibiting root respiration, damaging the rhizosphere environment, obstructing nutrient uptake, and aggravating disease. In field studies on industrial hemp, both severe drought and waterlogging caused by excessive water reduced photosynthesis and decreased plant growth and yield by more than 50%, with only partial recovery after stress relief (Kumar et al., 2025). This further demonstrates that both excessively dry and excessively wet conditions can cause productivity losses. For *F. thunbergii*, cultivation should avoid large fluctuations in water supply, especially problems such as drought in the early stage affecting emergence, water shortage in the middle stage limiting growth, and waterlogging in the late stage causing rot. A stable, moderate, and well-coordinated irrigation and drainage environment is an important condition for ensuring stable yield in *F. thunbergii*.

4.3 Effects of rational water regulation on peimine accumulation and quality stability

Water conditions not only affect yield formation in *F. thunbergii*, but also influence the accumulation of secondary metabolites such as peimine. The synthesis and accumulation of peimine depend on normal physiological metabolism, while water supply affects photosynthesis, nutrient uptake, carbon-nitrogen metabolism, intracellular metabolic balance, and stress signal transduction. Appropriate soil moisture can maintain strong photosynthetic capacity and a relatively stable growth state, providing a material basis for peimine biosynthesis. If water is insufficient or excessive, normal plant metabolism may be disrupted, leading to unstable accumulation of active components and affecting medicinal quality. Studies on related medicinal plants have shown that moderate water deficit can sometimes increase alkaloids or other secondary metabolites, whereas severe stress leads to decreased biomass and quality fluctuations. For example, in summer snowflake (*Leucojum aestivum*), moderate water deficit stress, namely 50% deficit irrigation, resulted in higher levels of bulb alkaloids such as galanthamine and lycorine, as well as phenolic compounds and antioxidant capacity, whereas severe stress or waterlogging reduced fresh weight and did not further increase alkaloid content (Baba et al., 2024).

Moderate water regulation helps achieve coordinated improvement of yield and quality. In the early growth stage of *F. thunbergii*, soil should be kept moderately moist to promote sprouting, emergence, and root formation. During vegetative growth and bulb enlargement, stable water supply should be ensured to avoid premature leaf senescence caused by water shortage. In the late growth stage and before harvest, water should be appropriately controlled according to soil conditions and weather changes to reduce waterlogging and disease occurrence and promote bulb maturation and filling. Studies on *Atractylodes chinensis* have shown that moderate irrigation levels can maintain relatively high yield while maximizing alkaloid-related enzyme activities and quality indicators; the quality peak occurs at an intermediate irrigation level rather than under maximum water supply (Lv et al., 2026). In *Datura stramonium*, gradient irrigation creates different tropane alkaloid profiles in different organs, indicating that soil water supply can serve as a cultivation measure for regulating the accumulation of specific alkaloids (Moreno-Pedraza et al., 2019). These studies provide insights for water regulation in *F. thunbergii*: controlled and non-severe mild water deficit may help enhance peimine accumulation, provided that bulb biomass and marketability are not significantly sacrificed.

In production practice, water regulation should be integrated with soil improvement, ridge and ditch construction, disease control, and water-fertilizer coordinated management. Selecting well-drained fields, adopting high-ridge cultivation, improving ditch drainage systems, applying mulching for moisture conservation, and conducting scientific irrigation according to rainfall conditions can all help maintain suitable soil moisture. Reviews on drought and medicinal plant physiology indicate that mild to moderate stress usually stimulates the formation of secondary metabolites such as phenols, flavonoids, and alkaloids, whereas severe or prolonged stress leads to yield collapse and unstable quality (Bistgani et al., 2024; Tan and Gören, 2024). Studies combining water and nutrient management have also shown that under 70%~75% of maximum water-holding capacity combined with moderate nitrogen supply, *Sophora alopecuroides* can achieve relatively high biomass and alkaloid accumulation while promoting the formation of specific rhizosphere microbial communities (Huang et al., 2024b). Therefore, for *F. thunbergii*, water management should avoid long-term drought and frequent waterlogging, with stable soil moisture close to field capacity as the basic goal. After experimental verification, short-term, precise, and mild water deficit treatments may be explored to promote peimine accumulation. Establishing a management system centered on soil moisture monitoring, rational irrigation and drainage, and rhizosphere environment optimization can improve yield stability and consistency of peimine content in *F. thunbergii*, thereby providing support for the production of high-quality medicinal materials.

5 Effects of Soil Environment on the Yield of *Fritillaria thunbergii* and Peimine Accumulation

5.1 Relationship among soil texture, aeration, and bulb development

Soil is an important medium for root growth, bulb enlargement, and active constituent accumulation in *Fritillaria thunbergii*, and its texture and structure directly affect the development of underground organs. Since the bulb is the medicinal part of *F. thunbergii*, whether the underground part can fully enlarge is closely related to soil looseness, pore distribution, water and nutrient retention capacity, and mechanical resistance. Soil texture determines pore size distribution, aeration, and water-holding capacity, thereby influencing root penetration capacity and the supply of carbohydrates to underground storage organs. Relevant meta-analyses have shown that coarse sandy soils drain rapidly but have weak nutrient retention capacity, whereas heavy clay soils have stronger water and nutrient retention capacity but are prone to poor aeration and waterlogging. Loamy soils with appropriate proportions of sand, silt, and clay usually balance aeration, water retention, and fertility, making them more favorable for crop productivity (Bhatt et al., 2025). Therefore, for bulbous medicinal plants such as *F. thunbergii*, deep, loose, well-aggregated loamy soils with good drainage are more conducive to root extension, assimilate transport, and continuous bulb enlargement. In contrast, overly heavy, compacted, or extremely sandy soils may restrict bulb development due to excessive root penetration resistance, rhizosphere waterlogging, or insufficient water and nutrient retention.

Soil aeration is an important factor affecting the physiological activities of the underground parts of *F. thunbergii*. Roots and bulbs require normal respiration during growth to maintain cellular metabolism, energy supply, and nutrient absorption. Well-aerated soil can ensure oxygen supply in the rhizosphere, promote root vitality and nutrient absorption efficiency, and reduce the risk of root diseases. Conversely, poorly drained soils, low porosity, or long-term excessive moisture easily create hypoxic conditions, inhibiting root respiration and leading to root weakness, bulb rot, and pathogen proliferation. Studies on crops such as maize and tomato have shown that soil aeration-enhancing technologies, including aerated seepage irrigation and micro/nano-bubble systems, can increase soil oxygen content, soil respiration, microbial biomass, root length, and root surface area, and significantly improve yield. At the same time, soil aeration can also increase the activities of nutrient-cycling enzymes such as urease, thereby enhancing nitrogen transformation and the supply of available nutrients to roots (Li et al., 2022; Yu et al., 2024). These findings suggest that good soil aeration not only directly affects root respiration, but also indirectly promotes the development of underground storage organs by regulating microbial activity and nutrient cycling.

In production practice, priority should be given to selecting fields with loose and fertile soil, convenient irrigation and drainage, and good soil permeability for *F. thunbergii* cultivation. During land preparation, deep plowing and soil exposure, high-ridge cultivation, and the application of well-decomposed organic fertilizer can be used to improve soil aggregate structure, reduce compaction, and enhance the coordination between water retention and drainage. Heavy clay soils or low-lying waterlogged fields should be avoided for large-scale continuous cultivation of *F. thunbergii*, or the rhizosphere environment should be improved through ditch drainage, soil replacement or amendment, increased organic matter input, and improved irrigation and drainage systems. In highly moist or compacted soils, limited oxygen diffusion reduces root respiration and nutrient absorption capacity and promotes root diseases. Even when nutrient inputs are sufficient, poor aeration may restrict fertilizer effectiveness (Yang et al., 2025). Given that *F. thunbergii* bulbs are sensitive to rot and require a relatively high oxygen supply in the rhizosphere, maintaining suitable soil structure and aeration is an important basis for supporting healthy bulb development, stable yield, and peimine accumulation.

5.2 Effects of soil fertility and ph on nutrient absorption and yield formation

Soil fertility is directly related to nutrient supply and yield formation in *F. thunbergii*. During growth, *F. thunbergii* needs to absorb nitrogen, phosphorus, potassium, and various medium and trace elements from the soil to support leaf establishment, root development, and bulb enlargement. Nitrogen promotes vegetative growth and leaf formation, phosphorus contributes to root development and energy metabolism, and potassium is closely associated with assimilate transport, stress resistance, and bulb filling. Studies on fertilization in medicinal crops have shown that yield responses to nutrient inputs depend largely on soil properties and climatic context. Long-term high fertilizer input or unfavorable water conditions may increase biomass in the short term, but may also weaken medicinal quality (Yang et al., 2025). A systematic review of nitrogen management in medicinal plants further indicated that moderate nitrogen application generally improves both yield and plant metabolite content, whereas excessive nitrogen reduces quality and may even suppress yield (Hao et al., 2024). This suggests that fertilization in *F. thunbergii* should not simply pursue high input, but should provide balanced nutrients according to the soil fertility basis and growth-stage requirements.

Soil nutrient supply should remain coordinated, rather than focusing excessively on a single nutrient or fertilizer type. Excessive nitrogen application may lead to excessive aboveground vegetative growth, tender plant tissues, reduced disease resistance, and impaired assimilate accumulation in bulbs. Insufficient phosphorus and potassium supply, meanwhile, can restrict root development, energy metabolism, assimilate transport, and bulb filling.

Studies on bulbous medicinal plants such as *Pinellia ternata* have shown that phosphorus application alone can increase bulbil biomass by 43%, while combined phosphorus and potassium fertilization can double biomass compared with the unfertilized control, highlighting the importance of balanced macronutrient supply for the development of underground storage organs (Ng et al., 2023). Therefore, for *F. thunbergii*, organic fertilizer should be used as the basis, combined with appropriate supplementation of nitrogen, phosphorus, potassium, and medium and trace elements, while emphasizing coordination among vegetative growth, bulb enlargement, and active constituent formation. Long-term improper fertilization may also lead to salt accumulation, aggravated soil acidification, and microbial community imbalance, further affecting the growth and medicinal quality of *F. thunbergii*.

Soil pH affects nutrient availability, root vitality, microbial activity, and photosynthetic performance, and is one of the important factors determining the ecological suitability of *F. thunbergii*. Excessively acidic or alkaline environments may reduce the availability of certain mineral elements, impair root absorption capacity, and induce nutrient imbalance. In medicinal plants such as *Melissa officinalis*, *Taraxacum officinalis*, and *Ocimum basilicum*, germination, growth, and photosynthetic efficiency are significantly affected by soil pH, and pH changes also alter the uptake of micronutrients such as manganese, copper, and zinc (Adamczyk-Szabela and Wolf, 2022). Studies on continuous cropping obstacles further emphasize that pH and cation exchange capacity are key factors determining soil biochemical and biological properties, and they can regulate microbial community structure and nutrient accessibility. Under continuous cropping conditions, soil acidification or alkalization can intensify nutrient imbalance and weaken root nutrient absorption capacity (Haq et al., 2023; Li et al., 2024). Therefore, in production, soil pH can be regulated through soil testing and formula fertilization, increasing organic matter, and rational application of lime or soil conditioners, so that nitrogen, phosphorus, potassium, and trace elements remain highly available while beneficial microbial activity is promoted, thereby providing a stable soil chemical environment for yield formation and peimine biosynthesis in *F. thunbergii*.

5.3 Effects of soil microecology and continuous cropping obstacles on peimine accumulation

Soil microecology is an important hidden factor affecting the healthy growth and quality formation of *F. thunbergii*. Rhizosphere microorganisms participate in organic matter decomposition, nutrient transformation, pathogen suppression, and plant stress regulation, playing important roles in root growth, bulb development, and secondary metabolite formation. A healthy soil microecology can improve soil nutrient cycling efficiency, promote root uptake of nutrients and water, and enhance plant adaptability to unfavorable environments. In *F. thunbergii* cultivation, organic fertilizer can significantly reshape fungal communities by increasing saprotrophic fungal groups such as Pezizales and Sordariales, reducing the proportion of pathotrophic fungi, enhancing enzyme activities, lowering the soil NH_4^+/NO_3^- ratio, and increasing bulb yield by nearly sevenfold compared with the unfertilized control (Du et al., 2024). This shift toward beneficial saprotrophic fungal communities is associated with improved soil health and nutrient turnover capacity, and may help support both biomass formation and the accumulation of alkaloids such as peimine in *F. thunbergii*. Broader studies have also shown that beneficial microorganisms can enhance stress resistance, suppress pathogens, improve nutrient absorption, and regulate secondary metabolite biosynthesis in medicinal plants, making them environmentally friendly tools for improving medicinal material quality (Wang et al., 2022).

Continuous cropping obstacles are common in *F. thunbergii* cultivation. Long-term continuous planting in the same field can easily lead to imbalanced soil nutrient ratios, soil acidification or alkalization, accumulation of harmful root exudates and autotoxic substances, increased pathogens, and reduced beneficial microorganisms, thereby disrupting the balance of rhizosphere microecology (Haq et al., 2023). Continuous cropping obstacles not only reduce emergence rate, weaken plant growth, and aggravate disease, but also affect bulb development and active constituent accumulation. Studies on other medicinal plants can provide references for *F. thunbergii*. For example, in long-term monoculture systems of *Codonopsis pilosula*, soil total phosphorus and available potassium increased, whereas pH decreased, bacterial diversity declined, and autotoxic compounds such as 2,6-di-tert-butylphenol accumulated. These changes were associated with declines in yield and quality (Li et al., 2024). Reviews focusing on the rhizosphere of medicinal plants have pointed out that autotoxic substances and pH shifts can disrupt microbial structural stability, reducing beneficial microorganisms while increasing harmful microorganisms, thereby impairing nutrient acquisition and secondary metabolite profiles (Liao and Xia, 2024). Although direct data on changes in peimine under continuous cropping conditions in *F. thunbergii* remain limited, it can be inferred that soil microecological degradation, increased pathogens, and intensified chemical stress may interfere with steroidal alkaloid biosynthesis and regulation, leading to fluctuations in medicinal quality.

Improving soil microecology and alleviating continuous cropping obstacles are important directions for enhancing yield and quality stability in *F. thunbergii*. In production, soil-borne disease pressure can be reduced and soil microbial diversity restored through rational crop rotation, intercropping, application of well-decomposed organic fertilizer and microbial fertilizer, removal of diseased residues, and necessary soil disinfestation and ecological restoration. Meanwhile, excessive use of chemical fertilizers and pesticides should be reduced to avoid further disruption of the rhizosphere ecological environment. Studies have shown that crop rotation, organic amendments, and targeted microbial inoculation have demonstrated potential in other medicinal plants to restore microbial balance, alleviate continuous cropping obstacles, and increase secondary metabolite levels (Wang et al., 2022; Haq et al., 2023; Li et al., 2024). By constructing a healthy and stable soil microecological system, it is possible not only to improve stress resistance and bulb yield in *F. thunbergii*, but also to promote stable peimine content, thereby supporting the production of high-quality geo-authentic medicinal materials.

6 Effects of Regional Ecological Conditions and Cultivation Patterns on Quality Formation in *Fritillaria thunbergii*

6.1 Effects of altitude and production-area ecological environment on the growth of *Fritillaria thunbergii*

Regional ecological conditions constitute an important external basis affecting the growth, development, and quality formation of *Fritillaria thunbergii*. Different production areas vary in altitude, air temperature, precipitation, light, diurnal temperature difference, soil type, and field moisture conditions. Together, these factors determine the growth rhythm, degree of bulb enlargement, and level of active constituent accumulation in *F. thunbergii*. The suitable distribution of *Fritillaria* species is clearly constrained by macroecological factors. Jiang et al. (2022) modeled the potential geographical distribution of three *Fritillaria* species and found that precipitation, altitude, and temperature were the dominant variables determining suitable habitats. In particular, annual precipitation below approximately 336 mm significantly reduced the probability of occurrence. Suitable precipitation around the sowing period, namely September to October, and during the bulb filling period, namely May, was especially important for seed germination, early growth, and nutrient accumulation, whereas imbalanced water supply increased the risk of disease (Jiang et al., 2022). Therefore, for *F. thunbergii*, ecological suitability evaluation should not focus on a single climatic factor alone, but should comprehensively analyze the matching relationships among temperature, precipitation, light, soil drainage, and disease pressure.

Altitude changes affect the growth of *F. thunbergii* by regulating temperature, light intensity, air humidity, and diurnal temperature difference. A relatively suitable altitude environment usually provides mild or cool climatic conditions, which can delay aboveground senescence to some extent, prolong the photosynthetic functional period of leaves, and allow more assimilates to be transported to the underground bulbs. Meanwhile, an appropriate diurnal temperature difference helps reduce nighttime respiratory consumption and promotes dry matter accumulation and bulb filling. A review on the taxonomy and cultivation of *Fritillaria* species indicated that biomass and morphology change systematically with altitude: *Fritillaria* species growing at high altitudes, namely 2 700~4 000 m, are usually shorter and single-flowered, whereas species distributed below 1 500 m tend to be taller, multi-flowered, and have greater biomass. Altitude also changes together with thermal regime and solar radiation, thereby regulating plant height, phenology, and the skeleton types of isosteroidal alkaloids (Qu et al., 2022). This indicates that higher altitude is not necessarily more favorable. If temperature is too low or the growing season is too short, sprouting, leaf expansion, and bulb enlargement may also be restricted.

The ecological environment of the production area also affects the quality stability of *F. thunbergii*. Interannual climatic variation, soil fertility basis, and field management conditions differ among regions, which may lead to differences in peimine content and bulb marketability. Existing studies show that *F. thunbergii* is usually cultivated in mid- to low-altitude areas, such as Pan'an County in Zhejiang Province at an altitude of approximately 600 m. The warm and humid monsoon climate and relatively favorable soil fertility in this region are conducive to vigorous plant growth and high bulb productivity (Huang et al., 2024a). For *F. thunbergii* production, selecting production areas with stable ecological environments, suitable soil conditions, and low disease pressure is beneficial for achieving high and stable yield and quality. Therefore, evaluating production-area ecological factors and defining suitable cultivation regions are important prerequisites for promoting standardized production and quality control of *F. thunbergii*.

6.2 Environmental characteristics of geo-authentic production areas and quality advantages of *Fritillaria thunbergii*

As a traditional geo-authentic medicinal material of Zhejiang Province, the quality advantages of *F. thunbergii* are closely associated with the long-established ecological environment of its production areas. Geo-authentic production areas usually possess suitable climatic conditions, soil types, rhizosphere microecology, and cultivation experience. These factors together shape a relatively stable growth environment and quality characteristics for *F. thunbergii*. Suitable temperature and humidity conditions meet the ecological requirements of *F. thunbergii*, which prefers cool and moist conditions but is intolerant of waterlogging. Good soil structure supports root growth and bulb enlargement, while mature cultivation management techniques further guarantee medicinal material yield and commercial quality. Shi et al. (2011) compared three major production areas, namely the Ningbo geo-authentic production area, Pan'an, and Nantong, and found that soil pH ranged from 4.48 to 7.73 across different regions, indicating that *F. thunbergii* can tolerate acidic to slightly alkaline soil conditions. Among them, Ningbo, as the geo-authentic production area, had the highest soil organic matter content, phosphatase activity, and urease activity, reflecting superior soil fertility and enzyme activity (Shi et al., 2011).

The advantages of geo-authentic production areas are reflected not only in natural ecological conditions, but also in cultivation systems and quality awareness formed through long-term production practice. Growers can usually arrange sowing, fertilization, irrigation and drainage, shading, and harvesting reasonably according to local climatic changes and soil characteristics, enabling *F. thunbergii* to obtain suitable environmental conditions during key growth stages. This coordinated relationship among "ecological environment-cultivation technology-medicinal material quality" is an important basis for the formation of geo-authentic medicinal quality. It is worth noting that geo-authentic areas are not the only spaces where quality can form. Shi et al. (2011) showed that Nantong, a non-geo-authentic production area with relatively alkaline soil, had higher rhizobacterial diversity and bulb alkaloid content, suggesting that alkaline pH and abundant microbial communities may also favor secondary metabolite accumulation. This indicates that both geo-authentic areas and high-quality non-geo-authentic areas may possess favorable soil nutrient status, active microbial processes, and suitable ecological environments, jointly shaping bulb quality.

From the perspective of quality formation, geo-authentic production areas provide a relatively stable environment for material accumulation and secondary metabolism in *F. thunbergii*. Within Zhejiang Province, the soil properties of Pan'an and Ningbo are relatively similar, which provides a practical basis for large-scale cultivation of *F. thunbergii* in Pan'an while maintaining quality comparable to that of the geo-authentic area (Shi et al., 2011; Huang et al., 2024a). Multi-regional LC-MS chemometric studies further found that *F. thunbergii* bulbs produced in Zhejiang differed significantly in alkaloid profiles from samples from other provinces. Through targeted quantification of key alkaloids and non-targeted analysis, Zhejiang-produced bulbs could be distinguished from non-Zhejiang samples, and 11 characteristic markers associated with bulb appearance traits were identified (Zhang et al., 2026). This indicates that geo-authentic ecological conditions not only affect the external morphology of *F. thunbergii*, but also confer specific alkaloid fingerprints. In the future, based on the protection of traditional production-area advantages, ecological suitability evaluation, metabolomics, and modern quality testing technologies should be combined to further clarify the relationships between environmental factors in geo-authentic areas and peimine accumulation, thereby providing a basis for quality improvement and origin authentication of *F. thunbergii*.

6.3 Effects of open-field cultivation, understory cultivation, facility cultivation, and other patterns on yield and quality

Open-field cultivation is a relatively common production pattern for *F. thunbergii*, with the advantages of relatively simple management, low production cost, and suitability for large-scale cultivation. In suitable production areas and under good field management conditions, open-field cultivation can meet the basic growth requirements of *F. thunbergii* and produce relatively stable bulb yield. Traditional open-field cultivation of *F. thunbergii* in areas such as Pan'an mainly depends on local climatic conditions and fertilization management, while optimized organic fertilizer application and potassium fertilization have been shown to simultaneously increase bulb yield and peimine content (Sui et al., 2021; Huang et al., 2024a). However, open-field cultivation is highly dependent on natural climate and is vulnerable to strong light, high temperature, continuous rainfall, drought, and disease. Without effective shading, drainage, and soil management measures, premature senescence of aboveground parts, poor bulb development, or quality fluctuations may occur. Therefore, open-field cultivation should focus on coordinated management of light, temperature, water, and fertilizer, as well as disease control. Especially in years with large climatic fluctuations, cultivation stability should be improved through shading, water-fertilizer regulation, and drainage measures.

Understory cultivation and semi-wild cultivation patterns can improve the growth environment of *F. thunbergii* to some extent. Understory environments are characterized by moderate shading, buffered temperature changes, higher air humidity, richer soil organic matter, and more complex microbial communities. These conditions help alleviate strong light and high-temperature stress, prolong the functional period of leaves, and create a relatively stable ecological environment for bulb enlargement and active constituent accumulation. Reviews on understory cultivation indicate that the lower light intensity, buffered temperature and humidity, altered soil fertility, and microbial communities in understory environments may significantly increase or decrease the yield and quality of medicinal plants compared with open-field cultivation, depending on species characteristics and stand structure (Li et al., 2025; Wen et al., 2025). For *F. thunbergii*, understory cultivation combined with soil amendments such as organic fertilizer and biochar can optimize soil and rhizosphere microecology, helping improve bulb yield and alkaloid quality compared with traditional cultivation patterns (Liu et al., 2026). However, understory or semi-wild patterns also have limitations, such as greater management difficulty, larger yield fluctuations, and limited mechanization. Therefore, refined regulation should be carried out according to forest stand type, canopy closure, soil conditions, and water status.

Facility cultivation provides a new approach for precise environmental regulation in *F. thunbergii*. Through temperature and humidity control, shading management, water-fertilizer regulation, and disease control under facility conditions, the adverse effects of extreme weather on production can be reduced, while emergence uniformity, plant growth stability, and yield controllability can be improved. Studies on other medicinal plants help explain the mechanisms of different cultivation patterns. For example, in *Epimedium pubescens*, inter-row understory cultivation under different tree species can produce yields and active constituent contents comparable to or higher than open-field controls when microclimatic conditions such as air humidity are suitable, whereas excessive shading under dense canopies reduces yield (Li et al., 2026). Shading experiments and agroforestry studies on aromatic and medicinal plants have also shown that mild to moderate shading, approximately 30%~40%, usually slightly reduces biomass but can increase essential oil or active constituent contents; heavy shading, exceeding 50%~75%, significantly reduces yield and does not necessarily bring further quality improvement (Zubay et al., 2021; Şeker et al., 2023). Therefore, different cultivation patterns each have advantages and limitations. They should be selected according to production-area conditions, production goals, and cost effectiveness. Guided by ecological and omics data, the advantages of open-field cultivation, understory cultivation, and facility cultivation should be integrated to construct standardized production patterns that balance high bulb yield, high peimine content, and ecological sustainability.

7 Mechanistic Analysis of Cultivation Environment Regulation of Yield and Peimine Accumulation in *Fritillaria thunbergii*

7.1 Regulatory mechanisms of environmental factors on photosynthesis and dry matter accumulation

The basis of yield formation in *Fritillaria thunbergii* lies in plant photosynthesis, carbon assimilation, and dry matter accumulation, which are jointly affected by environmental factors such as light, temperature, water, soil fertility, and the root-zone environment. Leaves are the main organs for photosynthesis in *F. thunbergii*. Appropriate light can improve leaf light-use efficiency and promote organic matter synthesis, while suitable temperature helps maintain enzyme activity and cellular metabolism, allowing plants to sustain strong physiological activity. Existing studies have shown that, in *F. thunbergii*, shading within a certain range reduces the net photosynthetic rate, but plants can partially compensate by increasing chlorophyll content and adjusting leaf traits. However, excessive shading markedly inhibits biomass accumulation and bulb yield (Liu et al., 2025a). Meanwhile, appropriate potassium fertilization under shading conditions can alleviate the decline in bulb biomass, indicating that improved mineral nutrition can partially restore photosynthetic capacity and carbon fixation. Studies on other medicinal plants have also shown that moderate nitrogen application or balanced nitrogen, phosphorus, and potassium supply can optimize leaf dry weight, total biomass, and photosynthetic rate, whereas nitrogen deficiency or excessive nitrogen application may reduce photosynthesis by limiting chlorophyll formation, inducing reactive oxygen species damage, or downregulating photosynthetic antenna-related genes (Yang et al., 2024). Therefore, the influence of environmental factors on the yield of *F. thunbergii* is first reflected in the regulation of leaf photosynthetic carbon capture capacity.

The transport of dry matter from the aboveground parts to the underground bulbs is a key process in yield formation in *F. thunbergii*. During the vegetative growth stage, plants synthesize carbohydrates through leaves and use them for stem and leaf growth, root development, and bulb filling. After entering the bulb enlargement stage, assimilates are gradually transferred to the underground parts, and the bulbs become the main storage organs. At this stage, the stability of environmental conditions directly determines the efficiency of dry matter accumulation. Suitable soil moisture and nutrient supply can enhance root absorption capacity and maintain continuous photosynthesis in the aboveground parts, while good soil aeration supports root respiration and energy metabolism, thereby promoting the transport of assimilates to the bulbs. Temperature and root-zone conditions also regulate photosynthetic performance and biomass formation. Studies on hydroponically grown medicinal plants have shown that air temperature and root-zone temperature significantly affect photosynthesis, nutrient uptake, leaf growth, and secondary metabolite accumulation. Unsuitable temperatures can induce oxidative stress and reduce water uptake, whereas appropriate temperatures promote growth and metabolite formation (Venkatasai et al., 2025). Metabolomics-based stress studies have further shown that abiotic factors such as drought, salinity, extreme temperature, and pH can alter the levels of primary metabolites, including amino acids and carbohydrates. These substances function as osmotic regulators and energy reserves under stress conditions and also reflect adjustments in photosynthetic carbon flow and respiratory metabolism (Salam et al., 2023).

Different environmental factors do not act in isolation, but influence yield by comprehensively regulating plant growth status. For example, moderate shading can reduce strong light and high-temperature stress and delay premature leaf senescence; rational water and fertilizer management can maintain the functional period of leaves and enhance root vitality; and good soil structure can improve water and nutrient use efficiency. Only when light, temperature, water, fertilizer, and aeration conditions are coordinated can *F. thunbergii* establish a stable vegetative growth foundation and accumulate more dry matter in the bulbs. Therefore, the mechanism by which environmental factors regulate yield is essentially realized through their effects on photosynthesis, carbon assimilation, root absorption, assimilate transport, and bulb storage processes. At the same time, these primary metabolic processes also provide carbon skeletons and energy for the biosynthesis of steroidal alkaloids such as peimine.

7.2 Induction mechanisms of environmental stress on secondary metabolism and peimine biosynthesis

Peimine is an important steroidal alkaloid secondary metabolite in *F. thunbergii*, and its formation is closely related to plant growth status and environmental responses. Plant secondary metabolism is usually associated with defense, adaptation, and stress resistance. When plants are exposed to a certain degree of environmental stimulation, corresponding metabolic regulatory mechanisms may be activated, promoting the synthesis and accumulation of active components such as alkaloids, terpenoids, flavonoids, and phenylpropanoids. Extensive studies have shown that light intensity and quality, temperature, soil moisture, fertility, and salinity can significantly increase or decrease plant secondary metabolite levels, and different types of stress often induce the accumulation of different classes of compounds (Yang et al., 2018; Pant et al., 2021; Qaderi et al., 2023). Therefore, changes in peimine accumulation in *F. thunbergii* can be understood as the result of the combined regulation of primary metabolism, stress signaling, and secondary metabolic pathways by environmental factors.

Under abiotic stress conditions, plants usually activate a series of signal transduction processes, including reactive oxygen species, phytohormones such as jasmonic acid, abscisic acid, and salicylic acid, Ca^{2+} signaling, and mitogen-activated protein kinase (MAPK) cascades. These signals further converge on transcription factors such as MYB, bHLH, AP2/ERF, WRKY, bZIP, and NAC, which coordinately upregulate or downregulate biosynthetic genes in alkaloid, terpenoid, and phenylpropanoid pathways (Kajla et al., 2023; Rabeh et al., 2025). Metabolomics studies have also confirmed that stress-induced changes in primary metabolism, such as alterations in the shikimate pathway, terpenoid backbone pathway, and amino acid metabolism, can further provide precursors, energy, and metabolic flux for the formation of nitrogen-containing alkaloids and other defensive secondary metabolites (Salam et al., 2023). Therefore, moderate environmental stress may promote peimine biosynthesis through a chain reaction involving “signal activation-transcriptional regulation-metabolic pathway redistribution.”

In *F. thunbergii*, existing omics studies have provided direct evidence for this mechanism. The combined treatment of shading and potassium fertilization can significantly increase the contents of peimine, peiminine, imperialine, and other steroidal alkaloids in bulbs. Transcriptomic analysis has identified multiple upregulated genes in the terpenoid/steroidal alkaloid pathway, among which farnesyl pyrophosphate synthase (FtFPS) is regarded as a key hub gene. FtFPS catalyzes the formation of farnesyl pyrophosphate, which is an important precursor for sterol and steroidal alkaloid biosynthesis. Meanwhile, FtFPS can interact with AP2/ERF transcription factors, thereby linking external environmental signals with the activation of the steroidal alkaloid pathway (Liu et al., 2025a). Another fertilization study on *F. thunbergii* showed that organic fertilizer can increase the contents of peimine and peiminine, possibly through the upregulation of ABA signaling and the induction of putative genes related to steroidal alkaloid biosynthesis (Huang et al., 2024a). Therefore, environmental stress has a dual effect on peimine biosynthesis: moderate stimulation can act as an inducing signal to activate secondary metabolic pathways, whereas excessive stress may inhibit growth, reduce photosynthetic carbon supply, and cause metabolic disorder, ultimately leading to unstable accumulation of active constituents.

7.3 Coordination mechanisms between yield formation and peimine accumulation

The goal of *F. thunbergii* production is not only to increase bulb yield, but also to ensure the content of active constituents such as peimine. Therefore, it is necessary to correctly understand the relationship between yield formation and quality formation. Yield mainly depends on photosynthesis, dry matter accumulation, and bulb enlargement, while peimine accumulation is closely associated with secondary metabolic activity. The two processes are both consistent and potentially contradictory. A favorable growth environment can improve plant vigor and bulb yield while providing sufficient substrates for peimine biosynthesis. However, if the environment excessively promotes vegetative growth, dry matter allocation and metabolic direction may shift toward biomass expansion, and active constituent accumulation may not increase synchronously. Studies have shown that shading alone can significantly increase the total active ingredient content in *F. thunbergii* bulbs, but it reduces bulb biomass and yield, showing a typical “high-quality/low-yield” pattern (Liu et al., 2025a).

The coordination between yield and peimine accumulation depends on regulating the growth focus and metabolic allocation of plants at different developmental stages. In the early growth stage, priority should be given to promoting sprouting, leaf expansion, and root establishment, thereby laying the foundation for subsequent material accumulation. During the vegetative growth stage, high photosynthetic efficiency and moderate population growth should be maintained to ensure sufficient assimilate supply. During bulb enlargement and maturation, dry matter transfer to the underground bulbs should be promoted, while suitable light, temperature, water, and soil conditions should be maintained to support secondary metabolic activity. Existing studies have shown that when shading is combined with appropriate potassium fertilization, yield loss in *F. thunbergii* can be alleviated while peimine and related steroidal alkaloids remain at relatively high levels. Moreover, antitussive, expectorant, and anti-inflammatory activities are relatively optimal under moderate potassium treatment (Liu et al., 2025a). Similarly, organic fertilizer treatment can achieve relatively high bulb yield while increasing peimine and peiminine contents, indicating that an appropriate nutrient regime can shift the system from a strict yield-quality trade-off toward a more coordinated outcome (Huang et al., 2024a).

Mechanistic studies on other medicinal plants also support this coordination strategy. Moderate resource supply can generally optimize carbon-nitrogen balance and carbon allocation, thereby promoting both biomass and secondary metabolite accumulation. For example, in *Epimedium pubescens*, moderate nitrogen treatment can produce relatively high total dry weight and higher levels of icariin-type flavonoids, whereas both low and high nitrogen weaken photosynthesis, disrupt carbon-nitrogen homeostasis, reduce soluble sugar and starch contents, and suppress flavonoid biosynthesis (Liu et al., 2025b). Reviews on medicinal plant cultivation have also pointed out that environmental factors such as temperature, light, soil fertility, and water need to be precisely controlled to stabilize secondary metabolite content and yield. At the same time, harvest timing should be regulated so that the peak of secondary metabolite accumulation coincides with an acceptable biomass level, thereby achieving the so-called “optimal harvest time” (Yang et al., 2018; Qaderi et al., 2023). By extension, scientific environmental management for *F. thunbergii* should aim at the coordinated improvement of yield and quality. Through ecological suitability zoning, moderate shading, rational water and fertilizer supply, soil improvement, rotation and intercropping, and disease control, a stable and suitable growth environment can be constructed. On this basis, incorporating bulb yield, marketable traits, dry matter content, peimine content, and safety indicators into comprehensive evaluation will help establish a more scientific cultivation technology system for *F. thunbergii* and achieve coordinated development of medicinal material yield, quality, and industrial benefits.

8 Future Perspectives and Prospects

High-quality and high-yield production of *Fritillaria thunbergii* should first be based on the selection of ecologically suitable areas. Since *F. thunbergii* prefers cool, moist, and well-ventilated environments and is intolerant of high temperature and waterlogging, cultivation areas should preferably be selected in regions with a mild climate, appropriate diurnal temperature difference, relatively balanced precipitation, loose and fertile soil, and favorable irrigation and drainage conditions. The screening of ecologically suitable areas should not rely solely on traditional cultivation experience, but should comprehensively consider factors such as altitude, temperature, light, precipitation, soil texture, pH, disease risk, as well as transportation and processing conditions, so as to form a regionalized cultivation layout. On this basis, standardized cultivation strategies should be promoted, including the selection of high-quality seed bulbs, seed source grading, pre-sowing treatment, rational close planting, scientific fertilization, green pest and disease control, and timely harvesting. By establishing unified production technical procedures and field management standards, differences in management among growers can be reduced, thereby improving yield stability and quality consistency of *F. thunbergii* and laying a foundation for geo-authentic medicinal material brand development and industrial-scale production.

The core of cultivation environment optimization for *F. thunbergii* lies in the comprehensive coordination of light, temperature, water, fertility, and soil conditions. In production, refined management should be carried out according to the requirements of different growth stages. During sprouting and emergence, soil should be kept moderately moist with good aeration to promote uniform emergence and root formation. During vegetative growth, moderate shading, rational irrigation, and balanced fertilization should be used to maintain leaf photosynthetic function and promote assimilate accumulation. During bulb enlargement, stable water and fertilizer supply should be emphasized, while premature senescence of aboveground parts caused by high temperature, drought, or wet injury should be avoided. In the late growth stage, water should be appropriately controlled to promote bulb maturation and stable accumulation of active constituents. In fertilizer management, the principle of using organic fertilizer as the basis, applying chemical fertilizers appropriately, and reasonably supplementing medium and trace elements should be followed, while avoiding excessive nitrogen application or overfertilization that may cause excessive vegetative growth and soil degradation. Meanwhile, measures such as deep plowing and soil exposure, high-ridge cultivation, application of well-decomposed organic fertilizer, crop rotation and intercropping, use of microbial fertilizers, and construction of drainage systems should be adopted to improve soil structure and rhizosphere microecology, alleviate continuous cropping obstacles, reduce the risk of soil-borne diseases, and provide a favorable environment for peimine accumulation and medicinal quality stability.

In the future, the development of the *F. thunbergii* industry should shift from a single yield-oriented approach toward the coordinated improvement of yield and quality. When evaluating cultivation effects, attention should be paid not only to yield per unit area, single-bulb weight, and commercial appearance, but also to dry matter content, contents of active constituents such as peimine and peiminine, incidence of pests and diseases, pesticide residues, heavy metal safety, and environmental parameters of the production area. By establishing an evaluation model integrating "environmental factors-growth indicators-yield indicators-quality indicators," the comprehensive effects of different cultivation environments and management measures on the overall quality of *F. thunbergii* can be more accurately reflected. Future research should further strengthen studies on the physiological and molecular mechanisms by which cultivation environment regulates peimine biosynthesis, and clarify the effects of light, temperature, water, fertilizer, soil microecology, and environmental stress on peimine metabolic pathways. Meanwhile, the application of digital monitoring, precise water and fertilizer management, facility cultivation, ecological cultivation, and quality traceability technologies in *F. thunbergii* production should be promoted. Through the integration of basic research and production practice, high-quality and high-yield cultivation patterns suitable for different production areas can be gradually established, thereby promoting the standardized, green, and high-quality development of the *F. thunbergii* industry.

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.

References

Adamczyk-Szabela D., and Wolf W., 2022, The impact of soil pH on heavy metals uptake and photosynthesis efficiency in *Melissa officinalis, Taraxacum officinalis, Ocimum basilicum*, Molecules, 27(15): 4671.
https://doi.org/10.3390/molecules27154671

Baba Y., Cimen A., Yildirim A.B., and Turker A.U., 2024, How does water stress affect the bioaccumulation of galanthamine and lycorine, growth performance, phenolic content and defense enzyme activities in summer snowflake (*Leucojum aestivum* L.)?, Physiology and Molecular Biology of Plants, 30(5): 775-790.
https://doi.org/10.1007/s12298-024-01451-8

Bhatt R., Kunal, Garg A.K., Majumder D., Verma K.K., and De Oliveira M.W., 2025, Soil texture: unlocking fertility and productivity for better crops, AATCC Review, 13(3): 396-408.
https://doi.org/10.21276/aatccreview.2025.13.03.396

Bistgani Z.E., Barker A.V., and Hashemi M., 2024, Physiology of medicinal and aromatic plants under drought stress, The Crop Journal, 12(2): 330-339.
https://doi.org/10.1016/j.cj.2023.12.003

Ceolin S., Schymanski S.J., van Dusschoten D., Koller R., and Klaus J., 2025, Root growth dynamics and allocation as a response to rapid and local changes in soil moisture, Biogeosciences, 22: 691-703.
https://doi.org/10.5194/bg-22-691-2025

Chen C.C., Lee M.R., Wu C.R., Ke H., Xie H., Tsay H.S., Agrawal D.C., and Chang H.C., 2020, LED lights affecting morphogenesis and isosteroidal alkaloid contents in *Fritillaria cirrhosa* D. Don-an important Chinese medicinal herb, Plants, 9(10): 1351.
https://doi.org/10.3390/plants9101351

Cheng X., Li D., Jiang Z., Qu C., Yan H., and Wu Q., 2023, Metabolite profiling and transcriptomic analyses demonstrate the effects of biocontrol agents on alkaloid accumulation in *Fritillaria thunbergii*, BMC Plant Biology, 23(1): 435.
https://doi.org/10.1186/s12870-023-04459-6

Du J., Yu Y., Tang C., Zong K., Zhang S., Zhang Q., Fang L., and Li Y., 2024, Organic fertilizers increase the proportion of saprotrophs favoring soil nitrification under medicinal plants *Fritillaria thunbergii*, Industrial Crops and Products, 219: 119129.
https://doi.org/10.1016/j.indcrop.2024.119129

Duan Y., Liu X., Wu J., You J., Wang F., Guo X.L., Tang T., Liao M., and Guo J., 2022, Transcriptomic and metabolic analyses reveal the potential mechanism of increasing steroidal alkaloids in *Fritillaria hupehensis* through intercropping with *Magnolia officinalis*, Frontiers in Plant Science, 13: 997868. https://doi.org/10.3389/fpls.2022.997868

Duan Y.Y., Wu J.Q., Wang F.F., Zhang K.Q., Guo X.L., Tang T., Mu S., You J., and Guo J., 2023, Transcriptomic and metabolomic analyses provide new insights into the appropriate harvest period in regenerated bulbs of *Fritillaria hupehensis*, Frontiers in Plant Science, 14: 1132936. https://doi.org/10.3389/fpls.2023.1132936

Fujita S., Noguchi K., and Tange T., 2021, Different waterlogging depths affect spatial distribution of fine root growth for *Pinus thunbergii* seedlings, Frontiers in Plant Science, 12: 614764. https://doi.org/10.3389/fpls.2021.614764

Hao D.C., Luan Y., Wang Y., and Xiao P.G., 2024, Unveiling nitrogen fertilizer in medicinal plant cultivation, Agronomy, 14(8): 1647. https://doi.org/10.3390/agronomy14081647

Haq M.Z.U., Yu J., Yao G., Yang H., Iqbal H.A., Tahir H., Cui H., Liu Y., and Wu Y.G., 2023, A systematic review on the continuous cropping obstacles and control strategies in medicinal plants, International Journal of Molecular Sciences, 24(15): 12470. https://doi.org/10.3390/ijms241512470

Huang L., Liang S., Luo L., Wu M., Fu H.L., and Zhong Z., 2024a, Transcriptomic analysis reveals effects of fertilization towards growth and quality of *Fritillariae thunbergii* bulbus, PLOS ONE, 19(9): e0309978. https://doi.org/10.1371/journal.pone.0309978

Huang X., Niu P.X., Gao Y.D., Rong W.W., Luo C.K., Zhang X.X., Jiang P., Wang M., and Chu G.M., 2024b, Effects of water and nitrogen on growth, rhizosphere environment, and microbial community of *Sophora alopecuroides*: their interrelationship, Plants, 13(14): 1970. https://doi.org/10.3390/plants13141970

Jeong J., Kim J.W., Kim J.H., Chung E.H., Ko J.W., Hwang Y.H., and Kim T.W., 2024, Investigating changes in pharmacokinetics of steroidal alkaloids from a hydroethanolic *Fritillariae thunbergii* bulbus extract in 2,4-dinitrobenzene sulfonic acid-induced colitis rats, Pharmaceuticals, 17(8): 1001. https://doi.org/10.3390/ph17081001

Jeong S.J., Zhen S., Zhang Q., and Niu G., 2025, Lowering light intensity while extending photoperiod at a constant daily light integral synergistically interacts with warm temperature to enhance leaf expansion and crop yield in lettuce in the absence of far-red light, Frontiers in Plant Science, 16: 1529455. https://doi.org/10.3389/fpls.2025.1529455

Jiang R., Zou M., Qin Y., Tan G., Huang S., Quan H., Zhou J., and Liao H., 2022, Modeling of the potential geographical distribution of three *Fritillaria* species under climate change, Frontiers in Plant Science, 12: 749838. https://doi.org/10.3389/fpls.2021.749838

Kajla M., Roy A., Singh I., and Singh A.K., 2023, Regulation of the regulators: Transcription factors controlling biosynthesis of plant secondary metabolites during biotic stresses and their regulation by miRNAs, Frontiers in Plant Science, 14: 1126567. https://doi.org/10.3389/fpls.2023.1126567

Kumar I.V., Lisson S., Hardie M., and Acuña T., 2025, Effect of different water regimes on physiology, growth and yield of industrial hemp in field conditions, Crop and Pasture Science, 76(11): CP25137. https://doi.org/10.1071/cp25137

Li D., Zhang H., Wen D., Suo F., and Guo B., 2026, Unraveling the environmental and physiological controls on yield and quality of *Epimedium pubescens* through a shading gradient experiment in agroforestry systems, Forests, 17(3): 320. https://doi.org/10.3390/f17030320

Li G., Long H., Zhang R., Drohan P., Xu A., and Niu L., 2023, Stable soil moisture alleviates water stress and improves morphogenesis of tomato seedlings, Horticulturae, 9(3): 391. https://doi.org/10.3390/horticulturae9030391

Li H., Yang Y., Lei J., Gou W., Crabbe M.C., and Qi P., 2024, Effects of continuous cropping of *Codonopsis pilosula* on rhizosphere soil microbial community structure and metabolomics, Agronomy, 14(9): 2014. https://doi.org/10.3390/agronomy14092014

Li X., Liang H., Liang J., Huang Y., and Liang Y., 2025, Understory cultivation of medicinal plants promotes sustainable forestry development, Agroforestry Systems, 99(2): 39. https://doi.org/10.1007/s10457-025-01141-8

Li Y., Zhang Z., Wang J., and Zhang M., 2022, Soil aeration and plastic film mulching increase the yield potential and quality of tomato (*Solanum lycopersicum*), Agriculture, 12(2): 269. https://doi.org/10.3390/agriculture12020269

Liao H., Quan H., Huang B., Ji H., Zhang T., Chen J., and Zhou J., 2023, Integrated transcriptomic and metabolomic analysis reveals the molecular basis of tissue-specific accumulation of bioactive steroidal alkaloids in *Fritillaria unibracteata*, Phytochemistry, 214: 113831. https://doi.org/10.1016/j.phytochem.2023.113831

Liao J., and Xia P., 2024, Continuous cropping obstacles of medicinal plants: focus on the plant-soil-microbe interaction system in the rhizosphere, Scientia Horticulturae, 331: 112927. https://doi.org/10.1016/j.scienta.2024.112927

Liu J., Sheng X., Zhu Z., Zhang K., Yuan Q., Wang H., and Sui N., 2026, Co-application of biochar and organic fertiliser enhances the yield and quality of understory *Fritillaria thunbergii* Miq. by optimising soil and rhizosphere microecological structure, Industrial Crops and Products, 246: 123387.
https://doi.org/10.1016/j.indcrop.2026.123387

Liu J., Zhu Z., Wang L., Yuan Q., Zhu H., Sheng X., Zhang K., Liang B., Jin H., Wang S., Weng W., Wang H., and Sui N., 2025a, Regulation of steroidal alkaloid biosynthesis in bulbs of *Fritillaria thunbergii* Miq. by shading and potassium application: Integrating transcriptomics and metabolomics analyses, Biology, 14(6): 633.
https://doi.org/10.3390/biology14060633

Liu S., An X., Xu C., He D., Li X., Chen C., Guo B., Xu D., and Huang J., 2025b, Integrative transcriptomic-physiological analysis deciphers nitrogen-mediated carbon reallocation balancing growth and flavonoid metabolism in *Epimedium pubescens*, Frontiers in Plant Science, 16: 1539445.
https://doi.org/10.3389/fpls.2025.1539445

Lv G., Wu Y., Li Z., Zhuang D., Guo Y., Wang Z., Gao C., Sun D., and Jia J., 2026, Effects of drip irrigation regimes on leaf structure, photosynthesis, yield, and quality in *Atractylodes chinensis* (DC.) Koidz., Frontiers in Agronomy, 7: 1711027.
https://doi.org/10.3389/fagro.2025.1711027

Maan C., Veldhuis M.C.T., and Van De Wiel B.J.H., 2023, Dynamic root growth in response to depth-varying soil moisture availability: a rhizobox study, Hydrology and Earth System Sciences, 27: 2341-2359.
https://doi.org/10.5194/hess-27-2341-2023

Manghwar H., Hussain A., Alam I., Khoso M.A., Ali Q., and Liu F., 2024, Waterlogging stress in plants: unraveling the mechanisms and impacts on growth, development, and productivity, Environmental and Experimental Botany, 224: 105824.
https://doi.org/10.1016/j.envexpbot.2024.105824

Marković M., Momčilović M.T., Uzelac B., Cingel A., Milošević S., Jevremović S., and Subotić A., 2020, Breaking the dormancy of snake's head fritillary (*Fritillaria meleagris* L.) in vitro bulbs-Part 1: Effect of GA3, GA inhibitors and temperature on fresh weight, sprouting and sugar content, Plants, 9(11): 1449.
https://doi.org/10.3390/plants9111449

Marković M., Momčilović M.T., Uzelac B., Jevremović S., and Subotić A., 2021, Bulb dormancy in vitro-*Fritillaria meleagris*: initiation, release and physiological parameters, Plants, 10(5): 902.
https://doi.org/10.3390/plants10050902

Moreno-Pedraza A., Gabriel J., Treutler H., Winkler R., and Vergara F., 2019, Effects of water availability in the soil on tropane alkaloid production in cultivated *Datura stramonium*, Metabolites, 9(7): 131.
https://doi.org/10.3390/metabo9070131

Ng C., So P., Coo J.L., Lau S.Y., and Wong J.F., 2023, Interactions between nutrient types and soil hydrological properties on yield and quality of *Pinellia ternata*, a medicinal plant, Industrial Crops and Products, 199: 116423.
https://doi.org/10.1016/j.indcrop.2023.116423

Nile S.H., Su J., Wu D., Wang L., Hu J., Sieniawska E., and Kai G., 2021, *Fritillaria thunbergii* Miq. (Zhe Beimu): a review on its traditional uses, phytochemical profile and pharmacological properties, Food and Chemical Toxicology, 153: 112289.
https://doi.org/10.1016/j.fct.2021.112289

Omidi H., Shams H., Sahandi S.M., and Rajabian T., 2018, Balangu (*Lallemantia* sp.) growth and physiology under field drought conditions affecting plant medicinal content, Plant Physiology and Biochemistry, 130: 641-646.
https://doi.org/10.1016/j.plaphy.2018.08.014

Pant P., Pandey S., and Dall'Acqua S., 2021, The influence of environmental conditions on secondary metabolites in medicinal plants: a literature review, Chemistry and Biodiversity, 18(11): e2100345.
https://doi.org/10.1002/cbdv.202100345

Peng M., Liu Z., Chen X., Xiao Y., Wang S., Yan Z., Zhou T., and Xu B., 2024, LED blue light enhances the accumulation and synthesis of steroidal alkaloids in *Fritillaria unibracteata* Hsiao et K. C. Hsia in vitro, Industrial Crops and Products, 216: 118836.
https://doi.org/10.1016/j.indcrop.2024.118836

Qaderi M.M., Martel A.B., and Strugnell C.A., 2023, Environmental factors regulate plant secondary metabolites, Plants, 12(3): 447.
https://doi.org/10.3390/plants12030447

Qu A., Wu Q., Su J., Li C., Yang L., Wang Z., Wang Z., Li Z., Ruan X., Zhao Y., and Wang Q., 2022, A review on the composition and biosynthesis of alkaloids and on the taxonomy, domestication, and cultivation of medicinal *Fritillaria* species, Agronomy, 12(8): 1844.
https://doi.org/10.3390/agronomy12081844

Rabeh K., Hnini M., and Oubohssaine M., 2025, A comprehensive review of transcription factor-mediated regulation of secondary metabolites in plants under environmental stress, Stress Biology, 5(1): 15.
https://doi.org/10.1007/s44154-024-00201-w

Salam U., Ullah S., Tang Z.H., Elateeq A.A., Khan Y., Khan J., Khan A., and Ali S., 2023, Plant metabolomics: an overview of the role of primary and secondary metabolites against different environmental stress factors, Life, 13(3): 706.
https://doi.org/10.3390/life13030706

Şeker S., Çakaloğulları U., Bayram E., and Tatar Ö., 2023, Production of sage, oregano and rosemary under shading conditions and the effects of light on growth and essential oil properties, Industrial Crops and Products, 197: 116254.

Shan T., Shi Y., Xu J., Zhao L., Tao Y., and Wu J., 2022, Transcriptome analysis reveals candidate genes related to steroid alkaloid biosynthesis in *Fritillaria anhuiensis*, Physiologia Plantarum, 174(5): e13755.
https://doi.org/10.1111/ppl.13755

Shi J., Yuan X., Lin H., Yang Y., and Li Z., 2011, Differences in soil properties and bacterial communities between the rhizosphere and bulk soil and among different production areas of the medicinal plant *Fritillaria thunbergii*, International Journal of Molecular Sciences, 12(6): 3770-3785.
https://doi.org/10.3390/ijms12063770

Sui N., Wang L., Sun J., Wu J., Chen M., Zhang S., Yuan Q., and Kai G., 2021, Estimating *Fritillaria thunbergii* Miq. yield, quality, and potassium use efficiency in response to potassium application rate, Industrial Crops and Products, 164: 113409.
https://doi.org/10.1016/j.indcrop.2021.113409

Tan U., and Gören H.K., 2024, Comprehensive evaluation of drought stress on medicinal plants: a meta-analysis, PeerJ., 12: e17801.
https://doi.org/10.7717/peerj.17801

Venkatasai N.N., Shetty D.N., Vinay C., Sekar M., Muthusamy A., and Rai P., 2025, A comprehensive review of factors affecting growth and secondary metabolites in hydroponically grown medicinal plants, Planta, 261(2): 48.
https://doi.org/10.1007/s00425-025-04619-y

Wang G., Ren Y., Bai X., Su Y., and Han J., 2022, Contributions of beneficial microorganisms in soil remediation and quality improvement of medicinal plants, Plants, 11(23): 3200.
https://doi.org/10.3390/plants11233200

Wen D., Zhang H., Qin F.Y., Xu C.Q., Li D., and Guo B.L., 2025, Effects of understory environmental factors on understory planting of medicinal plants, Zhongguo Zhong Yao Za Zhi, 50(5): 1164-1171.
https://doi.org/10.19540/j.cnki.cjcmm.20241214.101

Xu Z., Wang Y., Song W., Dong L., Wang Z., and Yang Y., 2026, Functions of FtGGPS and its role in the bulb development of *Fritillaria thunbergii*, Sheng Wu Gong Cheng Xue Bao, 42(1): 436-457.
https://doi.org/10.13345/j.cjb.250616

Yang D., Liu X., Xu X., Niu T., Fu G., Song C., and Hou X., 2024, Effect of soil and community factors on the yield and medicinal quality of *Artemisia argyi* growth at different altitudes of the Funiu Mountain, Frontiers in Plant Science, 15: 1430758.
https://doi.org/10.3389/fpls.2024.1430758

Yang L., Wen K.S., Ruan X., Zhao Y.X., Wei F., and Wang Q., 2018, Response of plant secondary metabolites to environmental factors, Molecules, 23(4): 762.
https://doi.org/10.3390/molecules23040762

Yang P., Wang R., Liu J., Xu X., Xu Q., Liu S., Dong M., Shen Q., Shen Z., and Li R., 2025, The influence of environmental heterogeneity on fertilization-driven patterns of distribution and yield in medicinal plants, Agronomy, 15(9): 2142.
https://doi.org/10.3390/agronomy15092142

Yu Z., Wang H., Yu D.S., Yin N.X., and Zhang J., 2024, The effect of aeration and irrigation on the improvement of soil environment and yield in dryland maize, Frontiers in Plant Science, 15: 1464624.
https://doi.org/10.3389/fpls.2024.1464624

Zhang J., Li Y., Yang T., Liu D., Liu X., and Jiang N., 2021, Spatiotemporal variation of moisture in rooted-soil, Catena, 200: 105144.
https://doi.org/10.1016/j.catena.2021.105144

Zhang M.J., Zhang L., Gan J., Fang C., Chen B., Zheng C., and Zhou J.L., 2026, Exploring the differences in alkaloids of *Fritillariae thunbergii bulbus* from different regions using liquid chromatography-mass spectrometry and chemometrics, Chemistry and Biodiversity, 23(4): e03442.
https://doi.org/10.1002/cbdv.202503442

Zhou A.Z., Li X., Zou J., Wu L., Cheng B., and Wang J., 2023, Discovery of potential quality markers of *Fritillariae thunbergii bulbus* in pneumonia by combining UPLC-QTOF-MS, network pharmacology, and molecular docking, Molecular Diversity, 28: 1-18.
https://doi.org/10.1007/s11030-023-10620-y

Zou L., Fu Y., Wu L., Cheng J., Yang Y., Li M., Xu Y., Jiang Y., Wang Q., and Wu C., 2026, Edible and medicinal *Fritillaria thunbergii* Miq. aqueous extract improves metabolic health via modulation of gut microbiota in mice fed on a high-sugar and high-fat diet, Journal of Food Biochemistry, 2026(1): 2627240.
https://doi.org/10.1155/jfbc/2627240

Zubay P., Ruttner K., Ladányi M., Deli J., Németh É.Z., and Szabó K., 2021, In the shade-screening of medicinal and aromatic plants for temperate zone agroforestry cultivation, Industrial Crops and Products, 170: 113764.
https://doi.org/10.1016/j.indcrop.2021.113764